Soil and plant health in relation to dynamic sustainment of Eh and pH homeostasis: A review

Olivier Husson, Jean-Pierre Sarthou, Lydia Bousset, Alain Ratnadass, Hans-Peter Schmidt, John Kempf, Benoit Husson, Sophie Tingry, Jean-Noël Aubertot, Jean-Philippe Deguine, et al.

HAL Id: hal-03287577
https://hal.inrae.fr/hal-03287577

Submitted on 14 Oct 2021

1 **Soil and plant health in relation to dynamic maintenance of Eh and pH homeostasis: A review**

2

3 **Olivier Husson[a,b], Jean Pierre Sarthou[c], Lydia Bousset[d], Alain Ratnadass[e,f], Hans-Peter Schmidt[g], John**

4 **Kempf[h], Benoit Husson[i], Sophie Tingry[j], Jean-Noël Aubertot[c], Jean-Philippe Deguine[k], François-Régis**

5 **Goebel[a,b], Jay Ram Lamichhane[c].**

6

7 [a.] CIRAD, UPR AIDA, F-34398 Montpellier, France.

8 [b.] AIDA, Univ Montpellier, CIRAD, Montpellier, France. [c.] Université de Toulouse, INRAE, INP-ENSAT

9 Toulouse, UMR AGIR, F-31320, Castanet-Tolosan, France

10 [d.] INRAE, UMR 1349 IGEPP – Agrocampus Ouest Rennes- Université Rennes 1 ; BP35327

11 35653, Le Rheu cedex, France

12 [e.] CIRAD, UPR HortSys, F-97455 Saint-Pierre, Réunion, France

13 [f.] HortSys, Univ Montpellier, CIRAD, Montpellier, France

14 [g.] Ithaka Institute for Carbon Strategies, Ancienne Eglise 9, Arbaz 1974, Switzerland

15 [h.] Advancing Eco Agriculture, 4551 Parks West Rd, Middlefield Ohio 44062, United States

16 [i.] IDEEAQUACULTURE, Parc Euromedecine 2, 39 Rue Jean Giroux, 34080 Montpellier, France

17 [j.] Institut Européen des Membranes, IEM UMR-5635, Université de Montpellier, ENSCM, CNRS, Place Eugène

18 Bataillon, 34095 Montpellier Cedex 5, France

19 [k.] CIRAD, UMR PVBMT, F-97410 La Réunion, Saint Pierre, France

20

21 **ORCID numbers : Olivier Husson :** 0000-0001-9587-5819; **Jean Pierre Sarthou :** 0000-0003-4096-6291;
22 **Lydia Bousset :** 0000-0002-1600-1900 ; **Alain Ratnadass :** 0000-0002-8873-5671 ; **Hans-Peter Schmidt :**
23 0000-0001-8275-7506 ; **Sophie Tingry:** /0000-0001-6311-9330 ; **Jean-Noël Aubertot :** /0000-0001-6048-
24 1553 ; **Jean-Philippe Deguine :** 0000-0002-3689-3707 ; **François-Régis Goebel :** 0000-0002-5438-1078 ; **Jay**
25 **Ram Lamichhane :** 0000-0001-9780-0941

26

27 Glossary

28 ABA: Abscissic acid
29 ACP: Agroecological Crop Protection
30 AsA: Ascorbic Acid
31 ASC: Reduced AsA
32 ATP: Adenosine Tri Phosphate
33 DHA: De Hydro Ascorbic acid (Oxidized AsA)
34 EC: Electrical conductivity
35 Eh: Redox Potential
36 ET: Ethylene
37 G x E x M x P Interactions: Genotype x Environment x Management x Pest *sensu lato* interactions
38 GSH: Reduced Glutathione
39 GSSG: Oxidized Glutathione
40 ISR: Induced Systemic resistance
41 JA: Jasmonic Acid
42 NADPH: Reduced form of Nicotinamide Adenine Dinucleotide Phosphate
43 NO: Nitric Oxide
44 pH: Hydrogen potential
45 RAS: Root-Adhering Soil
46 ROS: Reactive Oxygen species
47 SA: Salicylic Acid

48 SAR: Systemic Acquired Resistance
49 SOM: Soil Organic Matter
50

51 **Introduction**

52 *"Research is to see what everybody has seen, and think what nobody has thought"* Albert Szent-Gyorgyi, Nobel

53 prize laureate.

54 Since the late 19th century and until quite recently, medical microbiology was based on the assumption that a few

55 microorganisms are pathogens while most are not. Although this binary view has now been strongly criticized,

56 and considered untenable (Méthot and Alizon 2014), it is generally recognized that the interaction of the three

57 factors of the host, pathogenic agent, and environment (plant disease triangle) determine whether a disease

58 develops or not. Thus, plant stage of growth, pathogen virulence, and environmental changes result in a dynamic

59 relationship over space and time (Agrios et al. 2005). Variations in any of the three interacting factors could

60 significantly alter expected patterns of disease spread and development (Farber and Mundt 2017). Even if a host

61 plant and a potential virulent pathogen are present in a certain area, serious disease epidemics will not occur

62 unless the environment fosters their development (Bateman 1978; Keane and Kerr 1997; Agrios et al. 2005).

63 Abiotic stresses can dramatically alter the outcome of plant-pathogen interactions and, depending on the

64 pathosystem and stress intensity, the stress may enhance or reduce diseases. Even mild, episodic stresses can

65 predispose plants to levels of pathogen inoculum that would not be damaging in the absence of the stress

66 (Bostock et al. 2014). Environmental stresses also influence overall plant tolerance to insect pests (Louda and

67 Collinge 1992).

68 The idea that a pathogenic organism is essentially a static or unchanging entity distinct from other types of

69 microbes would mean that such a microorganism possessed an inherent capacity to cause disease in hosts.

70 Pathogenicity is a dynamic feature of an interaction between a host and microbes as influenced by the

71 environment (Agrios et al. 2005; Méthot and Alizon 2014). The role of beneficial or commensal microorganisms

72 in plant health is now widely acknowledged, both in soil (especially the rhizosphere microbiome), and in leaves

73 (the phyllosphere microbiome; Andrews and Harris 2000; Paszkowski 2006; Leveau 2019; Teixeira et al. 2019;

74 Yu et al. 2019). Although knowledge of plant–plant and plant–microbe interactions has been greatly extended in

75 recent years, the chemical communication leading to defense priming is not well-understood (Mhlongo et al.

76 2018) and highlights the need to further elucidate microbial functions and interactions (Toyota and Shirai 2018).

77 Thus, two of the major questions remaining are "what makes a commensal or an opportunistic microorganism

78 become pathogenic?" and "how do pathogenic microorganisms impact plant health?"

79 Understanding the impacts of stresses on plant health is, therefore, important for obtaining optimum crop

80 production efficiency. Stress is defined as "a sudden change in the environment that exceeds the organism's

81 optimum to cause homeostatic imbalance which must be compensated for" (Kilian et al. 2012). Homeostasis is

82 considered an underestimated focal point of ecology and evolution (Giordano 2013) although "cellular redox

83 homeostasis in plants" is understood to be central to the plant stress defense system (Anjum et al. 2016). More

84 generally, Eh and pH signaling and homeostasis should be regarded as key processes in many aspects of plant

85 biology (Rengel 2002; Foyer and Noctor 2016) since plants function in a specific Eh-pH spectrum and rely on

86 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):
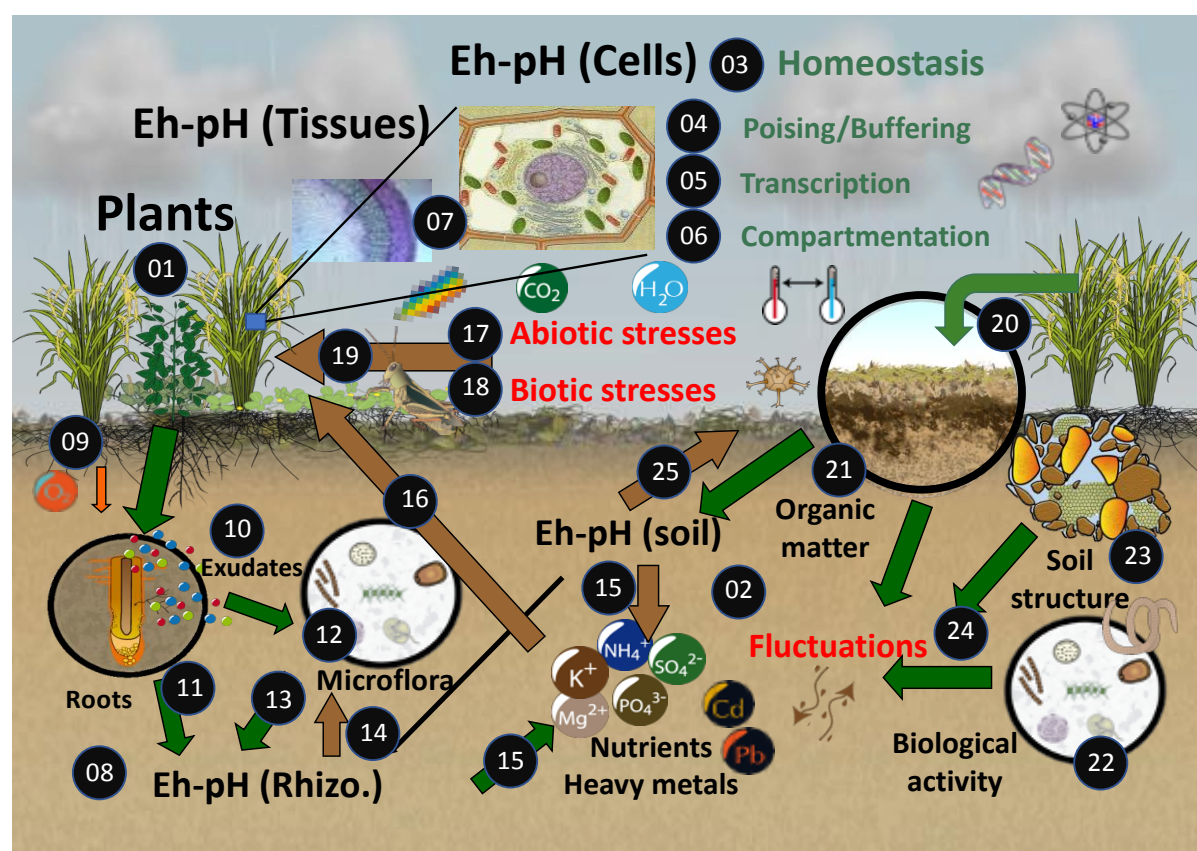

Fig. 1: The Eh-pH driven conceptual model of how the soil-plant-microorganism system could function to indicate the key role of dynamic maintenance of Eh-pH homeostasis for soil and plant health. Plants (01) grow in soil with highly fluctuating Eh-pH characteristics (02). To insure the necessary Eh-pH 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

4

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.

187

188 Although redox regulation is also involved in plant-weed interactions, especially in parasitic weeds (Yoder
189 2001) and through redox-associated mechanisms for allelopathy (Downum and Rodriguez 1986; Cheng and
190 Cheng 2015), we excluded weeds from this review and limit it to only two kinds of pests (pathogens and insects
191 or nematodes) for which Eh-pH interactions are better documented.

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

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

219

220 Eh-pH conditions at which pests can thrive

221 Plant pathogens

222 Each organism has an optimal Eh-pH range for its development. Pathogens having a broad host range are able to
223 develop under a large range of Eh-pH conditions, as for instance *Pseudomonas syringae* (Morris et al. 2019).
224 However, most pathogens are adapted to specific hosts, and have a relatively narrow optimal range of Eh-pH in
225 which they are pathogenic (Rabotnova and Schwartz 1962). The Eh-pH conditions at which some plant

226 pathogenic fungi and oomycetes can thrive are summarized in Table 1 while those for bacteria and viruses are

227 reported in Table 2.

228

229 *Table 1. Optimal Eh-pH conditions at which key plant pathogenic fungi and oomycetes are pathogenic. Most*

230 *fungal pathogens develop under both oxidized (Eh>400mV) and acidic conditions. Necrotrophic fungi develop*

231 *better in more acidic (and less oxidized) conditions than hemi-biotrophic and biotrophic fungi. A number of*

232 *plant pathogenic fungi thrive in slightly acidic to alkaline conditions, as for example Gaeumannomyces,*

233 *Verticillium, Colletotrichum sp. etc. Fungi developing in the apoplast develop at lower pH than those growing in*

234 *the phloem. Many oomycetes develop in less oxidized conditions than their fungal counterparts, in a wide range*

235 *of pH although with large species-specific variations in optimal pH. pH values in brackets indicate possible*

236 *range of survival while na means non-available. These are only indications of the tendency of the main groups of*

237 *pathogens. As large differences can exist between species, each pathogen should be characterized by its specific*

238 *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)

7

		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)

239

240

241 *Table 2. Some Eh-pH conditions where various types of plant pathogenic bacteria and viruses can develop.*

242 *Many plant pathogenic bacteria grow under more reduced (lower Eh) conditions than their fungal counterparts,*

243 *in alkaline or slightly acidic plants or plant parts. These conditions are met in reduced (anaerobic) soils, and*

244 *correspond to relatively oxidized plants as nutrient balanced plants are reduced (pe+pH<10). Viruses develop*

245 *under both reduced and alkaline conditions, that also correspond to conditions found in reduced soils, but in*

246 *strongly oxidized plants as the phloem is buffered at very low Eh in nutrient balanced plants. The listed Eh-pH*

247 *values are indicative of where microorganisms are pathogenic on plants although some of them (notably Gram-*

248 *negative bacteria) can thrive under different Eh-pH conditions, especially in reduced soil conditions for*

249 *bacteria, and then become pathogenic when conditions become more oxidized.*

250 *Aerobic conditions correspond to pe+pH >10 according to Rabotnova and Schwartz (1962). pe+pH is*

251 *equivalent to the chemical notion of rH_2 or to correct Eh to pH 7, which better characterizes oxidation in*

252 *organic chemistry than Eh alone. At 25°C, pe +pH = Eh(V)/0.059 + pH. Electrical neutrality corresponds to*

253 *pe+pH=14 or Eh@pH7=402mV (Husson et al. 2016).*

254

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	

8

		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		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)
	Phloem Epidermis cells	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	

257 Insect pests

258 Although it is well-known that insect pest interactions with plants are affected by both regulation and balance of

259 pH (Harrison 2001), and by redox signaling (Zebelo and Maffei 2015), little is known about the influence of the

260 combined Eh-pH levels (reflected in pe+pH) of the plant parts that insects feed upon.

261 The redox state of the apoplast exerts a strong influence on the extent of the plant response to aphid infestation in

262 terms of altered cell wall composition and nutritional quality (Rasool et al. 2017). Eh-pH conditions affect plant

263 digestibility by insects, and redox active components such as phenols are regarded as antifeedant, digestibility

264 reducers and toxic (Fürstenberg-Hägg et al. 2013; Usha Rani and Pratyusha 2013; Napoleão et al. 2017). The

265 Eh-pH in insect intestinal tracts is related to digestive enzymes and reflects different digestive strategies. The

266 effects of plant allelochemicals, especially phenols, on insect herbivores are influenced by gut redox conditions.

267 Therefore, the regulation of gut redox conditions is an important adaptation strategy of insect herbivores to the

268 plant chemical defenses that must be included in the analysis of plant-insect interactions (Appel and Martin

269 1990). Herbivores may have multiple strategies to deal with foliar phenolics such as a "reducing strategy" in

270 which reducing conditions in the gut prevent phenolic oxidation, and an "oxidative or polymerization strategy"

271 in which phenolics are oxidized and rapidly polymerized. Herbivores feeding on foliage with a high

272 concentration of readily oxidized and polymerized phenolics and low concentration of nutrients (e.g., many

273 trees) may use the oxidative polymerization strategy. Conversely, herbivores feeding on foliage with a low

274 concentration of phenolics but high concentration of nutrients for reducing potential (e.g., many herbs) may

275 employ the reducing strategy (Appel 1993). Saprophytic larvae of *Penthetria holosericea*, which feed selectively

276 on decomposed leaves and their own microbe-rich faeces, present very alkaline (pH>11) conditions with

277 moderately low Eh (230 mV) and thus, have a high pe+pH (>15) in the midgut. These conditions differ

278 fundamentally from those of detritivorous and humivorous insects which host a highly active, fermentative

279 microbiota in their alkaline midgut or hindgut compartments (Šustr et al. 2014).

280 In a study of Lepidopteran larvae, midgut pH of *Helicoverpa zea, Heliothis virescens* and *Hyphantria cunea*

281 (Noctuidae) revealed significant differences between insect species, but no host plant effect (geranium, cotton,

282 clover or soybean), since all were strongly alkaline at pH 9.3 to 10.6 (Johnson and Felton 1996a). In contrast,

283 midgut Eh was influenced by both insect and host plant species. Midguts of larvae feeding on clover and

284 soybean had more positive potentials, with redox values about 100 mV higher than those of larvae feeding on

285 geranium. In this interaction, much of the variation in midgut redox conditions was due to the redox activity of

286 host plant chemicals at the alkaline pH of the gut (Johnson and Felton 1996a).

287 Midgut Eh-pH, in relation to plant Eh-pH, therefore, can help discriminate insects based on their feeding mode

288 and capacity to cope with an oxidized diet. Adults or nymphs of sucking insects preferentially feed on plant parts

289 at neutral to basic pH, e.g. the phloem (Giaquinta 1977; Gerendás and Schurr 1999). They dislike strongly

290 reduced plants or plant parts that are rich in phenols and ascorbic acid (Farkas et al. 1960). It is interesting that

291 these insects often are vectors of viruses that require high pH.

292 Also, a lower level of ROS and a higher antioxidant potential in the adult than in the larval midgut indicate stage

293 specificity in the management of oxidative stress as reported for *Leptinotarsa decemlineata* (Coleoptera,

294 Chrysomelidae), the Colorado Potato Beetle, which has a midgut with low pH of 5.38 to 6.30, and pe+pH of

295   5.93 to 6.95 (Krishnan et al. 2007). Phytophagous Lepidopteran larvae have a higher midgut pH, with a low Eh

296   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

297   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

298   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

299   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).

300

301   Regarding phytophagous insects, little is known about the Eh-pH levels of the plant parts they feed upon.

302   Johnson and Felton (1996b) reported midgut Eh and pH values for 13 Lepidopteran, two Coleopteran, one

303   Orthopteran and one Isopteran species feeding on natural host plants or plant-derived foods. Table 3 reports new

304   information published in the literature.

305

306   *Table 3. Eh-pH physicochemical status of some phytophagous-saprophagous insect midguts (based on literature*

307   *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)

308

309   Similar information is not available for phloem-feeding species (e.g. aphids), since studies were conducted

310   mainly for insects whose body size allows gut dissection (e.g. Lepidoptera, Orthoptera, and some Coleoptera,

311   particularly Scarab beetles). Although Isoptera have a small body size there is interest in studying their digestive

312   processes because they involve symbiotic microbiota (in the hindgut). Still, there are some reservations about the

313   accuracy of Eh measurements for the latter (Eutick et al. 1976; Veivers et al. 1980; Brune et al. 1995). In

314   addition, information is often lacking as to whether redox potentials indicated in these studies are Eh (according

315   to the Standard Hydrogen Electrode) or potentials measured via the reference electrode (Ag-AgCl or calomel).

316   Information on Eh-pH midgut conditions is also missing for species whose diet differs between immature and

317   adult stages, e.g. chafer beetles (*Pachnoda spp.*), cockchafers (*M. melolontha*) or blackbeetles (*O. nasicornis*). *L.*

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

323

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

333

334 Gastropods and nematodes
335 Charrier and Brune (2003) showed that two phyllophageous species of starved helicid snails (Gastropoda and
336 Pulmonata), (*Helix pomatia* and *Cornu aspersum*, syn. *Helix aspersa*) had a pH increasing from the crop (an
337 expanded portion of the alimentary tract used for the storage of food prior to digestion) to the distal intestine of
338 pH 6.4 and 7.4, respectively. In the saprophagous *Elona quimperiana*, the pH along the gut axis remained acidic
339 (5.1–6.6). Oxygen was not detected in the gut lumen of any of these species to highlight anaerobic conditions.
340 This clearly illustrates that the morpho-anatomical differentiation of the intestinal tract corresponds to different
341 physicochemical microenvironments. The increasing alkalinity along the gut should have repercussions for the
342 microbial communities colonizing the intestine. Intestinal microbiota, in turn, may cause changes in the pH of
343 the host tissue during anaerobiosis (Pörtner 1987; Charrier and Brune 2003).

344

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

356

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

358 Studying the effect of plant age and leaf position on susceptibility to wheat stripe rust, Farber and Mundt (2017)
359 suggested that the distribution of the rust could be driven more by differences in host susceptibility than by
360 propagule dispersal. Benada (2017) hypothesized that Eh and pH are major players in plant physiology and
361 pathogen resistance in order to explain the variable changes in resistance that occur during ontogeny of the host
362 and environment that involve: i) the disease gradients on a plant, ii) the evolution of susceptibility of organs
363 during ontogeny and growth, and iii) the difference in resistance of individual plant cells and relatively swift
364 changes of its resistance within a couple of hours. From an evolutionary point of view, the circadian rhythmic
365 cell is a hydro-electro-chemical oscillator driven or synchronized by sunlight with a temporal compartmentation
366 of metabolism and a network of metabolic sequences to compensate for oxidative stress (Wagner et al. 2000). It
367 is, therefore, not surprising to observe a strong spatial and temporal variability of Eh and pH in plants.
368
369 Spatial variability of Eh and pH in plants
370 Plants have five key nutrient tissues, namely the phloem, xylem, leaf apoplast, root apoplast, and cellular
371 organelles that serve as nutrient reservoirs. Each of these are the target of certain pathogens and pests (Fatima
372 and Senthil-Kumar 2015). The nutrient content in these tissues differ in types of minerals and carbon sources
373 (sugars, amino- and organic acids, and organic alcohols) (Fatima and Senthil-Kumar 2015), all of which affect
374 Eh or pH. Eh and pH have been recognized as important factors defining ecological niches for microorganisms
375 (Köpke et al. 2005; Vartoukian et al. 2010; Cardinale 2011; Jones et al. 2015; Koch and Harnisch 2016). The
376 difference in Eh-pH between roots and shoots, as well as between apoplast, xylem and phloem, can therefore be
377 used to characterize Eh-pH niches.
378
379 *Eh-pH niches: Roots vs shoots or grains*
380 The assessment of redox state based on ratios of ASC/DHA (reduced *vs.* oxidized AsA) or GSH/GSSG (reduced
381 *vs.* oxidized Glutathione) ratios logically shows that roots (i. e. non photosynthetic organs) are more oxidized
382 than leaves (i.e. photosynthetic organs) in maize (Ahmad et al. 2016), soybean (Borella et al. 2019), sunflower
383 (Ortega et al. 2017), onion (García et al. 2020) and poplar (Morabito and Guerrier 2000). Roots show
384 tremendous variability in rhizospheric-apoplastic pH, especially in relation to nitrogen mineral nutrition. There
385 is strong acidification related to NH_4^+ absorption and pronounced alkalization related to NO_3^- absorption
386 (Marschner et al. 1986). Masiello et al. (2008) measured a higher carbon oxidation state in maize grains than in
387 maize stover. Internal oxygen concentrations are lower within bulky storage organs such as fruits (apple, banana)
388 or tubers than other tissues. This results in different oxygen gradients within growing potato tubers which have a
389 very low oxygen level in the center of the tuber (Geigenberger 2003).
390
391 Leaf Eh-pH also has high spatial variability. Husson et al. (2018a) plotted the spatial distribution of Eh and pH
392 in rice plants and showed that average leaf pH decreased from younger leaves (located on the upper part of the
393 canopy) to the older ones (located on the lower part of the canopy). The youngest leaves had the highest Eh
394 values, which were negatively correlated with their length (the shorter the leaf, the higher the Eh value). The last
395 fully expanded leaf had the lowest Eh, and Eh of mature leaves increased with leaf age, with the lowest leaves
396 being the most oxidized (higher Eh). The tip of the leaves was also more acidic and in a reduced (lower pH and
397 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)

414

415 The low antioxidant efficiency in the apoplast allows ROS to easily accumulate and provides a condition for

416 ROS signaling. Therefore, the apoplastic ROS-antioxidant homeostasis is actively engaged in the reception of,

417 and reaction to, many biotic and abiotic stresses (Podgórska et al. 2017). Similarly, pH signals light intensity

418 changes, drought, lack of oxygen, and the presence of symbiotic partners or microbial attackers (Felle 2001).

419 The plant apoplast is the first site of direct contact with a pathogen and is thus an interface that mediates the first

420 crosstalk between host and pathogens to perform a crucial role in initiation and coordination of many defense

421 responses (Bolwell et al. 2001; Gupta et al. 2015). Any deviations from the basal cellular redox balance may

422 induce responses that continuously readjust cellular functions; however, diversion of resources to stress

423 responses may limit growth and may thus be detrimental to the plant. The ultimate outcome of these responses

424 must therefore be tightly controlled by the redox signaling networks between organellar and apoplastic signaling

425 systems (Sierla et al. 2013). This is also valid for pH that acts as a messenger in situations where pH changes are

426 preconditions for certain processes, e.g., the gravity response, activation of certain transporters in stomatal

427 movements, and possibly for growth in general (Felle 2001).

428

429 *Intra-cellular variability of Eh-pH*

430 Eh-pH conditions in the cell organelles are summarized in Table 5. Cell Eh-pH is strongly buffered to permit

431 marked differences and interplay between organelles.

432

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 pratense*; 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.

			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)
		xylem pH Decreased cytosol pH Increased vacuolar pH		
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)

512

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

532 et al. 2009). In *Vicia faba*, alkalization was acropetally moved to the leaves after first arriving in the older leaves
533 where it spread systemically throughout the entire apoplast, starting from the leaf base towards the tip. The
534 alkalization then increased ABA in the leaf apoplast and guard cells (Geilfus 2017). Apoplast pH affected
535 functionality by reducing the stomatal pore size in *Vicia faba* during the onset of Cl⁻ salinity via effects on ABA.
536 Based on this mode of action, it was hypothesized that, under conditions of soil salinity, Cl⁻-inducible
537 alkalization of the leaf apoplast reduces the transpiration rate and, thus, reduces the uptake of Na+ and Cl⁻ from
538 the soil solution (Geilfus 2017).
539
540 Aluminum (Al) is a major plant growth-limiting factor in acid soils (Melakerberhan et al. 1995). The primary
541 site of Al accumulation and toxicity is the root meristem. Al triggers lipid peroxidation and ROS production in
542 roots, inhibits respiration and depletes ATP (Yamamoto et al. 2003). In barley, alleviation of aluminum toxicity
543 by hydrogen sulfide was related to elevated ATPase and suppressed oxidative stress (Dawood et al. 2012).
544 Several other toxic elements are known to lead to plant oxidation, including cadmium (leading to formation of
545 callose in phloem cells), zinc, mercury, and antimony (Cuypers et al. 2001; Benitez-Alfonso et al. 2011;
546 Sobrino-plata et al. 2014; Ortega et al. 2017).
547 In general, high levels of metal ions such as Co, Cu, Fe, Mn, Mo, Ni,and Zn, and trace levels of toxic metals (Pb,
548 Cd, Hg, As, Cr, Ag, Al, Cs, Sr, U) have been reported to negatively affect plant growth, metabolism,
549 development, and overall productivity, due mainly to accelerated ROS formation and, to a lower extent, through
550 other reactions (Anjum et al. 2014). High soil pe+pH also increases Cd availability from increased bacterial
551 activity (Wang et al. 2020). Finally, GSH is a key antioxidant for the plant to cope with mercury and cadmium
552 stress (Sobrino-plata et al. 2014). Likewise, the ascorbic acid (AsA) redox system efficiently protects the plant
553 and plays a key role in metal-metalloid stress tolerance (Chen et al. 2017b). A deficiency of GSH and AsA leads
554 to susceptibility to toxic elements such as Cadmium (Jozefczak et al. 2015).
555
556 *Mineral nutrition and plant Eh-pH*
557 Mineral nutrition impacts plant photosynthesis and, as a consequence, plant Eh-pH. Any kind of N, P or K
558 deficiency leads to plant oxidation. While N deficiency results in alkalization, P or K deficiency results in
559 acidification (Table 8). The concentration of amino acids and sugars in the apoplast of leaf and stem tissue may
560 increase with Ca, B, Zn or K deficiency (Huber et al. 2011), which leads to an increase in EC. Furthermore, Si
561 content decreases with excess applications of N, which can also affect disease tolerance (Gupta et al. 2017).
562 Besides the availability of N, the form in which it is absorbed by the plant influences soil Eh-pH and has a
563 dramatic impact on plant physiology (Marschner et al. 1986).
564
565 *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

	Eh	Oxidation and altered antioxidant responses	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)

566

567 The form of nitrogen absorbed by the plant and the solubility of essential elements are related not only to the

568 type of fertilizer applied but also to soil Eh-pH conditions. The main form of N absorbed is mainly determined

569 by pe+pH with a balance between both forms being reached close to pe+pH=14 (Husson 2013). Drought limits

570 biological activity and thus leads to a raise in soil Eh and pe+pH, with a strong negative impact on Fe and Mn

571 solubility, and increased nitrification. For example, a four-fold reduction in nitrate reductase activity was

572 observed following 6 days of severe drought (Li et al. 2014). In contrast, submersion causes a strong and rapid

573 decrease in soil Eh, with a slight raise in pH, leading to low pe+pH, thus to reduced, soluble Fe and Mn, and to

574 ammonification (Ponnamperuma 1972; Cottes 2019). Thus, the dominant form of mineral nitrogen in soil is

575 nitrate in dry-oxidized-alkaline soils and ammonium in waterlogged-reduced-acidic soils.

576

577 Nitrate absorption strongly alkalizes plant roots and shoot (apoplast) while ammonium absorption leads to strong

578 acidification, with a strong impact on other nutrients solubility-absorption. Absorption of nitrate is an active

579 process that increases root respiration to reduce Eh in the rhizosphere while leading to shoot oxidation (Table 9).

580

581 *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

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

617   Hence, this "redox" model (Fig. 2) correlates: i) the Eh-pH conditions of the plants in their various
618   compartments (roots, shoots, stems, grains, fruits and apoplast, xylem, phloem, cell, and organelles) which are
619   the result of genotype, age, management practices and the various stresses related to the abiotic and biotic
620   environments, their intensity and their duration; ii) the specific conditions at which specific pests can thrive
621   depending on the pest type, their reproductive cycle, metabolism and living style (soil-borne vs air-borne,
622   biotrophic-hemi-biotrophic-necrotrophic, intracellular-extracellular, chewing-sucking, etc.).
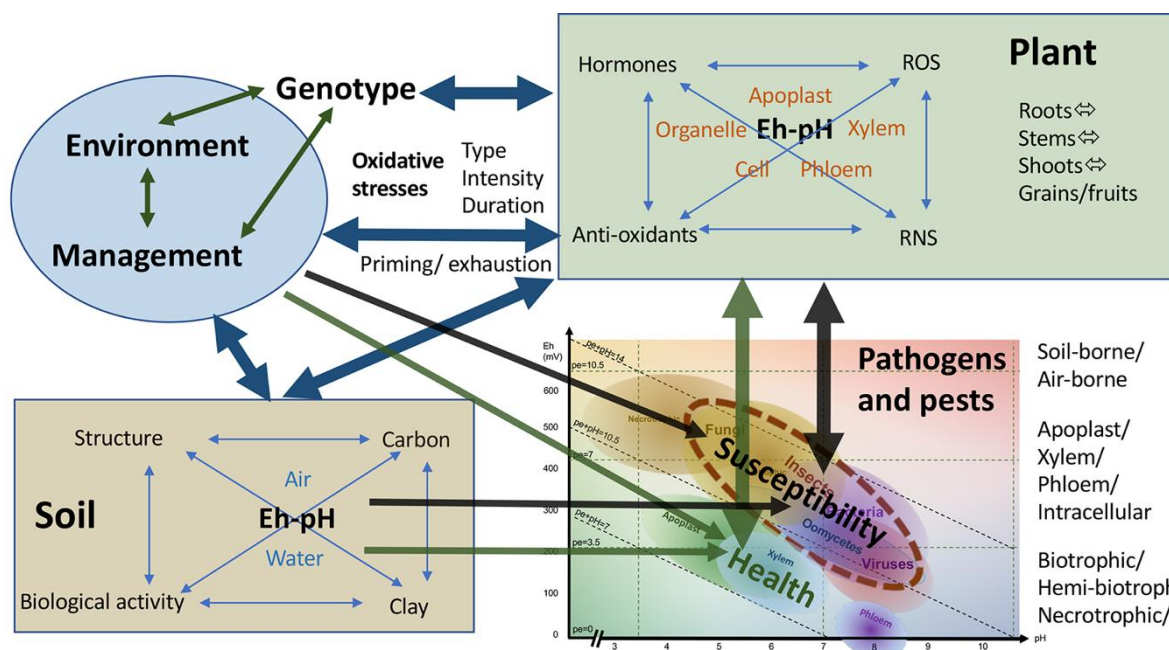
623
624

625
626   *Fig. 2: Model of GxExMxP interactions in a "Redox" perspective. Environment and management practices*
627   *impact soil Eh-pH (water and air in interaction with soil structure, carbon, biological activity and clay).*
628   *Environment (management practices) and soil Eh-pH induce oxidative stresses in plants, which together with*
629   *genotype affect plant Eh-pH in the various plant compartments through interactions between ROS, RNS,*
630   *hormones and antioxidants. These antioxidants can be primed or inversely exhausted in relation to type,*
631   *duration and intensity of the various stresses. In this model, plants become susceptible when imbalanced Eh-pH*
632   *conditions in plant compartments match the specific Eh-pH conditions at which the various pests can thrive.*

633
634   The effects of the multiple and complex abiotic and biotic factors and their interactions can be integrated into
635   these simple parameters to provide a powerful tool for analyzing *GxExMxP* interactions in a temporal and
636   spatialized perspective.

637

24

638 Can spatio-temporal variability in plant Eh-pH explain locations-periods of plant susceptibility-tolerance-
639 resistance to various pests?
640
641 The "Eh-pH zones", where the various types of pests can thrive in space (relation to the various plant parts) and
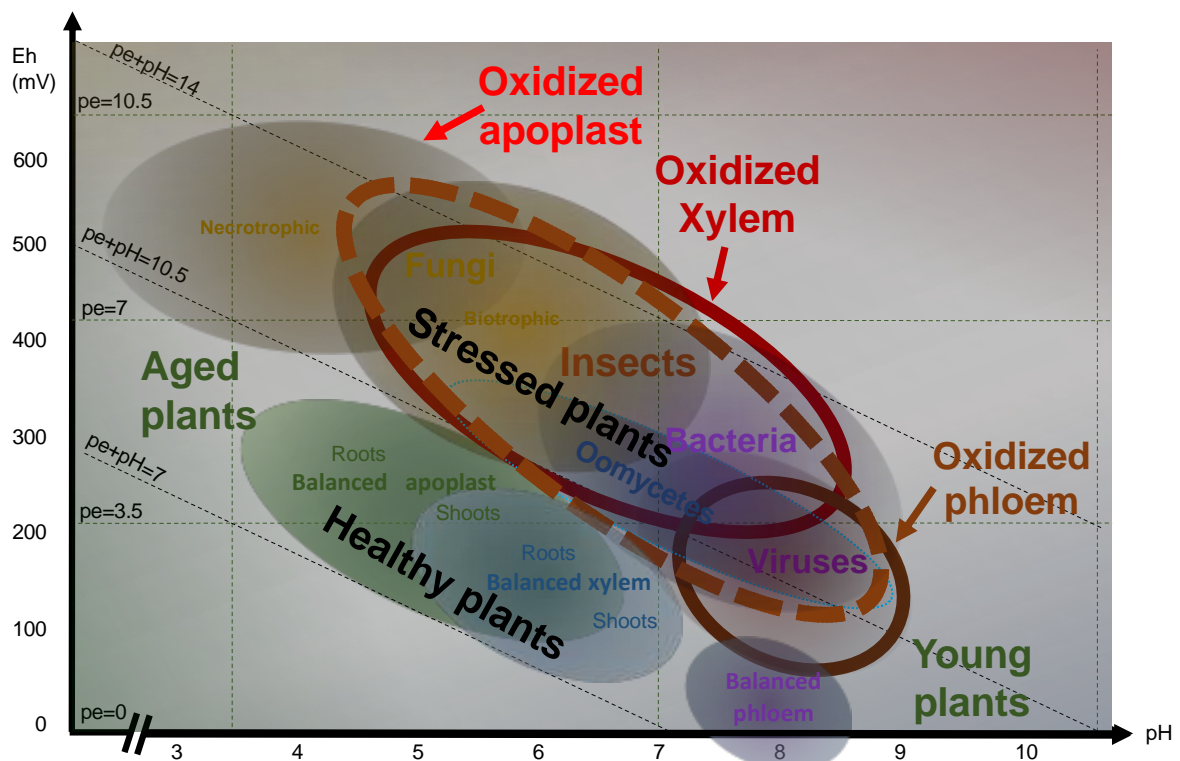642 time is summarized in Fig. 3.
643
644

645
646 *Fig. 3. Eh-pH map of indicative zones where the main groups of pests can thrive, corresponding to oxidized*
647 *plants. Adapted from section 2 (Tables 1 and 2) and section 3. Viruses develop in alkaline phloem and possibly*
648 *xylem, as do most bacteria. Inversely, most fungi prefer the acidic and more oxidized apoplast. Oomycetes often*
649 *thrive in moderately oxidized apoplast, usually at higher pH than their fungal counterparts. Insects have*
650 *different preferences, according to their feeding mode: xylem or phloem sucking insect at higher pH and lower*
651 *Eh compared with biting-chewing insects; larvae at lower pe+pH and higher pH compared with adults. These*
652 *are only tendencies for the main groups of pathogens and pests, as optimal Eh-pH conditions are specific.*
653 *Although some pathogens are ubiquistic, able to develop in a large range of Eh-pH conditions, most pathogens*
654 *can develop only in a specific, narrow Eh-pH range (Rabotnova and Schwartz 1962).*
655
656 The spatial variations in plant Eh-pH correlate well with, and may explain the spatial distribution of pests within
657 plant organs as illustrated by four examples: i) the initial development of fungi (fungal wilt pathogens) in the
658 apoplast (more acidic and oxidized than the vascular system), and where many soil-borne fungi are necrotrophic
659 (developing in the more acidic-oxidized conditions of the roots) while most of the biotrophic pathogens, such as
660 rusts and powdery mildews, occur on the above-ground portions of the plants that are less acidic and oxidized
661 than the roots (Raaijmakers et al. 2009); ii) the preferential development of many Gram-positive bacteria,

25

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).
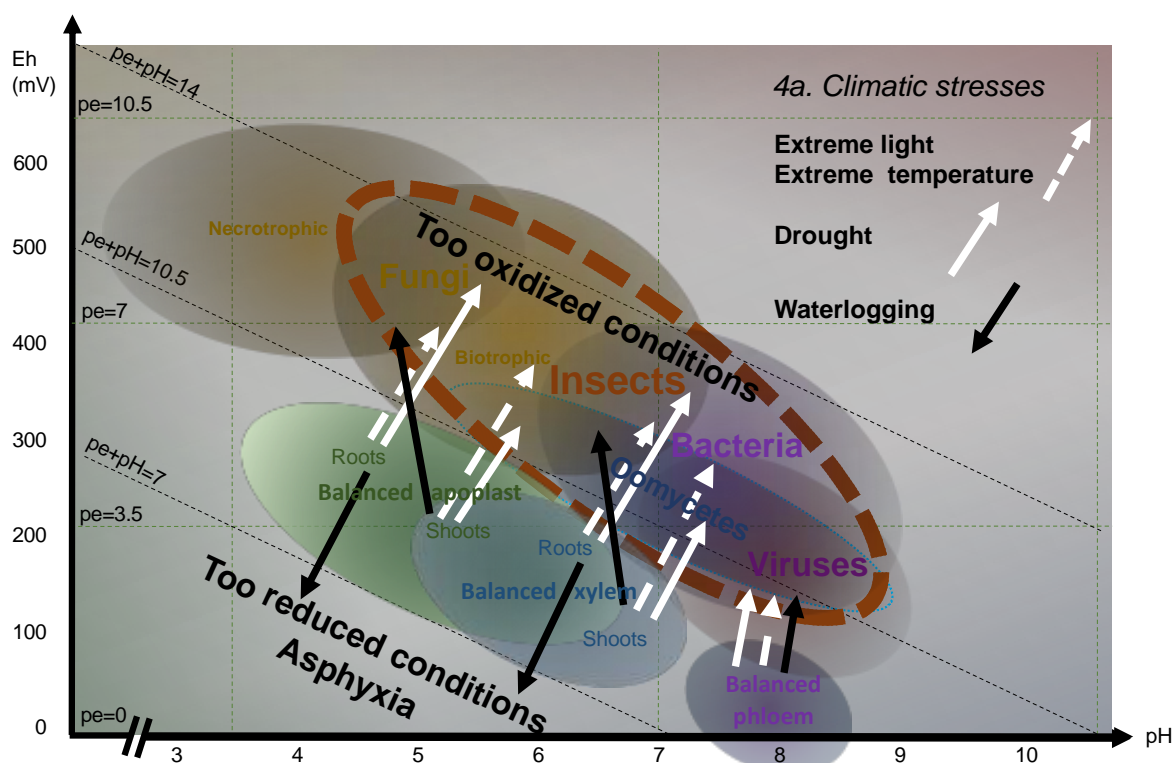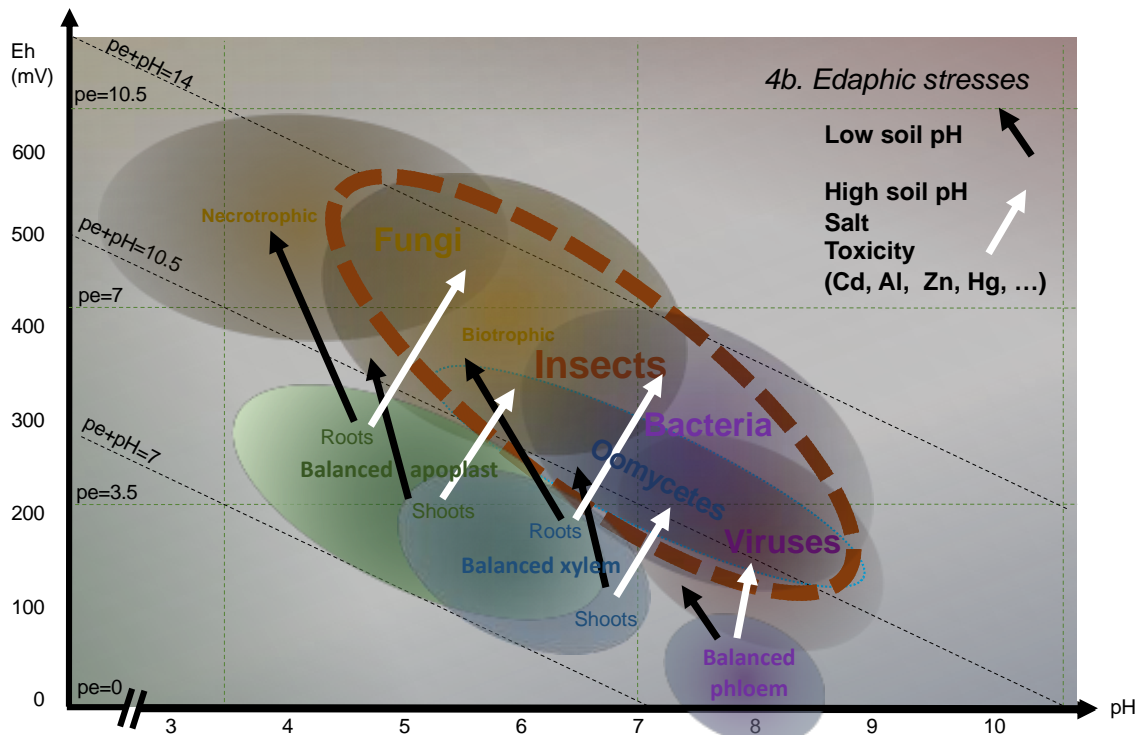
Fig. 4: Impact of abiotic stresses leading to unbalanced redox conditions in plant parts (pH-Eh map) in relation zones indicating optima where the main pest groups can thrive (adapted from Tables 1 and 2). 4a. Climatic stresses. 4b. Edaphic stresses. Edaphic stresses often lead to plant oxidation and 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

786   effects (Lamichhane 2015); and iii) availability of anti-oxidant pools in the plant, their ability to counterbalance
787   the oxidative stresses and their possible exhaustion.

788

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

790   Stress may affect plant diseases through a range of effects on the pathogen, host, or the host-pathogen

791   interaction. The concept of predisposition implies an effect on the host rather than on the pathogen (Sorauer

792   1974). Stresses or nutrition that cause stomatal closure or formation of a thicker cuticle may prevent invasion by

793   pathogens. In some cases, however, pathogens may enter a plant regardless of stress and affect disease

794   development more than infection (Schoeneweiss 1975). Drought-induced pathogen resistance is presumably due

795   to enhanced induction of antimicrobial and PR-proteins activated by drought. These compounds can protect

796   plants during early stages of pathogen infection. Plant susceptibility to drought may be attributed to high levels

797   of ABA in drought stressed plants since this hormone interferes with pathogen-induced plant defense signaling

798   and thereby reduces the expression of defense-related genes (Ramegowda and Senthil-Kumar 2015).

799

800   Bostock et al. (2014) developed a model of plant response to integrate the general adaptation syndrome with the

801   concept of disease severity, disease duration and disease predisposition. In this model, there is an alarm stage

802   following an abiotic stress event which corresponds to the maximum predisposition before the acclimation-

803   resistance stage (maximum resistance) to conclude with a final collapse, exhaustion and death stage.

804   In an Eh-pH perspective (Fig. 5a), this could be seen as a first phase for the increase in ROS (and ABA) that is

805   followed by the production of antioxidants and phytoalexins by the plants (acclimation stage, maximum

806   resistance). The collapse stage could be regarded as the exhaustion of the antioxidant capacity of the plant that

807   leads to a further increase in oxidation level. The collapse, exhaustion and death phase could, therefore, be split

808   into two sub-phases: i) a high susceptibility phase that could still be reversible, especially to viruses and

809   necrotrophic pathogens, that is related to strongly oxidized conditions upon exhaustion of antioxidants, and ii) a

810   death phase related to irreversible oxidation. Furthermore, the high production of antioxidants following ROS

811   activation after a moderate stress could have a priming effect to induce a greater capacity to respond to further

812   stimulus, lowering the plant redox state, and, thus, preparing it for a rapid response in case of pest attacks. One

813   hypothesis could be that plants that sustain a lower Eh level can more readily produce reduced primary and

814   secondary metabolites such as phenolics, SA and phytoalexins or redox regulated molecules such as plant

815   pathogenesis-related proteins (Fobert and Després 2005; Balmer et al. 2015). Indeed, compounds that induce

816   priming are reported to promote stronger and faster responses to stress by modulating the oxidative environment

817   and interacting with signaling pathways mediated by SA, JA and ET (González-Bosch 2018).

818

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

820   Under natural conditions, biotic and abiotic stresses frequently co-occur. As a consequence, common molecular

821   signaling pathways governing adaptive responses to individual stresses can interact (Nguyen et al. 2016). A

822   mechanism to study multiple-stress interactions (Bateman, 1978) recognizes that plant responses to a

823   combination of stresses such as heat and drought may differ from those to individual stresses. Abiotic stress

824   applications are likely to influence plant-pathogen interactions and vice versa (Prasch and Sonnewald 2015). For

825   instance, when applied in combination, drought and herbivory had an additive effect on specific processes

826 involved in secondary metabolism and defense responses, including protease inhibitor activity (Nguyen et al.
827 2016). Abiotic and biotic stress interactions can occur at multiple levels, depending on the type of stress
828 (osmotic, ionic), growth characteristics, infection strategy of the pest (biotroph-necrotroph, mode of infection by
829 direct penetration or through plant openings such as stomata, etc.) or infection stage of the host (Kissoudis et al.
830 2014).

831

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

839

840 In their seminal review on enhancing crop resilience to combined abiotic and biotic stress, Kissoudis et al.
841 (2014) showed that stress factors affect the homeostasis of chemical signals in the apoplasm such as Ca^{2+}, ROS,
842 and pH levels. A combination of abiotic stress with pathogen infection potentially derails hormone and systemic
843 ROS homeostasis. Under multiple stresses, the intensity of one stress affects the plant's responses to further
844 stresses. For instance, plants exposed to mild drought stress activate the basal defense response that enables them
845 to defend against pathogen infection. In contrast, severe drought causes leakage of cellular nutrients into the
846 apoplast that facilitates successful pathogen infection (Ramegowda and Senthil-Kumar 2015).
847 Considering both the oxidative stress and the regulation of antioxidant systems, Lushchak (2014) proposed four
848 levels of an intensity-based classification of oxidative stress, namely: i) a basal oxidative level; ii) a low intensity
849 oxidative stress, in which markers of ROS-induced and ROS-sensitive functions can be measured; iii) an
850 intermediate intensity oxidative stress, and iv) a high intensity oxidative stress where markers of oxidatively
851 modified components dominate.
852 In the proposed hypothesis in this paper we integrate the various models and classifications through an Eh-pH
853 perspective. Consideration of oxidative stresses in combination with plant responses (antioxidant systems in
854 interaction with hormones) results in a dynamic and spatialized plant Eh-pH model (Fig. 5). In this model, low to
855 moderate stress after an alarm stage (predisposition upon oxidation), leads to the production of antioxidants (in
856 relation to ABA) and priming of plant defense mechanisms and decreased plant susceptibility in an acclimation
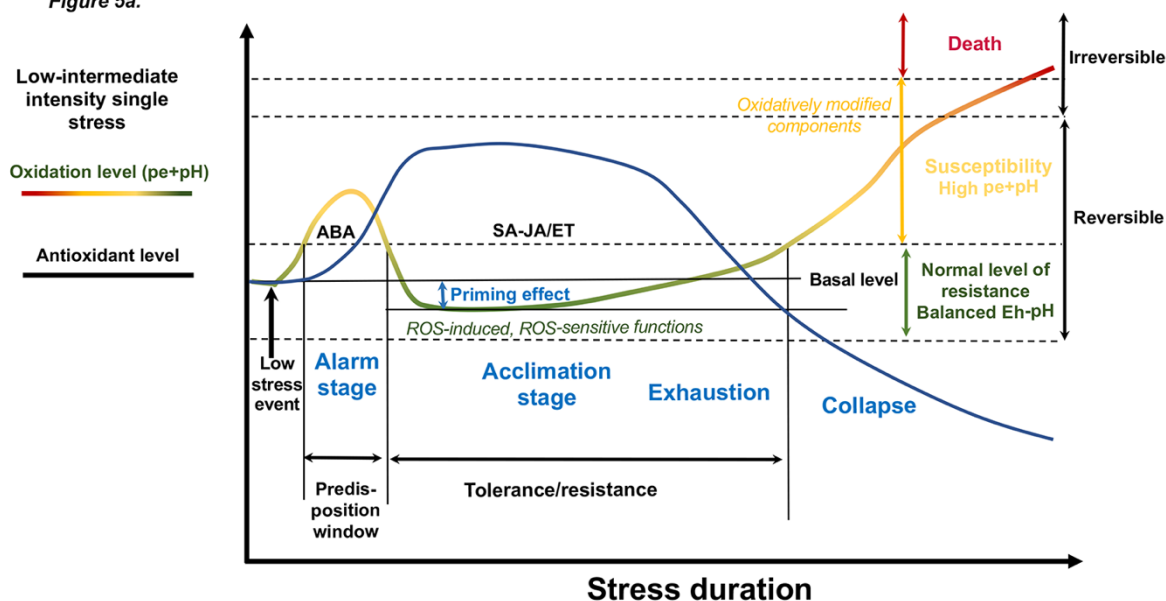857 stage in which SA, JA-ET induce SAR-ISR.
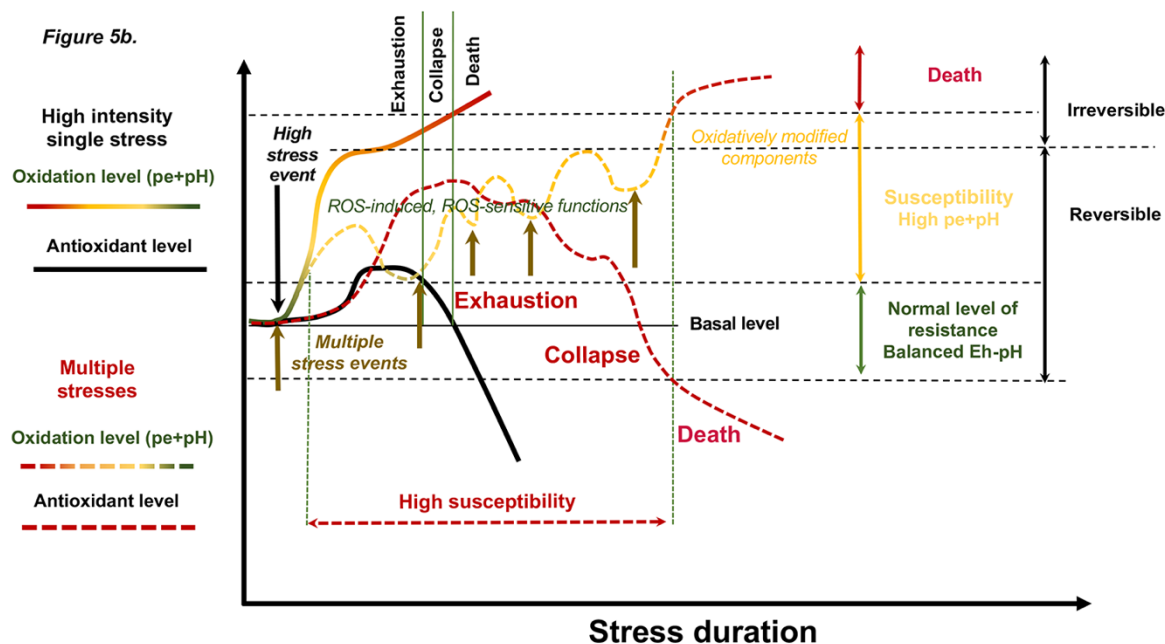
Figure 5a.

Figure 5b.

858

859

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

869

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

909 plant nutrition can significantly influence the growth and condition of phytophagous insects that influence their
910 susceptibility to pathogens (Shikano et al. 2010).

911

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

923

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

932

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

944

945 Revisiting mineral nutrition and plant-pest interactions with an Eh-pH perspective
946 Interactions between mineral nutrition and plant pests include how nutrient supply alters pest prevalence and
947 influences competitive interactions among coinfecting pathogens (Lacroix et al. 2014). However, several
948 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.

35

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).
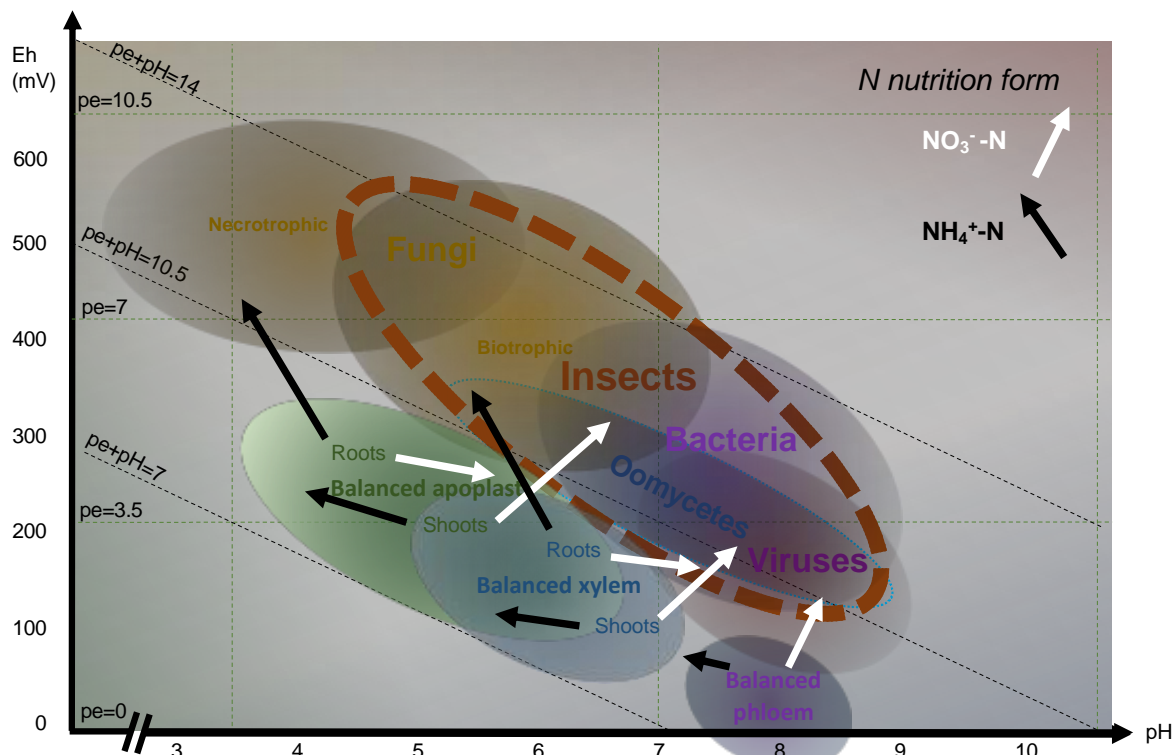

Fig. 6: Impact of N-form of nutrition, creating unbalanced redox conditions in plant parts (pH-Eh map) in relation to optimum zones where the main groups of pathogenic microorganisms and pests can thrive. NH_4^+ absorption (red arrows) leads to plant acidification, reduction (decreased pe+pH) of shoots 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

1051　homeostasis perspective could also be used to analyze the incidence of insect pests under mineral vs organic

1052　fertilizations (Altieri and Nicholls 2003).

1053

1054　*Micronutrients and plant-pest interactions in a Eh-pH perspective*

1055　Manganese is a good illustration of the benefit in considering Eh-pH to decipher relations between mineral

1056　nutrition and plant pests. Mn absorption is strongly influenced by soil-rhizosphere Eh-pH conditions, and is

1057　soluble only in its reduced form (Mn^{2+}), at low pe+pH. Mn has a tremendous impact on plant Eh-pH. Of central

1058　importance are its structural, redox and electron transport roles in photosynthesis, which results in the splitting of

1059　water and electron harvesting during the light reaction. Aside from Mn superoxide dismutase and a few Mn

1060　containing enzymes, Mn functions primarily as an activator of enzymes, including dehydrogenases, transferases,

1061　hydroxylases and decarboxylases (Thompson and Huber 2007).

1062

1063　Due to its role in plant Eh-pH regulation, it is not surprising that Mn availability reduces diseases in 89% of the

1064　cases (reviewed by Thompson and Huber (2007)). All the conditions leading to Mn reduction and, thus to its

1065　increased availability, decreased the development and severity of pathogenic fungi such as *Gaeumannomyces*

1066　*graminis* and *M. oryzae*. Interestingly, these pathogens possess the ability to oxidize Mn, and their virulence

1067　depends on this capacity. Mn oxidation was, thus, highly correlated with fungal virulence and disease

1068　development (Thompson and Huber 2007). The battle for Mn between host and bacterial pathogens, in relation

1069　to oxidative stress, was, indeed, a major determinant defining the outcome of infections (Juttukonda and Skaar

1070　2015).

1071

1072　Other essential micronutrients in redox regulation have a strong impact on a large range of pests. Examples are

1073　sulfur (Bloem et al. 2005), copper and boron, which were reported to decrease diseases in 93 and 91% of the

1074　studied cases, respectively (Datnoff et al. 2007).

1075　The first-row transition metals—manganese (Mn), iron (Fe), cobalt (Co), nickel (Ni) and copper (Cu)—provide

1076　the necessary redox and catalytic activity for many important biological processes (Ranieri et al. 2001; Bárcenas-

1077　Moreno et al. 2011; Gerwien et al. 2018). A process aptly named 'nutritional immunity' makes the host actively

1078　sabotage and counteract metal uptake by microorganisms and it can also fight invaders by deploying toxic levels

1079　of certain metals. Iron, Cu and Mn, for example, are intrinsically toxic via Fenton chemistry (generation of

1080　oxygen radical species from hydrogen peroxide, catalyzed by the metal), leading to oxidative damage to the

1081　microbes at high metal concentrations (Gerwien et al. 2018). Finally, silicon, which has been reported to play an

1082　important role in resistance to fungal and bacterial diseases, and to herbivory (Epstein 1994; Fauteux et al. 2005;

1083　Sakr 2016; Liu et al. 2017), is also known to improve antioxidant capacity and redox homeostasis (Manivannan

1084　et al. 2018; Soundararajan et al. 2018). For example, silicon induces resistance of cassava to bacterial blight by

1085　altering antioxidant enzyme activity (Njenga et al. 2017).

1086

1087　Revisiting pathogenicity and virulence in an Eh-pH perspective

1088　The Eh-pH perspective described herein provides a simple answer to the question "what makes commensal or

1089　opportunistic microorganisms become pathogenic?" The answer is that "A commensal or opportunistic

1090   microorganism becomes pathogenic when it encounters or can develop Eh-pH niches favorable for its
1091   development".

1092   This hypothesis is supported by the fact that pH has now been recognized as a key factor in reducing fungal
1093   pathogenicity (Fernandes et al. 2017). In addition, cellular redox balance may serve as an inducer for the
1094   defense-related genes, including pathogenesis-related proteins (Foyer 2005). Oxalic acid indirectly aids
1095   *Sclerotinia sclerotiorum* pathogenicity by acting as a signaling molecule via manipulation of host ROS
1096   (Williams et al. 2011). Furthermore, ROS and redox regulation are also involved in the perception of pests and
1097   activation of plant defense. For instance, mitogen-activated protein kinase cascade, involved in pattern-triggered
1098   and effector-triggered immunity, is activated and regulated by ROS (Bigeard et al. 2015; Liu and He
1099   2017).Indeed, the Rice Yellow Mottle Virus-encoded viral suppressor of RNA silencing P1 is a protein with
1100   redox-dependent flexibility (Gillet et al. 2013).
1101

1102   It can also be hypothesized that the virulence of a pathogen is related to its ability to alter and sustain host plant
1103   Eh-pH to its benefits despite the plant attempts to make it unfavorable, especially during the oxidative burst in
1104   the hypersensitive response (Torres et al. 2006). This is observed with *Sclerotinia sclerotorium* and *Botrytis*
1105   *cinerea* through oxalic acid production (Mbengue et al. 2016; Wang et al. 2016), or in bacteria through
1106   production of thiol antioxidants such as GSH and detoxification enzymes that consume ROS (Reniere 2018).
1107   Fungal pH modulations of the host environment regulate an arsenal of enzymes to increase fungal pathogenicity.
1108   This arsenal includes genes and processes that compromise host defenses, contribute to intracellular signaling,
1109   produce cell wall-degrading enzymes, regulate specific transporters, induce redox protectant systems, and
1110   generate factors needed by the pathogen to effectively cope with the hostile environment within the host (Alkan
1111   et al. 2013). The ability of the pathogen to actively increase or decrease its surrounding pH allows it to select the
1112   specific virulence factor, out of its vast arsenal, to best fit a particular host (Prusky and Yakoby 2003).
1113

1114   The evolution of pathogenicity towards novel hosts may be based on traits that were originally developed to
1115   ensure survival in the microorganism's original habitat, including former hosts (Van Baarlen et al. 2007). An Eh-
1116   pH perspective could help understand cross-kingdom host jumps or why and how pests can expand their host
1117   range. This perspective can also provide new insights on the "disease triangle" that integrate pathogenicity, host
1118   susceptibility, and environment. This can be done by stating that compatible interactions between a pathogen and
1119   a host will only result in disease symptoms when environmental conditions are also fulfilled (Van Baarlen et al.
1120   2007). This review suggests that Eh-pH are major determinants of environmental conditions impacting pest-host
1121   interactions.
1122

1123   Microorganisms thriving in slightly reduced and acidic conditions could be commensal or even beneficial to
1124   plants in such situations; however, they may become detrimental when Eh-pH conditions change (especially
1125   increase in pe+pH) to alter their interactions. This could be the case for Cyanobacteria which exhibit
1126   characteristics of higher plants (photosynthetic organisms) as well as bacteria. These bacteria are able to reduce
1127   the effect of salinity by producing extracellular polysaccharide or compatible solutions, increase rice seed
1128   germination in drought situations, and remove pollutants (heavy metals and pesticides) from soil and water
1129   (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 efficient 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.
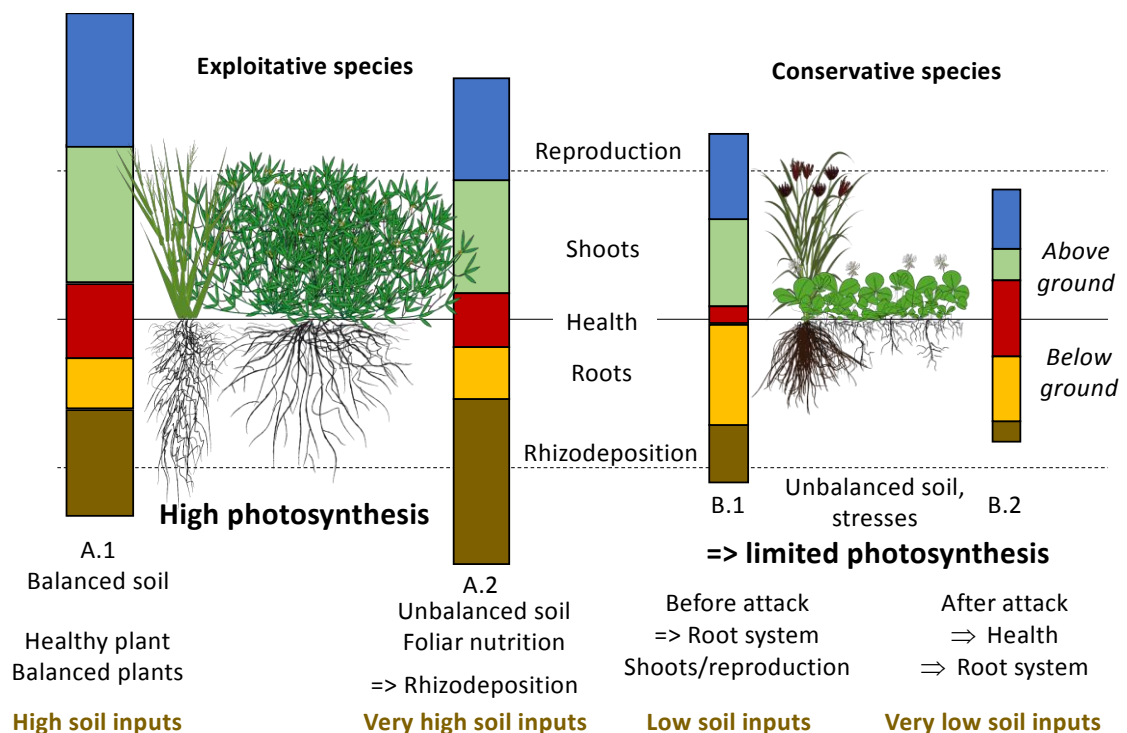

Fig. 7. Hypothesized model of energy allocation to reproduction, growth, health and rhizodeposition as a function of growing conditions. The energy investment distribution and aboveground-belowground interactions in this Fig. vary with plant strategies. A1: Under optimal soil conditions, the high energy 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

1314 plants to favor beneficial rhizosphere communities via modification of plant exudation patterns in response to
1315 exposure to aboveground pathogens to the benefit of subsequent plant generations (Yuan et al. 2018).

1316

1317 The rhizosphere microbiome results from an interplay between soil and seed microbiota, beneficial and
1318 pathogenic microorganisms colonizing aerial parts of plants, and root exudation; all of which appears to be
1319 largely regulated by Eh and pH. Microorganisms play a key role in the numerous interactions between plant and
1320 soil, but soil is in part derived from the activity of plants (Fig. 8) since they supply organic matter and play a
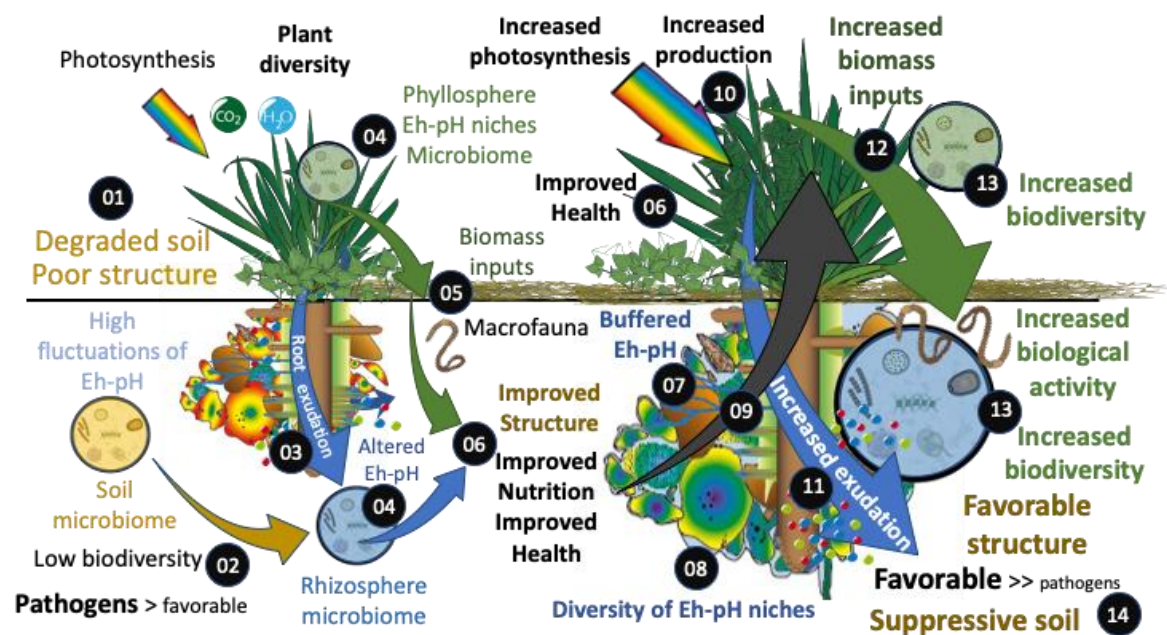1321 pivotal role in weathering rocks and minerals (Lambers et al. 2009).

1322

1323

1324
1325 *Fig. 8: Schematic presentation of the soil-plant-microorganism system showing the central role of*
1326 *photosynthesis by plant that provides the "fuel" for soil system regeneration. On degraded soils (01), poor*
1327 *structure and high Eh-pH fluctuations lead to low diversity of the soil microbiome, with pests dominating*
1328 *beneficial organisms (02) to result in poor plant growth. As a consequence, plants have limited capacity and*
1329 *energy to sustain an efficient pest or pathogen defense system, leading to poor plant health. Increasing*
1330 *photosynthetic activity by various means leads to increased root exudation (03) that alters Eh-pH and allows the*
1331 *development of a diversity of microorganisms in the rhizosphere and phyllosphere (04). The inputs of biomass*
1332 *on the soil surface from decaying plant parts create a litter (05) that, promotes the development of active*
1333 *macrofauna. Together with the active macrofauna, feeding on root exudates microorganisms in the rhizosphere*
1334 *improve soil structure, plant nutrition and plant health (06). The improved soil structure and active microbiota*
1335 *buffer the Eh-pH, both in soil and plants (07) to create a diversity of Eh-pH niches (08) and food supplies for*
1336 *microorganisms. All of this activity favors the completion of major biogeochemical cycles and increases plant*
1337 *defense against pests. Improved soil structure, plant nutrition and health (09) result in increased photosynthesis*
1338 *and biomass production (10). Consequently, both root exudation (11) and biomass inputs on the soil surface*
1339 *(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).

1342

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

1345 Competitive interactions in soil microbial communities are regarded as the major driving factor of general soil

1346 suppressiveness. To infect root tissue, pathogens have to compete with members of the rhizosphere microbiome

1347 for available nutrients and microsites (Chapelle et al. 2016). In disease-suppressive soils, pathogen activity is

1348 strongly restricted by specific rhizosphere microorganisms. For instance, the rhizosphere microbiome of sugar

1349 beet seedlings grown in a soil suppressive to the fungal pathogen *Rhizoctonia solani* showed that

1350 *Oxalobacteraceae, Burkholderiaceae, Sphingobacteriaceae* and *Sphingomonadaceae* were significantly more

1351 abundant in the rhizosphere upon fungal invasion and that stress-related genes (ppGpp metabolism and oxidative

1352 stress) were upregulated in these bacterial families (Chapelle et al. 2016). It was postulated that the pathogenic

1353 fungus induces directly or via the plant, stress responses in the rhizobacterial community that lead to shifts in

1354 microbiome composition and to activation of antagonistic traits that restrict pathogen infection. Several root-

1355 colonizing microorganisms are known to improve the plants response to pathogens (Meisner and De Boer 2018).

1356 Upon pest attack, plants are able to stimulate protective microorganisms and enhance microbial activity that

1357 suppresses pests in the rhizosphere (Berendsen et al. 2012). Natural antibiotics are weapons in the microbial

1358 warfare in the rhizosphere that are integral to plant health (Cha et al. 2016). Plant response to increased pathogen

1359 abundance depends on the microbial community colonizing the root, which is affected by the amount and

1360 composition of rhizodeposits. For example, iron-mobilizing coumarins exuded by *A. thaliana* shape their root

1361 bacterial community by inhibiting the proliferation of a relatively abundant *Pseudomonas* species via a redox-

1362 mediated mechanism (Voges et al. 2019). Redox-active phenazine compounds also play a role in the persistence

1363 and survival of *Pseudomonas* spp. in the rhizosphere and, inversely, plant-beneficial phenazine-producing

1364 *Pseudomonas* spp. are proficient biocontrol agents of many soilborne pathogens (Biessy and Filion 2018).

1365 Melatonin, an amphiphilic antioxidant produced by cellular organisms able to scavenge both oxygenated and

1366 nitrogenated compounds, may decrease the deleterious physiological effect of various abiotic stresses through

1367 modulation of antioxidative enzymes and enhancement of organic acid anion exudation. In addition it may

1368 differentially modify some bacterial and fungal communities (Pisoschi and Pop 2015; Zhang et al. 2017;

1369 Madigan et al. 2019).

1370

1371 Redox states affect substrate availability and energy transformation and, thus, play a crucial role in regulating

1372 soil microbial abundance, diversity, and community structure (Song et al. 2008). Redox potential fluctuations are

1373 common in soils, and microbial community acclimation or avoidance strategies for survival shape microbial

1374 community diversity and biogeochemistry (DeAngelis et al. 2010). By characterizing redox-related soil

1375 microbial communities along a river flood plain continuum, Song et al. (2008) observed that, microorganisms, in

1376 general were highly abundant, diverse, and distributed more evenly in the oxic layers than the anoxic ones. The

1377 lower diversity in the anoxic than the oxic soils was primarily attributed to differences in oxygen availability in

1378 these soils. The decrease in abundance with increasing oxygen and substrate limitation, however, was

1379 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

1420 with the formation of microaggregates, sustains the activity of oxygen-sensitive anaerobic enzymes and leads to
1421 the direction of unsorted redox processes (i.e. not following the "redox tower" that would cause ecological
1422 niches of prokaryotes that consume electron acceptors in a thermodynamically determined order), within and
1423 between populations (Chen et al. 2017a). Various ecological services can be simultaneously ensured at any time
1424 by the rich soil biodiversity in a balanced environment.

1425

Conclusions and future perspectives

1427 Although causality cannot be demonstrated with the available literature, the literature does report many spatio-
1428 temporal correlations between Eh-pH conditions and plant susceptibility, tolerance and resistance to pests across
1429 various stress conditions that could support our initial hypothesis that Eh-pH homeostasis is central to soil and
1430 plant health. The Eh-pH homeostasis model is strengthened by the fact that this model: i) represents a unifying
1431 paradigm that comprises a large range of processes in a very logical and consistent manner; ii) encompasses
1432 various other models in crop protection (priming-exhaustion, optimal defense theory, susceptibility-tolerance-
1433 resistance, soil legacy, etc.); iii) enlightens our understanding of these processes without contradicting any
1434 observation or current knowledge; and, finally iv) provides a useful perspective to disentangle G x E x M x P
1435 interactions.

1436

1437 The new perspective this model proposes could help: i) plant pathologists and entomologists understand plant-
1438 pathogen and plant-pest interactions, and develop new approaches to pest management; ii) epidemiologists and
1439 modelers refine their models; iii) breeders improve and accelerate breeding for improved plant resistance,
1440 adaptability and tolerance to various stresses, pests and pathogens; and enhance energy allocation between
1441 growth and defense in selected varieties; iv) plant nutrition specialists design advanced fertilizers adapted to pH-
1442 Eh conditions of a given soil to meet the requirements of a given crop; and v) agronomists develop
1443 agroecological crop protection (ACP; Deguine et al. 2017) or biodiversity-based agriculture by developing
1444 ecosystem services provided by biological diversity based on a redesign of the farming system (Wezel et al.
1445 2014; Duru et al. 2015).

1446

1447 Overall, an Eh-pH perspective could become a very powerful tool to develop a "one health approach"
1448 (Mackenzie and Jeggo 2019; Ratnadass and Deguine 2021) as the same parameters explain fundamental
1449 processes and could be used to characterize the "health" of soils (Husson et al. 2018b), plants (Husson et al.
1450 2018a), animals and humans. This is consistent with the increasing recognition of the importance of Eh and pH
1451 homeostasis in health (Aoi and Marunaka 2014; Ursini et al. 2016; Kruk et al. 2019) and the role of microbiota
1452 and pathobiota in healthy and unhealthy host immune responses (Littman and Pamer 2011).

1453

1454 This review emphasizes the importance of jointly considering Eh and pH in further studies since most studies
1455 conducted to date disconnect these two interacting parameters. In order to accomplish this, improved
1456 measurement methods and other tools are needed to assess plant and soil Eh-pH conditions. These could include
1457 spectrometric methods to overcome limitations of electrochemical ones for plants and the use of bio-indicators
1458 as natural vegetation species to surmount problems related to the high spatio-temporal variability in soils.

1459

1476 **References**

1477

1478 Aarti PD, Tanaka R, Tanaka A (2006) Effects of oxidative stress on chlorophyll biosynthesis in cucumber
1479 (*Cucumis sativus*) cotyledons. Physiol Plant 128:186–197. doi: 10.1111/j.1399-3054.2006.00720.x

1480 Abdullah AS, Moffat CS, Lopez-Ruiz FJ, et al (2017) Host–multi-pathogen warfare: Pathogen interactions in co-
1481 infected plants. Front Plant Sci 8:1–12. doi: 10.3389/fpls.2017.01806

1482 Agrios GN, Sonnack KD, Beattie L, Decicco E (2005) Plant pathology, Fifth. Elsevier Academic Press

1483 Ah-Fong AMV, Kagda MS, Abrahamian M, Judelson HS (2019) Niche-specific metabolic adaptation in
1484 biotrophic and necrotrophic oomycetes is manifested in differential use of nutrients, variation in gene
1485 content, and enzyme evolution. PLoS Pathog 15:1–30. doi: 10.1371/journal.ppat.1007729

1486 Ahmad N, Malagoli M, Wirtz M, Hell R (2016) Drought stress in maize causes differential acclimation
1487 responses of glutathione and sulfur metabolism in leaves and roots. BMC Plant Biol 16:1–15. doi:
1488 10.1186/s12870-016-0940-z

1489 Alexandre G, Zhulin IB (2001) More than one way to sense chemicals. J Bacteriol 183:4681–4686. doi:
1490 10.1128/JB.183.16.4681-4686.2001

1491 Alkan N, Espeso EA, Prusky D (2013) Virulence Regulation of Phytopathogenic Fungi by pH. Antioxid Redox
1492 Signal 19:1012–1025. doi: 10.1089/ars.2012.5062

1493 Alkhalfioui F, Renard M, Vensel WH, et al (2007) Thioredoxin-linked proteins are reduced during germination
1494 of Medicago truncatula seeds. Plant Physiol 144:1559–1579. doi: 10.1104/pp.107.098103

1495 Allen DJ, Ort DR (2001) Impacts of chilling temperatures on photosynthesis in warm-climate plants. Trends
1496 Plant Sci 6:36–42. doi: 10.1016/S1360-1385(00)01808-2

1497 Altieri MA, Nicholls CI (2003) Soil fertility management and insect pests: Harmonizing soil and plant health in
1498 agroecosystems. Soil Tillage Res 72:203–211. doi: 10.1016/S0167-1987(03)00089-8

1499 Amtmann A, Troufflard S, Armengaud P (2008) The effect of potassium nutrition on pest and disease resistance

in plants. Physiol Plant 133:682–691. doi: 10.1111/j.1399-3054.2008.01075.x

Andrews JH, Harris RF (2000) The ecology and biogeography of microorganisms on plant surfaces. Annu Rev Phytopathol 38:145–180. doi: 10.1146/annurev.phyto.38.1.145

Anjum N a, Gill SS, Gill R, et al (2014) Metal/metalloid stress tolerance in plants: role of ascorbate, its redox couple, and associated enzymes. Protoplasma 251:1265–83. doi: 10.1007/s00709-014-0636-x

Anjum NA, Khan NA, Sofo A, et al (2016) Redox homeostasis managers in plants under environmental stresses. Front Environ Sci 4:210. doi: 10.3389/fenvs.2016.00035

Anuradha M, Narayanan (1991) Promotion of root elongation by phosphorus deficiency. Plant Soil 136:273–275

Aoi W, Marunaka Y (2014) Importance of pH homeostasis in metabolic health and diseases : Crucial role of membrane proton transport. Biomed Res Int 2014:ID598986. doi: 10.1155/2014/598986

Appel HM (1993) Phenolics in ecological interactions: The importance of oxidation. J Chem Ecol 19:1521–1552

Appel HM, Joern A (1998) Gut physicochemistry of grassland grasshoppers. J Insect Physiol 44:693–700

Appel HM, Martin MM (1990) Gut redox conditions in herbivorous Lepidopteran larvae. J Chem Ecol 16:3277–3290

Arabi MIE, Jawhar M (2002) The ability of barley powdery mildew to grow in vitro. J Phytopathol 150:305–307. doi: 10.1046/j.1439-0434.2002.00751.x

Armijo G, Schlechter R, Agurto M, et al (2016) Grapevine pathogenic microorganisms: Understanding infection strategies and host response scenarios. Front Plant Sci 7:1–18. doi: 10.3389/fpls.2016.00382

Aubrey DP, Boyles JG, Krysinsky LS, Teskey RO (2011) Spatial and temporal patterns of xylem sap pH derived from stems and twigs of *Populus deltoides* L. Environ Exp Bot 71:376–381. doi: 10.1016/j.envexpbot.2011.02.006

Awasthi R, Bhandari K, Nayyar H (2015) Temperature stress and redox homeostasis in agricultural crops. Front Environ Sci 3:1–24. doi: 10.3389/fenvs.2015.00011

Babbar R, Karpinska B, Grover A, Foyer CH (2021) Heat-induced oxidation of the nuclei and cytosol. Front Plant Sci 11:1–16. doi: 10.3389/fpls.2020.617779

Backhausen JE, Scheibe R (1999) Adaptation of tobacco plants to elevated CO_2: influence of leaf age on changes in physiology, redox states and NADP-malate dehydrogenase activity. J Exp Bot 50:665–675. doi: 10.1093/jxb/50.334.665

Bahrun A, Jensen CR, Asch F, Mogensen VO (2002) Drought- induced changes in xylem pH, ionic composition, and ABA concentration act as early signals in field- grown maize (*Zea mays* L.). J Exp Bot 53:251–263

Baier M, Dietz KJ (2005) Chloroplasts as source and target of cellular redox regulation: A discussion on chloroplast redox signals in the context of plant physiology. J Exp Bot 56:1449–1462. doi: 10.1093/jxb/eri161

Ball P (2007) Bacteria may be wiring up the soil. Nature 449:388. doi: 10.1038/449388a

Ball P (2008) Water as an active constituent in cell biology. Chem Rev 108:74–108. doi: 10.1021/cr068037a

Balmer A, Pastor V, Gamir J, et al (2015) The "prime-ome": Towards a holistic approach to priming. Trends Plant Sci 20:443–452. doi: 10.1016/j.tplants.2015.04.002

Bárcenas-Moreno G, García-Orenes F, Mataix-Solera J, et al (2011) Soil microbial recolonisation after a fire in a Mediterranean forest. Biol Fertil Soils 47:261–272. doi: 10.1007/s00374-010-0532-2

1540 Bastiaans L, Kropff MJ (1993) Effects of leaf blast on photosynthesis of rice 2. Canopy photosynthesis.
1541   Netherlands J Plant Pathol 99:205–217. doi: 10.1007/BF01974665

1542 Bateman D (1978) The dynamic nature of disease. In: JG H, EB C (eds) Plant Disease, An Advanced Treatise
1543   Vol. III How Plants Suffer from Disease. Academic Press, pp 53–83

1544 Benada J (1966) The gradients of oxidation-reduction potentials in cereals and the dependance of obligate
1545   parasites on the redox potentials of the host tissues. Phytopathol Zeitschrift 55:265–269

1546 Benada J (2012) Redox potential and pH in plants and their function in the mechanism of resistance to diseases
1547   and in plant physiology. A review. Agrotest fyto, s.r.o. Zemedelsky vyzkumny ustav Kromeriz

1548 Benada J (2017) Measurement of redox potential and pH in plants and their function in the mechanism of plant
1549   resistance and in plant physiology. Int J Adv Res Electr Electron Instrum Eng 1111–1116. doi:
1550   10.15662/IJAREEIE.2015.0501001

1551 Benada J (1967) The distribution of redox potentials and pH values in the leaves of cereal tillers during the stem
1552   extension. Flora, Abt A, Bd 158:343–350

1553 Bendix C, Lewis JD (2018) The enemy within: Phloem-limited pathogens. Mol Plant Pathol 19:238–254. doi:
1554   10.1111/mpp.12526

1555 Benitez-Alfonso Y, Jackson D, Maule A (2011) Redox regulation of intercellular transport. Protoplasma
1556   248:131–140. doi: 10.1007/s00709-010-0243-4

1557 Berbara RLL, Morris BM, Fonseca HMAC, et al (1995) Electrical currents associated with arbuscular
1558   mycorrhizal interactions. New Phytol 129:433–438. doi: 10.1111/j.1469-8137.1995.tb04314.x

1559 Berendsen RL, Pieterse CMJ, Bakker PAHM (2012) The rhizosphere microbiome and plant health. Trends Plant
1560   Sci 17:478–486. doi: 10.1016/j.tplants.2012.04.001

1561 Berg G, Smalla K (2009) Plant species and soil type cooperatively shape the structure and function of microbial
1562   communities in the rhizosphere. FEMS Microbiol Ecol 68:1–13. doi: 10.1111/j.1574-6941.2009.00654.x

1563 Berger S, Sinha AK, Roitsch T (2007) Plant physiology meets phytopathology: Plant primary metabolism and
1564   plant-pathogen interactions. J Exp Bot 58:4019–4026. doi: 10.1093/jxb/erm298

1565 Bernacchi CJ, Leakey ADB, Heady LE, et al (2006) Hourly and seasonal variation in photosynthesis and
1566   stomatal conductance of soybean grown at future CO_2 and ozone concentrations for 3 years under fully
1567   open-air field conditions. Plant, Cell Environ 29:2077–2090. doi: 10.1111/j.1365-3040.2006.01581.x

1568 Berthelot E, Ducousso M, Macia J-L, et al (2019) Turnip Mosaic Virus is a second example of a virus using
1569   transmission activation for plant-to-plant propagation by Aphids. J Virol 93:1–11. doi: 10.1128/jvi.01822-
1570   18

1571 Bertrand PF (1976) Late season water deficits and development of *Cytospora* canker in French prune.
1572   Phytopathology 66:1318

1573 Best RJ (1968) Tomato Spotted Wilt Virus. Adv Virus Res 13:65–146. doi: 10.1016/S0065-3527(08)60251-1

1574 Best RJ, Samuel G (1936) The reaction of the viruses of tomato spotted wilt and tobacco mosaic to the pH value
1575   of media containing them. Ann Appl Biol 23:509–537. doi: 10.1111/j.1744-7348.1936.tb06108.x

1576 Bhuyan MHMB, Hasanuzzaman M, Mahmud J Al, et al (2019) Unraveling morphophysiological and
1577   biochemical responses of *Triticum aestivum* l. to extreme pH: Coordinated actions of antioxidant defense
1578   and glyoxalase systems. Plants 8:1–18. doi: 10.3390/plants8010024

1579 Bi JL, Felton GW (1995) Foliar oxidative stress and insect herbivory: Primary compounds, secondary

metabolites, and reactive oxygen species as components of induced resistance. J Chem Ecol 21:1511–1530. doi: 10.1007/BF02035149

Biessy A, Filion M (2018) Phenazines in plant-beneficial *Pseudomonas spp.*: biosynthesis, regulation, function and genomics. Environ Microbiol 20:3905–3917. doi: 10.1111/1462-2920.14395

Bigeard J, Colcombet J, Hirt H (2015) Signaling mechanisms in pattern-triggered immunity (PTI). Mol Plant 8:521–539. doi: 10.1016/j.molp.2014.12.022

Bignell DEE (1984) Direct potentiometric determination of redox potentials of the gut contents in the termites *Zootermopsis nevadensis* and *Cubitermes severus* and in three other arthropods. J Insect Physiol 30:169–174. doi: 10.1016/0022-1910(84)90122-7

Blancard D (2012) Tomato diseases: Identification, biology and control: A colour handbook, Second Edition, QUAE. CRC Press

Bloem E, Haneklaus S, Schnug E (2005) Significance of sulfur compounds in the protection of plants against pests and diseases. J Plant Nutr 28:763–784. doi: 10.1081/PLN-200055532

Blokhina OB, Virolainen E, Fagerstedt K V., et al (2000) Antioxidant status of anoxia-tolerant and -intolerant plant species under anoxia and reaeration. Physiol Plant 109:396–403. doi: 10.1034/j.1399-3054.2000.100405.x

Bolwell GP, Bindschedler L V., Blee KA, et al (2002) The apoplastic oxidative burst in response to biotic stress in plants: A three-component system. J Exp Bot 53:1367–1376. doi: 10.1093/jxb/53.372.1367

Bolwell PP, Page A, Piślewska M, Wojtaszek P (2001) Pathogenic infection and the oxidative defenses in plant apoplast. Protoplasma 217:20–32. doi: 10.1007/BF01289409

Borella J, Becker R, Lima MC, et al (2019) Nitrogen source influences the antioxidative system of soybean plants under hypoxia and re-oxygenation. Sci Agric 76:51–62. doi: 10.1590/1678-992x-2017-0195

Bostock RM, Pye MF, Roubtsova T V. (2014) Predisposition in plant disease: Exploiting the nexus in abiotic and biotic stress perception and response. Annu Rev Phytopathol 52:517–549. doi: 10.1146/annurev-phyto-081211-172902

Bousset L, Ermel M, Soglonou B, Husson O (2019) Fungal growth is affected by and affects pH and redox potential (Eh) of the growth medium. Fungal Biol 123:117–124. doi: 10.1002/adsc.201

Bové J., Garnier M (2003) Phloem-and xylem-restricted plant pathogenic bacteria. Plant Sci 164:423–438. doi: 10.1016/s0168-9452(03)00033-5

Browne G, Ott N, Poret-Peterson A, et al (2018) Efficacy of anaerobic soil disinfestation for control of *Prunus replant* disease. Plant Dis 102:209–219. doi: 10.1094/PDIS-09-16-1392-RE

Brugidou C, Opalka N, Yeager M, et al (2002) Stability of rice yellow mottle virus and cellular compartmentalization during the infection process in *Oryza sativa* (L .). Virology 297:98–108. doi: 10.1006/viro.2002.1398

Brune a, Emerson D, Breznak J a (1995) The termite gut microflora as an oxygen sink: Microelectrode determination of oxygen and pH gradients in guts of lower and higher termites. Appl Environ Microbiol 61:2681–7

Bueno E, Mesa S, Bedmar EJ, et al (2012) Bacterial adaptation of respiration from oxic to microoxic and anoxic conditions: Redox control. Antioxid Redox Signal 16:819–852. doi: 10.1089/ars.2011.4051

Bünemann EK, Bongiorno G, Bai Z, et al (2018) Soil quality – A critical review. Soil Biol Biochem 120:105–

125. doi: 10.1016/j.soilbio.2018.01.030

Burgin AJ, Yang WH, Hamilton SK, Silver WL (2011) Beyond carbon and nitrogen: How the microbial energy economy couples elemental cycles in diverse ecosystems. Front Ecol Environ 9:44–52. doi: 10.1890/090227

Burns NC (1971) Soil pH effects on nematode populations associated with soybeans. J Nematol 3:238–245

Bush DR (1992) The proton-sucrose symport. Photosynth Res 32:155–165

Cakmak I, Marschner H (1988) Increase in membrane permeability and exudation in roots of Zinc deficient plants. J Plant Physiol 132:356–361. doi: 10.1016/S0176-1617(88)80120-2

Calonnec A, Jolivet J, Vivin P, Schnee S (2018) Pathogenicity traits correlate with the susceptible *Vitis vinifera* leaf physiology transition in the biotroph fungus *Erysiphe necator:* An adaptation to plant ontogenic resistance. Front Plant Sci 871:1–17. doi: 10.3389/fpls.2018.01808

Campos WG, Schoereder JH, Picanço MC (2003) Performance of an oligophagous insect in relation to the age of the host plant. Neotrop Entomol 32:671–676. doi: 10.1590/s1519-566x2003000400019

Cardinale BJ (2011) Biodiversity improves water quality through niche partitioning. Nature 472:86–91. doi: 10.1038/nature09904

Cardoso EJBN, Vasconcellos RLF, Bini D, et al (2013) Soil health: Looking for suitable indicators. What should be considered to assess the effects of use and management on soil health? Sci Agric 70:274–289. doi: 10.1590/S0103-90162013000400009

Cardoza RE, Mora ME, Hermosa R, et al (2010) TvDim1 of *Trichoderma virens* is involved in redox-processes and confers resistance to oxidative stresses. Curr Genet 56:63–73. doi: 10.1007/s00294-009-0280-8

Carvalhais LC, Dennis PG, Fedoseyenko D, et al (2011) Root exudation of sugars, amino acids, and organic acids by maize as affected by nitrogen, phosphorus, potassium, and iron deficiency. J Plant Nutr Soil Sci 174:3–11. doi: 10.1002/jpln.201000085

Carvalho LC, Vidigal P, Amâncio S (2015) Oxidative stress homeostasis in grapevine (*Vitis vinifera* L.). Front Environ Sci 3:1–15. doi: 10.3389/fenvs.2015.00020

Cazemier AE, Den Camp HJMO, Hackstein JHP, Vogels GD (1997) Fibre digestion in arthropods. Comp Biochem Physiol - A Physiol 118:101–109. doi: 10.1016/S0300-9629(96)00443-4

Cazemier AE, Verdoes JC, Reubsaet FAG, et al (2003) *Promicromonospora pachnodae* sp. nov., a member of the (hemi)cellulolytic hindgut flora of larvae of the scarab beetle *Pachnoda marginata*. Antonie van Leeuwenhoek, Int J Gen Mol Microbiol 83:135–148. doi: 10.1023/A:1023325817663

Cha JY, Han S, Hong HJ, et al (2016) Microbial and biochemical basis of a Fusarium wilt-suppressive soil. ISME J 10:119–129. doi: 10.1038/ismej.2015.95

Chandrashekara C, Kumar R, Bhatt JC, et al (2012) Suppressive soils in plant disease management. In: Singh VK, Singh Y, Singh A (eds) Eco-friendly innovative approaches in plant disease management. pp 241–256

Chapelle E, Mendes R, Bakker PAH, Raaijmakers JM (2016) Fungal invasion of the rhizosphere microbiome. ISME J 10:265–268. doi: 10.1038/ismej.2015.82

Charrier M, Brune A (2003) The gut microenvironment of helicid snails (*Gastropoda: Pulmonata*): In-situ profiles of pH, oxygen, and hydrogen determined by microsensors. Can J Zool 81:928–935. doi: 10.1139/z03-071

Chen J, Hanke A, Tegetmeyer HE, et al (2017a) Impacts of chemical gradients on microbial community structur.

1660   ISME J 11:920–931. doi: 10.1038/ismej.2016.175

1661 Chen R, Song S, Li X, et al (2013) Phosphorus deficiency restricts plant growth but induces pigment formation

1662   in the flower stalk of Chinese kale. Hortic Environ Biotechnol 54:243–248. doi: 10.1007/s13580-013-

1663   0018-x

1664 Chen X, Mao A, Zhang Y, et al (2017b) Carbon and nitrogen forms in soil organic matter influenced by

1665   incorporated wheat and corn residues. Soil Sci Plant Nutr 63:377–387. doi:

1666   10.1080/00380768.2017.1359797

1667 Chen Z, Gallie DR (2004) The ascorbic acid redox state controls guard cell signaling and stomatal movement.

1668   Plant Cell 16:1143–1162. doi: 10.1105/tpc.021584

1669 Cheng F, Cheng Z (2015) Research progress on the use of plant allelopathy in agriculture and the physiological

1670   and ecological mechanisms of allelopathy. Front Plant Sci 6:1–16. doi: 10.3389/fpls.2015.01020

1671 Clarke D, Whitney H, Sutton G, Robert D (2013) Detection and learning of floral electric fields by bumblebees.

1672   Science 340:66–9. doi: 10.1126/science.1230883

1673 Clemente-Moreno MJ, Díaz-Vivancos P, Rubio M, et al (2013) Chloroplast protection in plum pox virus-

1674   infected peach plants by L-2-oxo-4-thiazolidine-carboxylic acid treatments: Effect in the proteome. Plant,

1675   Cell Environ 36:640–654. doi: 10.1111/pce.12003

1676 Clocchiatti A, Hannula SE, van den Berg M, et al (2020) The hidden potential of saprotrophic fungi in arable

1677   soil: Patterns of short-term stimulation by organic amendments. Appl Soil Ecol 147:103434. doi:

1678   10.1016/j.apsoil.2019.103434

1679 Conrad R (1996) Soil microorganisms as controllers of atmospheric trace gases (H2, CO, CH4, OCS, N2O, and

1680   NO). Microbiol Rev 60:609–640. doi: 10.1007/978-3-642-61096-7_11

1681 Cook JR, Baker KF (1983) The nature and practice of biological control of plant pathogens, American P. St

1682   Paul, Minnesota, USA

1683 Cook RJ (2014) Plant health management: Pathogen suppressive soils. In: Van Alfen NKBT-E of A and FS (ed).

1684   Academic Press, Oxford, pp 441–455

1685 Cornelissen JHC, Sibma F, Van Logtestijn RSP, et al (2011) Leaf pH as a plant trait: species-driven rather than

1686   soil-driven variation. Funct Ecol 25:449–455. doi: 10.1111/j.1365-2435.2010.01765.x

1687 Coskun D, Deshmukh R, Sonah H, et al (2019) The controversies of silicon's role in plant biology. New Phytol

1688   221:67–85. doi: 10.1111/nph.15343

1689 Cottes J (2019) Le couple Eh/pH du sol : Sa mesure, son impact sur la mobilité des nutriments et la croissance

1690   du tournesol. Ph.D Thesis, Université de Toulouse, France

1691 Cruz-Munoz M, Munoz-Beristain A, Petrone JR, et al (2019) Growth parameters of *Liberibacter crescens*

1692   suggest ammonium and phosphate as essential molecules in the Liberibacter-plant host interface. BMC

1693   Microbiol 19:1–16. doi: 10.1186/s12866-019-1599-z

1694 Cuypers A, Vangronsveld J, Clijsters H (2001) The redox status of plant cells (AsA and GSH) is sensitive to

1695   zinc imposed oxidative stress in roots and primary leaves of *Phaseolus vulgaris*. Plant Physiol Biochem

1696   39:657–664. doi: 10.1016/S0981-9428(01)01276-1

1697 Das P, Nutan KK, Singla-Pareek SL, Pareek A (2015) Oxidative environment and redox homeostasis in plants:

1698   dissecting out significant contribution of major cellular organelles. Front Environ Sci 2:1–11. doi:

1699   10.3389/fenvs.2014.00070

1700   Datnoff LE, Elmer WH, Huber DM (2007) Mineral nutrition and plant disease. APS Press, St Paul, Minnesota,
1701   USA

1702   Davet P (2004) Microbial ecology of the soil and plant growth. Science Publishers. Inc., Enfield, New
1703   Hampshire

1704   Dawood M, Cao F, Jahangir MM, et al (2012) Alleviation of aluminum toxicity by hydrogen sulfide is related to
1705   elevated ATPase, and suppressed aluminum uptake and oxidative stress in barley. J Hazard Mater 209–
1706   210:121–128. doi: 10.1016/j.jhazmat.2011.12.076

1707   De Corato U (2021) Soil microbiome manipulation gives new insights in plant disease-suppressive soils from the
1708   perspective of a circular economy: A critical review. Sustain 13:1–41. doi: 10.3390/su13010010

1709   De Deyn GB (2017) Plant life history and above–belowground interactions: missing links. Oikos 126:497–507.
1710   doi: 10.1111/oik.03967

1711   De Deyn GB, Cornelissen JHC, Bardgett RD (2008) Plant functional traits and soil carbon sequestration in
1712   contrasting biomes. Ecol Lett 11:516–531. doi: 10.1111/j.1461-0248.2008.01164.x

1713   DeAngelis KM, Silver WL, Thompson AW, Firestone MK (2010) Microbial communities acclimate to recurring
1714   changes in soil redox potential status. Environ Microbiol 12:3137–3149. doi: 10.1111/j.1462-
1715   2920.2010.02286.x

1716   Debona D, Rodrigues FÁ, Rios JA, Nascimento KJT (2012) Biochemical changes in the leaves of wheat plants
1717   infected by *Pyricularia oryzae*. Phytopathology 102:1121–9. doi: 10.1094/PHYTO-06-12-0125-R

1718   Deguine J-P, Gloanec C, Laurent P, et al (2017) Agroecological Crop Protection. Springer Netherlands,
1719   Dordrecht

1720   Di Gioia F, Ozores-Hampton M, Hong J, et al (2016) The effects of anaerobic soil disinfestation on weed and
1721   nematode control, fruit yield, and quality of florida fresh-market tomato. HortScience 51:703–711. doi:
1722   10.21273/hortsci.51.6.703

1723   Diéguez-Uribeondo J, Förster H, Adaskaveg JE (2008) Visualization of localized pathogen-induced pH
1724   modulation in almond tissues infected by *Colletotrichum acutatum* using confocal scanning laser
1725   microscopy. Phytopathology 98:1171–1178. doi: 10.1094/PHYTO-98-11-1171

1726   Dietz K-J (2003) Redox control, redox signaling, and redox homeostasis in plant cells. Int Rev Cytol 228:141–
1727   193. doi: 10.1016/S0074-7696(03)28004-9

1728   Dietz K-J, Turkan I, Krieger-Liszkay A (2016) Redox- and reactive oxygen species-dependent signalling in and
1729   from the photosynthesizing chloroplast. Plant Physiol 171:pp.00375.2016. doi: 10.1104/pp.16.00375

1730   Dini-Andreote F, Elsas JD (2013) Back to the basics: The need for ecophysiological insights to enhance our
1731   understanding of microbial behaviour in the rhizosphere. Plant Soil 373:1–15. doi: 10.1007/s11104-013-
1732   1687-z

1733   Dini-Andreote F, Stegen JC, Van Elsas JD, Salles JF (2015) Disentangling mechanisms that mediate the balance
1734   between stochastic and deterministic processes in microbial succession. Proc Natl Acad Sci U S A
1735   112:E1326–E1332. doi: 10.1073/pnas.1414261112

1736   Dodd IC, Tan LP, He J (2003) Do increases in xylem sap pH and/or ABA concentration mediate stomatal
1737   closure following nitrate deprivation? J Exp Bot 54:1281–1288. doi: 10.1093/jxb/erg122

1738   Dordas C (2008) Role of nutrients in controlling plant diseases in sustainable agriculture. A review. Agron
1739   Sustain Dev 28:33–46. doi: 10.1051/agro:2007051

1740   Downum KR, Rodriguez E (1986) Toxicological action and ecological importance of plant photosensitizers. J
1741   Chem Ecol 12:823–834. doi: 10.1007/BF01020254

1742   Dragičević V (2015) Thermodynamics of abiotic stress and stress tolerance of cultivated plants. Recent Adv
1743   Thermo Fluid Dyn 195–221. doi: 10.5772/60990

1744   Dubreuil G, Deleury E, Magliano M, et al (2011) Peroxiredoxins from the plant parasitic root-knot nematode,
1745   *Meloidogyne incognita*, are required for successful development within the host. Int J Parasitol 41:385–
1746   396. doi: 10.1016/j.ijpara.2010.10.008

1747   Duru M, Therond O, Fares M (2015) Designing agroecological transitions; A review. Agron Sustain Dev
1748   35:1237–1257. doi: 10.1007/s13593-015-0318-x

1749   Ebert A, Brune A (1997) Hydrogen concentration profiles at the oxic-anoxic interface: A microsensor study of
1750   the hindgut of the wood-feeding lower termite *Reticulitermes flavipes* (Kollar). Appl Environ Microbiol
1751   63:4039–4046. doi: 10.1128/aem.63.10.4039-4046.1997

1752   Egert M, Stingl U, Bruun LD, et al (2005) Structure and topology of microbial communities in the major gut
1753   compartments of *Melolontha melolontha* larvae (Coleoptera: Scarabaeidae). Appl Environ Microbiol
1754   71:4556–4566. doi: 10.1128/AEM.71.8.4556

1755   Ellakwa ET (2014) Effect of host plant on gut physicochemistry and digestive enzymes of the cutworn (*Agrotis
1756   ipsilon*) larvae. Am J drug Discov Dev 4:248–252

1757   Elmer WH, Datnoff LE (2014) Mineral nutrition and suppression of plant disease. Encycl Agric Food Syst
1758   4:231–244. doi: http://dx.doi.org/10.1016/B978-0-444-52512-3.00251-5

1759   Elstner EF, Osswald W (1994) Mechanisms of oxygen activation during plant stress. Proc R Soc Edinburgh Sect
1760   B Biol Sci 102:131–154. doi: 10.1017/s0269727000014068

1761   Endo RM, Linn MB (1960) The white-rust disease of Horseradish. Bull. Illinois Agric. Exp. Stn. 56 pp.

1762   Epstein E (1994) The anomaly of silicon in plant biology. Proc Natl Acad Sci USA 91:11–17

1763   Eutick ML, O'Brien RW, Slaytor M (1976) Aerobic state of gut of *Nasutitermes exitiosus* and *Coptotermes
1764   lacteus*, high and low caste termites. J Insect Physiol 22:1377–1380. doi: 10.1016/0022-1910(76)90161-X

1765   Exposito-Rodriguez M, Laissue PP, Yvon-Durocher G, et al (2017) Photosynthesis-dependent H_2O_2 transfer
1766   from chloroplasts to nuclei provides a high-light signalling mechanism. Nat Commun 8:1–10. doi:
1767   10.1038/s41467-017-00074-w

1768   Farber DH, Mundt CC (2017) Effect of plant age and leaf position on susceptibility to wheat stripe rust.
1769   Phytopathology 107:412–417. doi: 10.1094/phyto-07-16-0284-r

1770   Farkas GL, Király Z, Solymosy F (1960) Role of oxidative metabolism in the localization of plant viruses.
1771   Virology 12:408–421. doi: 10.1016/0042-6822(60)90163-X

1772   Fatima U, Senthil-Kumar M (2015) Plant and pathogen nutrient acquisition strategies. Front Plant Sci 6:1–12.
1773   doi: 10.3389/fpls.2015.00750

1774   Fauteux F, Rémus-Borel W, Menzies JG, Bélanger RR (2005) Silicon and plant disease resistance against
1775   pathogenic fungi. FEMS Microbiol Lett 249:1–6. doi: 10.1016/j.femsle.2005.06.034

1776   Felle HH (2005) pH regulation in anoxic plants. Ann Bot 96:519–532. doi: 10.1093/aob/mci207

1777   Felle HH (2001) pH: Signal and messenger in plant cells. Plant Biol 3:577–591. doi: 10.1055/s-2001-19372

1778   Felle HH (2006) Apoplastic pH during low-oxygen stress in barley. Ann Bot 98:1085–1093. doi:
1779   10.1093/aob/mcl193

1780   Felle HH, Herrmann A, Hanstein S, et al (2004) Apoplastic pH signaling in barley leaves attacked by the
1781   powdery mildew fungus *Blumeria graminis* f. sp. hordei. Mol Plant-Microbe Interact 17:118–123. doi:
1782   10.1094/MPMI.2004.17.1.118

1783   Fernandes TR, Segorbe D, Prusky D, Di Pietro A (2017) How alkalinization drives fungal pathogenicity. PLoS
1784   Pathog 13:1–8. doi: 10.1371/journal.ppat.1006621

1785   Ferreira M, Domingos M (2012) Seasonal characterization of antioxidant responses in plants of *Ipomoea nil* cv.
1786   Scarlet O'Hara. Brazilian J Biol 72:831–837. doi: 10.1590/s1519-69842012000500008

1787   Fiedler S, Scholich GU, Kleber M (2003) Construction and evaluation of redox electrode with summing
1788   operational amplifier: Application in study of methane emission. Commun Soil Sci Plant Anal 34:481–
1789   496. doi: 10.1081/CSS-120017833

1790   Fischer WR, Flessa H, Schaller G (1989) pH values and redox potentials in microsites of the rhizosphere.
1791   Zeitschrift für Pflanzenernährung und Bodenkd 152:191–195. doi: 10.1002/jpln.19891520209

1792   Fobert PR, Després C (2005) Redox control of systemic acquired resistance. Curr Opin Plant Biol 8:378–82. doi:
1793   10.1016/j.pbi.2005.05.003

1794   Footitt S, Cohn MA (1992) Seed dormancy in red rice. Plant Physiol 100:1196–1202. doi: 10.1104/pp.80.2.531

1795   Foyer CH (2005) Redox homeostasis and antioxidant signaling: A metabolic interface between stress perception
1796   and physiological responses. Plant Cell Online 17:1866–1875. doi: 10.1105/tpc.105.033589

1797   Foyer CH, Noctor G (2016) Stress-triggered redox signalling: What's in pROSpect? Plant, Cell Environ 39:951–
1798   964. doi: 10.1111/pce.12621

1799   Foyer CH, Noctor G (2013) Redox signaling in plants. Antioxid Redox Signal 18:2087–2090. doi:
1800   10.1089/ars.2013.5278

1801   Foyer CH, Shigeoka S (2011) Understanding oxidative stress and antioxidant functions to enhance
1802   photosynthesis. Plant Physiol 155:93–100. doi: 10.1104/pp.110.166181

1803   Frederickson Matika DE, Loake GJ (2013) Redox regulation in plant immune function. Antioxid Redox Signal
1804   21:1373–1388. doi: 10.1089/ars.2013.5679

1805   Fromm J, Bauer T (1994) Action potentials in maize sieve tubes change phloem translocation. J Exp Bot
1806   45:463–469. doi: 10.1093/jxb/45.4.463

1807   Fukuta Y, Suzuki T, Yanagihara S, et al (2019) Genetic variation of blast (*Pyricularia oryzae cavara*) resistance
1808   in rice (*Oryza sativa* l.) accessions widely used in kenya. Breed Sci 69:672–679. doi: 10.1270/jsbbs.19065

1809   Fürstenberg-Hägg J, Zagrobelny M, Bak S (2013) Plant defense against insect herbivores. Int J Mol Sci
1810   14:10242–10297. doi: 10.3390/ijms140510242

1811   García G, Clemente-Moreno MJ, Díaz-Vivancos P, et al (2020) The apoplastic and symplastic antioxidant
1812   system in onion: Response to long-term salt stress. Antioxidants 9:67. doi: 10.3390/antiox9010067

1813   Garnier M, Foissac X, Gaurivaud P, et al (2001) Mycoplasmas plants insect vectors: A matrimonial triangle.
1814   Comptes Rendus l'Academie des Sci - Ser III 324:923–928. doi: 10.1016/S0764-4469(01)01372-5

1815   Gaupels F, Durner J, Kogel KH (2017) Production, amplification and systemic propagation of redox messengers
1816   in plants? The phloem can do it all! New Phytol 214:554–560. doi: 10.1111/nph.14399

1817   Gebrie SA (2016) Biotrophic fungi infection and plant defense mechanism. J Plant Pathol Microbiol 7:. doi:
1818   10.4172/2157-7471.1000378

1819   Geigenberger P (2003) Response of plant metabolism to too little oxygen. Curr Opin Plant Biol 6:247–256. doi:

1820   10.1016/S1369-5266(03)00038-4

1821   Geilfus CM (2017) The pH of the Apoplast: Dynamic Factor with Functional Impact Under Stress. Mol Plant

1822   10:1371–1386. doi: 10.1016/j.molp.2017.09.018

1823   Geilfus CM, Mühling KH (2011) Real-time imaging of leaf apoplastic pH dynamics in response to NaCl stress.

1824   Front Plant Sci 2:1–11. doi: 10.3389/fpls.2011.00013

1825   Geilfus CM, Wang L, Wu J, Xue C (2020) The pH of the leaf apoplast is critical for the formation of

1826   Pseudomonas syringae-induced lesions on leaves of the common bean (*Phaseolus vulgaris*). Plant Sci

1827   290:110328. doi: 10.1016/j.plantsci.2019.110328

1828   Geiser E, Wiebach V, Wierckx N, Blank LM (2014) Prospecting the biodiversity of the fungal family

1829   *Ustilaginaceae* for the production of value-added chemicals. Fungal Biol Biotechnol 1:1–10. doi:

1830   10.1186/s40694-014-0002-y

1831   Gerendás J, Schurr U (1999) Physicochemical aspects of ion relations and pH regulation in plants - A

1832   quantitative approach. J Exp Bot 50:1101–1114. doi: 10.1093/jxb/50.336.1101

1833   Gerwien F, Skrahina V, Kasper L, et al (2018) Metals in fungal virulence. FEMS Microbiol Rev 42:1–21. doi:

1834   10.1093/femsre/fux050

1835   Gianfreda L (2015) Enzymes of importance to rhizosphere processes. J Soil Sci Plant Nutr 15:283–306. doi:

1836   10.4067/s0718-95162015005000022

1837   Giaquinta R (1977) Phloem loading of sucrose: pH dependence and selectivity. Plant Physiol 59:750–755. doi:

1838   10.1104/pp.59.4.750

1839   Gillet FX, Cattoni DI, Petiot-Bécard S, et al (2013) The RYMV-encoded viral suppressor of RNA silencing P1 is

1840   a zinc-binding protein with redox-dependent flexibility. J Mol Biol 425:2423–2435. doi:

1841   10.1016/j.jmb.2013.03.028

1842   Giordano M (2013) Homeostasis: an underestimated focal point of ecology and evolution. Plant Sci 211:92–101.

1843   doi: 10.1016/j.plantsci.2013.07.008

1844   Gjetting KSK, Ytting CK, Schulz A, Fuglsang AT (2012) Live imaging of intra-and extracellular pH in plants

1845   using pHusion, a novel genetically encoded biosensor. J Exp Bot 63:3207–3218. doi: 10.1093/jxb/ers040

1846   Gloser V, Korovetska H, Martín-Vertedor AI, et al (2016) The dynamics of xylem sap pH under drought: a

1847   universal response in herbs? Plant Soil 409:259–272. doi: 10.1007/s11104-016-2962-6

1848   Gnanamanickam SS (2006) Plant-associated bacteria. Springer, Dordrecht, The Netherlands

1849   Goggin FL, Avila C a., Lorence A (2010) Vitamin C content in plants is modified by insects and influences

1850   susceptibility to herbivory. BioEssays 32:777–790. doi: 10.1002/bies.200900187

1851   González-Bosch C (2018) Priming plant resistance by activation of redox-sensitive genes. Free Radic Biol Med

1852   122:171–180. doi: 10.1016/j.freeradbiomed.2017.12.028

1853   Goodman RN, Kiraly Z, Zaitlin M (1967) The biochemstry and physiology of infectious plant disease. Van

1854   Nostrand Company, Toronto

1855   Gour HN, Ashiya J, Mali BL, Nath R (2000) Influence of temperature and pH on the growth and toxin

1856   production by *Xanthomonas axonopodis* pv. vignicola inciting leaf blight of cowpea. J Mycol Plant Pathol

1857   30:389–392

1858   Grams TEE, Lautner S, Felle HH, et al (2009) Heat-induced electrical signals affect cytoplasmic and apoplastic

1859   pH as well as photosynthesis during propagation through the maize leaf. Plant, Cell Environ 32:319–326.

1860   doi: 10.1111/j.1365-3040.2008.01922.x

1861   Greggers U, Koch G, Schmidt V, et al (2013) Reception and learning of electric fields in bees. Proc R Soc B

1862   Biol Sci 280:. doi: 10.1098/rspb.2013.0528

1863   Grignon C, Sentenac H (1991) pH and ionic conditions in the apoplast. Annu Rev Plant Physiol Plant Mol Biol

1864   42:103–128. doi: 10.1146/annurev.pp.42.060191.000535

1865   Gupta N, Debnath S, Sharma S, et al (2017) Role of nutrients in controlling the plant diseases in sustainable

1866   agriculture. In: Meena V et al. (ed) Agriculturally Important Microbes for Sustainable Agriculture.

1867   Springer Nature, Singapore, pp 217–262

1868   Gupta R, Lee SE, Agrawal GK, et al (2015) Understanding the plant-pathogen interactions in the context of

1869   proteomics-generated apoplastic proteins inventory. Front Plant Sci 6:1–7. doi: 10.3389/fpls.2015.00352

1870   Guyonnet JP, Cantarel AAM, Simon L, Haichar FZ (2018a) Root exudation rate as functional trait involved in

1871   plant nutrient-use strategy classification. Int J Bus Innov Res 17:8573–8581. doi: 10.1002/ece3.4383

1872   Guyonnet JP, Guillemet M, Dubost A, et al (2018b) Plant nutrient resource use strategies shape active

1873   rhizosphere microbiota through root exudation. Front Plant Sci 871:1–13. doi: 10.3389/fpls.2018.01662

1874   Haapalainen M (2014) Biology and epidemics of *Candidatus Liberibacter* species, psyllid-transmitted plant-

1875   pathogenic bacteria. Ann Appl Biol 165:172–198. doi: 10.1111/aab.12149

1876   Haas C, Horn R (2018) Impact of small-scaled differences in micro-aggregation on physico-chemical parameters

1877   of macroscopic biopore walls. Front Environ Sci 6:1–12. doi: 10.3389/fenvs.2018.00090

1878   Hafke JB, Van Amerongen JK, Kelling F, et al (2005) Thermodynamic battle for photosynthate acquisition

1879   between sieve tubes and adjoining parenchyma in transport phloem. Plant Physiol 138:1527–1537. doi:

1880   10.1104/pp.104.058511

1881   Halliwell B, Gutteridge JMC (1984) Oxygen toxicity, oxygen radicals, transition metals and disease. Biochem J

1882   219:1–14. doi: 10.1042/bj2190001

1883   Handy D, Loscalzo J (2012) Redox regulation of mitochondrial function. Antioxid Redox Signal 16:1323–1368

1884   Harrison JF (2001) Insect acid-base physiology. Annu Rev Entomol 46:221–250. doi:

1885   10.1146/annurev.ento.46.1.221

1886   Hasanuzzaman M, Bhuyan MHMB, Nahar K, et al (2018) Potassium: A vital regulator of plant responses and

1887   tolerance to abiotic stresses. Agronomy 8:. doi: 10.3390/agronomy8030031

1888   Hemantaranjan A, Bhanu AN, Singh M, et al (2014) Heat stress responses and thermotolerance. Adv Plants

1889   Agric Res 1:62–70. doi: 10.15406/apar.2014.01.00012

1890   Hernández I, Munné-Bosch S (2015) Linking phosphorus availability with photo-oxidative stress in plants. J Exp

1891   Bot 66:2889–2900. doi: 10.1093/jxb/erv056

1892   Hernández JA, Gullner G, Clemente-Moreno MJ, et al (2016) Oxidative stress and antioxidative responses in

1893   plant–virus interactions. Physiol Mol Plant Pathol 94:134–148. doi: 10.1016/j.pmpp.2015.09.001

1894   Hess DT, Matsumoto A, Kim S-O, et al (2005) Protein S-nitrosylation: purview and parameters. Nat Rev Mol

1895   Cell Biol 6:150–166. doi: 10.1038/nrm1569

1896   Hijaz F, Killiny N (2014) Collection and chemical composition of phloem sap from *Citrus sinensis* L. Osbeck

1897   (sweet orange). PLoS One 9:1–11. doi: 10.1371/journal.pone.0101830

1898   Hinsinger P, Plassard C, Tang C, et al (2003) Origins of root-mediated pH changes in the rhizosphere and their

1899   responses to environmental constraints: A review. Plant Soil 248:43–59

1900 Hipper C, Brault V, Ziegler-Graff V, Revers F (2013) Viral and cellular factors involved in phloem transport of
1901   plant viruses. Front Plant Sci 4:1–24. doi: 10.3389/fpls.2013.00154

1902 Hogenhout SA, Loria R (2008) Virulence mechanisms of Gram-positive plant pathogenic bacteria. Curr Opin
1903   Plant Biol 11:449–456. doi: 10.1016/j.pbi.2008.05.007

1904 Howlett BJ, Idnurm A, Pedras MSC (2001) *Leptosphaeria maculans*, the causal agent of blackleg disease of
1905   Brassicas. Fungal Genet Biol 33:1–14. doi: 10.1006/fgbi.2001.1274

1906 Hua C, Li C, Jiang Y, et al (2020) Response of soybean cyst nematode (*Heterodera glycines*) and root-knot
1907   nematodes (*Meloidogyne spp.*) to gradients of pH and inorganic salts. Plant Soil 305–318. doi:
1908   10.1007/s11104-020-04677-z

1909 Hua J (2013) Modulation of plant immunity by light, circadian rhythm, and temperature. Curr Opin Plant Biol
1910   16:406–413. doi: 10.1016/j.pbi.2013.06.017

1911 Huber D, Römheld V, Weinmann M (2011) Relationship between nutrition, plant diseases and pests. In:
1912   Marschner's Mineral Nutrition of Higher Plants: Third Edition. pp 283–298

1913 Huber DM, Haneklaus S (2007) Managing nutrition to control plant disease. Landbauforsch Völkenrode 4
1914   57:313–322. doi: 10.1016/B978-0-12-803581-8.02518-2

1915 Huber DM, Thompson IA (2007) Nitrogen and plant disease. In: Datnoff LE, Elmer WE, Huber DM (eds)
1916   Mineral nutrition and plant disease, APS Press. The American phytopathological society, St Paul,
1917   Minnesota, USA, pp 31–44

1918 Huber DM, Watson RD (1974) Nitrogen form and plant disease. Annu Rev Phytopathol 12:139–165. doi:
1919   10.1146/annurev.py.12.090174.001035

1920 Huot B, Yao J, Montgomery BL, He SY (2014) Growth-defense tradeoffs in plants: A balancing act to optimize
1921   fitness. Mol Plant 7:1267–1287. doi: 10.1093/mp/ssu049

1922 Husson O (2013) Redox potential (Eh) and pH as drivers of soil/plant/microorganism systems: a
1923   transdisciplinary overview pointing to integrative opportunities for agronomy. Plant Soil 362:389–417.
1924   doi: 10.1007/s11104-012-1429-7

1925 Husson O, Audebert A, Benada J, et al (2018a) Leaf Eh and pH : A novel indicator of plant stress . Spatial ,
1926   temporal and genotypic variability in rice. Agronomy 8:1–24. doi: 10.3390/agronomy8100209

1927 Husson O, Brunet A, Babre D, et al (2018b) Conservation Agriculture systems alter the electrical characteristics
1928   (Eh, pH and EC) of four soil types in France. Soil Tillage Res 176:57–68. doi: 10.1016/j.still.2017.11.005

1929 Husson O, Husson B, Brunet A, et al (2016) Practical improvements in soil redox potential (Eh) measurement
1930   for characterisation of soil properties . Application for comparison of conventional and conservation
1931   agriculture cropping systems. Anal Chim Acta 906:98–109. doi: 10.1016/j.aca.2015.11.052

1932 Hwang H-H, Yu M, Lai E-M (2017) Agrobacterium -mediated plant transformation: Biology and applications.
1933   Arab B 15:e0186. doi: 10.1199/tab.0186

1934 Igamberdiev AU, Baron K, Manac'h-Little N, et al (2005) The haemoglobin/nitric oxide cycle: Involvement in
1935   flooding stress and effects on hormone signalling. Ann Bot 96:557–564. doi: 10.1093/aob/mci210

1936 Igamberdiev AU, Bykova N V. (2018) Role of organic acids in the integration of cellular redox metabolism and
1937   mediation of redox signalling in photosynthetic tissues of higher plants. Free Radic Biol Med 122:74–85.
1938   doi: 10.1016/j.freeradbiomed.2018.01.016

1939 Ilan T, Kim-Shapiro DB, Bock CH, Shapiro-Ilan DI (2013) Magnetic and electric fields induce directional

1940   responses in *Steinernema carpocapsae*. Int J Parasitol 43:781–784. doi: 10.1016/j.ijpara.2013.05.007

1941   Jackson MB, Saker LR, Crisp CM, et al (2003) Ionic and pH signalling from roots to shoots of flooded tomato

1942   plants in relation to stomatal closure. Plant Soil 253:103–113. doi: 10.1023/A:1024588532535

1943   Jacoby R, Peukert M, Succurro A, et al (2017) The role of soil microorganisms in plant mineral nutrition—

1944   current knowledge and future directions. Front Plant Sci 8:1–19. doi: 10.3389/fpls.2017.01617

1945   Janku M, Luhová L, Petrivalský M (2019) On the origin and fate of reactive oxygen species in plant cell

1946   compartments. Antioxidants 8:105

1947   Jashvantlal PS (2008) Management of bacterial blight of rice. PhD thesis Navsari Agricultural university, India

1948   Jha G, Sonti R V (2009) Attack and defense in Xanthomonas-rice interactions. Proc Indian Natn Sci Acad

1949   75:49–68

1950   Jiang Y (1996) Oxidative interactions between the spotted alfalfa aphid (*Therioaphis trifolii maculata*)

1951   (Homoptera: Aphididae) and the host plant Medicago sativa. Bull Entomol Res 86:533–540. doi:

1952   10.1017/S0007485300039328

1953   Jiang Y, Miles PW (1993) Responses of a compatible lucerne variety to attack by spotted alfalfa aphid: changes

1954   in the redox balance in affected tissues. Entomol Exp Appl 67:263–274. doi: 10.1111/j.1570-

1955   7458.1993.tb01677.x

1956   Johannes A, Matter A, Schulin R, et al (2017) Optimal organic carbon values for soil structure quality of arable

1957   soils. Does clay content matter? Geoderma 302:14–21. doi: 10.1016/j.geoderma.2017.04.021

1958   Johnson GN (2003) Thiol regulation of the thylakoid electron transport chain - A missing link in the regulation

1959   of photosynthesis? Biochemistry 42:3040–3044. doi: 10.1021/bi027011k

1960   Johnson KS, Felton GW (1996a) Physiological and dietary influences on midgut redox conditions in generalist

1961   lepidopteran larvae. J Insect Physiol 42:191–198. doi: 10.1016/0022-1910(95)00096-8

1962   Johnson KS, Felton GW (1996b) Potential Influence of midgut pH and redox potential on protein utilization in

1963   insect herbivores. Arch Insect Biochem Physiol 32:85–105

1964   Jones DL, Hodge A, Kuzyakov Y (2004) Plant and mycorrhizal regulation of rhizodeposition. New Phytol

1965   163:459–480. doi: 10.1111/j.1469-8137.2004.01130.x

1966   Jones DS, Kohl C, Grettenberger C, et al (2015) Geochemical niches of Iron-oxidizing acidophiles in acidic coal

1967   mine drainage. Appl Environ Microbiol 81:1242–1250. doi: 10.1128/AEM.02919-14

1968   Jonkers W, Estrada AER, Lee K, et al (2012) Metabolome and transcriptome of the interaction between *Ustilago

1969   maydis* and *Fusarium verticillioides* in vitro. Appl Environ Microbiol 78:3656–3667. doi:

1970   10.1128/AEM.07841-11

1971   Joseph A, Olufolaji D, Nwilene F, et al (2011) Effect of leaf age on rice yeallow mottle virus severity and

1972   chlorophyll content with echanical inoculation and vector transmission method. Trends Appl Sci Res

1973   6:691–698. doi: 10.3923/tasr.2011.1345.1351

1974   Jozefczak M, Bohler S, Schat H, et al (2015) Both the concentration and redox state of glutathione and ascorbate

1975   influence the sensitivity of arabidopsis to cadmium. Ann Bot 116:601–612. doi: 10.1093/aob/mcv075

1976   Jubany-Mari T, Alegre-Batlle L, Jiang K, Feldman LJ (2010) Use of a redox-sensing GFP (c-roGFP1) for real-

1977   time monitoring of cytosol redox status in *Arabidopsis thaliana* water-stressed plants. FEBS Lett 584:889–

1978   97. doi: 10.1016/j.febslet.2010.01.014

1979   Juttukonda LJ, Skaar EP (2015) Manganese homeostasis and utilization in pathogenic bacteria. Mol Microbiol

1980   97:216–228. doi: 10.1016/j.physbeh.2017.03.040

1981   Kapoor D, Sharma R, Handa N, et al (2015) Redox homeostasis in plants under abiotic stress: role of electron

1982   carriers, energy metabolism mediators and proteinaceous thiols. Front Environ Sci 3:1–12. doi:

1983   10.3389/fenvs.2015.00013

1984   Kappler A, Brune A (2002) Dynamics of redox potential and changes in redox state of iron and humic acids

1985   during gut passage in soil-feeding termites (*Cubitermes spp.*). Soil Biol Biochem 34:221–227

1986   Karmous I, Trevisan R, Ferjani E El, et al (2017) Redox biology response in germinating *Phaseolus vulgaris*

1987   seeds exposed to copper : Evidence for differential redox buffering in seedlings and cotyledon. PLoS One

1988   12:1–23

1989   Keane P, Kerr A (1997) Factors affecting disease development. In: Brown J, Ogle H (eds) Plant pathogens and

1990   plant diseases, APPS. Rockvale pubications, Amidale, NSW, pp 287–298

1991   Kilian J, Peschke F, Berendzen KW, et al (2012) Prerequisites, performance and profits of transcriptional

1992   profiling the abiotic stress response. Biochim Biophys Acta - Gene Regul Mech 1819:166–175. doi:

1993   10.1016/j.bbagrm.2011.09.005

1994   Killiny N (2017) Metabolite signature of the phloem sap of fourteen citrus varieties with different degrees of

1995   tolerance to *Candidatus Liberibacter asiaticus.* Physiol Mol Plant Pathol 97:20–29. doi:

1996   10.1016/j.pmpp.2016.11.004

1997   Király L, Hafez YM, Fodor J, Király Z (2008) Suppression of tobacco mosaic virus-induced hypersensitive-type

1998   necrotization in tobacco at high temperature is associated with downregulation of NADPH oxidase and

1999   superoxide and stimulation of dehydroascorbate reductase. J Gen Virol 89:799–808. doi:

2000   10.1099/vir.0.83328-0

2001   Kissoudis C, van de Wiel C, Visser RGF, van der Linden G (2014) Enhancing crop resilience to combined

2002   abiotic and biotic stress through the dissection of physiological and molecular crosstalk. Front Plant Sci

2003   5:1–20. doi: 10.3389/fpls.2014.00207

2004   Knight NL, Sutherland MW (2016) Histopathological assessment of *Fusarium pseudograminearum* colonization

2005   of cereal culms during crown rot infections. Plant Dis 100:252–259. doi: 10.1094/PDIS-04-15-0476-RE

2006   Koch C, Harnisch F (2016) Is there a specific ecological niche for electroactive iicroorganisms?

2007   ChemElectroChem 3:1282–1295. doi: 10.1002/celc.201600079

2008   Koch M. ;, Mew T. (1991) Effect of plant age and leaf maturity on the quantitative resitance of rice cultivars to

2009   *Xanthomonas campestris pv. oryzae*. Plant Dis September:901–904

2010   Kocsy G, Tari I, Vanková R, et al (2013) Redox control of plant growth and development. Plant Sci 211:77–91.

2011   doi: 10.1016/j.plantsci.2013.07.004

2012   Kong P, Moorman GW, Lea-Cox JD, et al (2009) Zoosporic tolerance to pH stress and its implications for

2013   Phytophthora species in aquatic ecosystems. Appl Environ Microbiol 75:4307–4314. doi:

2014   10.1128/AEM.00119-09

2015   Köpke B, Wilms R, Engelen B, et al (2005) Microbial diversity in coastal subsurface sediments: A cultivation

2016   approach using various electron acceptors and substrate gradients. Appl Environ Microbiol 71:7819–7830.

2017   doi: 10.1128/AEM.71.12.7819-7830.2005

2018   Korenblum E, Dong Y, Szymanski J, et al (2020) Rhizosphere microbiome mediates systemic root metabolite

2019   exudation by root-to-root signaling. Proc Natl Acad Sci U S A 117:3874–3883. doi:

10.1073/pnas.1912130117

Kováčik J, Bačkor M (2007) Changes of phenolic metabolism and oxidative status in nitrogen-deficient *Matricaria chamomilla* plants. Plant Soil 297:255–265. doi: 10.1007/s11104-007-9346-x

Kranzler C, Rudolf M, Keren N, Schleiff E (2013) Iron in Cyanobacteria. Adv Bot Res 65:57–105. doi: 10.1016/B978-0-12-394313-2.00003-2

Krasil'nikov NA (1958) Soil microorganisms and higher plants. Academy of Sciences of the USSR Institute of Microbiology, Moscow, USSR

Krasnow CS, Hausbeck MK (2017) Influence of pH and etridiazole on pythium species. Horttechnology 27:367–374. doi: 10.21273/HORTTECH03633-16

Krebelj AJ, Čepin U, Ravnikar M, Novak MP (2015) Spatio-temporal distribution of Grapevine fanleaf virus (GFLV) in grapevine. Eur J Plant Pathol 142:159–171. doi: 10.1007/s10658-015-0600-4

Krishnan N, Kodrík D (2006) Antioxidant enzymes in *Spodoptera littoralis* (Boisduval): Are they enhanced to protect gut tissues during oxidative stress? J Insect Physiol 52:11–20. doi: 10.1016/j.jinsphys.2005.08.009

Krishnan N, Kodrík D, Kłudkiewicz B, Sehnal F (2009) Glutathione-ascorbic acid redox cycle and thioredoxin reductase activity in the digestive tract of *Leptinotarsa decemlineata* (Say). Insect Biochem Mol Biol 39:180–188. doi: 10.1016/j.ibmb.2008.11.001

Krishnan N, Kodrík D, Turanli F, Sehnal F (2007) Stage-specific distribution of oxidative radicals and antioxidant enzymes in the midgut of *Leptinotarsa decemlineata*. J Insect Physiol 53:67–74. doi: 10.1016/j.jinsphys.2006.10.001

Kruk J, Aboul-Enein HY, Kładna A, Bowser JE (2019) Oxidative stress in biological systems and its relation with pathophysiological functions: the effect of physical activity on cellular redox homeostasis. Free Radic Res 53:497–521. doi: 10.1080/10715762.2019.1612059

Kuzniak E (2010) The ascorbate-gluathione cycle and related redox signals in plant-pathogen interactions. In: Ascorbate-Glutathione Pathway and Stress Tolerance in Plants. Springer, Dordrecht, pp 115–136

Kuzniak E, Skłodowska M, Kużniak E, Skłodowska M (2005) Fungal pathogen-induced changes in the antioxidant systems of leaf peroxisomes from infected tomato plants. Planta 222:192–200. doi: 10.1007/s00425-005-1514-8

Labudda M, Muszyńska E, Gietler M, et al (2020) Efficient antioxidant defense systems of spring barley in response to stress induced jointly by the cyst nematode parasitism and cadmium exposure. Plant Soil 189–206. doi: 10.1007/s11104-020-04713-y

Lacroix C, Seabloom EW, Borer ET (2014) Environmental nutrient supply alters prevalence and weakens competitive interactions among coinfecting viruses. J Physiol 204:424–433. doi: 10.1111/nph.12909

Lamb C, Dixon RA (1997) The oxidative burst in plant disease resistance. Annu Rev Plant Biol 48:251–275

Lambers H, Mougel C, Jaillard B, Hinsinger P (2009) Plant-microbe-soil interactions in the rhizosphere: an evolutionary perspective. Plant Soil 321:83–115. doi: 10.1007/s11104-009-0042-x

Lamichhane JR (2015) Bacterial diseases of crops: Elucidation of the factors that lead to differences between field and experimental infections. Adv Agron 134:227–246. doi: 10.1016/bs.agron.2015.06.006

Lamichhane JR, Venturi V (2015) Synergisms between microbial pathogens in plant disease complexes: A growing trend. Front Plant Sci 6:1–12. doi: 10.3389/fpls.2015.00385

Landraud P, Chuzeville S, Billon-Grande G, et al (2013) Adaptation to pH and role of PacC in the rice blast

2060   fungus *Magnaporthe oryzae*. PLoS One 8:. doi: 10.1371/journal.pone.0069236

2061 Lebreton L, Daval S, Guillerm-Erckelboudt AY, et al (2014) Sensitivity to pH and ability to modify ambient pH

2062   of the take-all fungus *Gaeumannomyces graminis var. tritici*. Plant Pathol 63:117–128. doi:

2063   10.1111/ppa.12062

2064 Lehmann S, Serrano M, Haridon FL, et al (2015) Reactive oxygen species and plant resistance to fungal

2065   pathogens. Phytochemistry 112:54–62. doi: 10.1016/j.phytochem.2014.08.027

2066 Lemke T, Stingl U, Egert M, et al (2003) Physicochemical conditions and microbial activities in the highly

2067   alkaline gut of the humus-feeding larva of *Pachnoda ephippiata* (Coleoptera: Scarabaeidae). Appl Environ

2068   Microbiol 69:6650–6658. doi: 10.1128/AEM.69.11.6650-6658.2003

2069 Leveau JH (2019) A brief from the leaf: latest research to inform our understanding of the phyllosphere

2070   microbiome. Curr Opin Microbiol 49:41–49. doi: 10.1016/j.mib.2019.10.002

2071 Li C, Lesnik KL, Liu H (2017) Stay connected : Electrical conductivity of microbial aggregates. Biotechnol Adv

2072   35:669–680. doi: 10.1016/j.biotechadv.2017.07.010

2073 Li H, Chen XW, Wu L, et al (2020) Effects of arbuscular mycorrhizal fungi on redox homeostasis of rice under

2074   Cd stress. Plant Soil 121–138. doi: 10.1007/s11104-020-04678-y

2075 Li J, Nishimura Y, Zhao X, Fukumoto Y (2014) Effects of drought stress on the metabolic properties of active

2076   oxygen species, nitrogen and photosynthesis in cucumber "Jinchun No. 5" seedlings. Japan Agric Res Q

2077   48:175–181. doi: 10.6090/jarq.48.175

2078 Li SX, Wang ZH, Stewart BA (2013) Responses of crop plants to ammonium and nitrate N. Adv Agron

2079   118:205–397. doi: 10.1016/B978-0-12-405942-9.00005-0

2080 Li Y, Yu S, Strong J, Wang H (2012) Are the biogeochemical cycles of carbon, nitrogen, sulfur, and phosphorus

2081   driven by the "FeIII–FeII redox wheel" in dynamic redox environments? J Soils Sediments 12:683–693.

2082   doi: 10.1007/s11368-012-0507-z

2083 Liao Y, Tian M, Zhang H, et al (2015) Salicylic acid binding of mitochondrial alpha-ketoglutarate

2084   dehydrogenase E2 affects mitochondrial oxidative phosphorylation and electron transport chain

2085   components and plays a role in basal defense against tobacco mosaic virus in tomato. New Phytol

2086   205:1296–1307. doi: 10.1111/nph.13137

2087 Littman DR, Pamer EG (2011) Role of the commensal microbiota in normal and pathogenic host immune

2088   responses. Cell Host Microbe 10:311–323. doi: 10.1016/j.chom.2011.10.004

2089 Liu G, Greenshields DL, Sammynaiken R, et al (2007) Targeted alterations in iron homeostasis underlie plant

2090   defense responses. J Cell Sci 120:596–605. doi: 10.1242/jcs.001362

2091 Liu J, Zhu J, Zhang P, et al (2017) Silicon supplementation alters the composition of herbivore induced plant

2092   volatiles and enhances attraction of parasitoids to infested rice plants. Front Plant Sci 8:1–8. doi:

2093   10.3389/fpls.2017.01265

2094 Liu Y, He C (2017) A review of redox signaling and the control of MAP kinase pathway in plants. Redox Biol

2095   11:192–204. doi: 10.1016/j.redox.2016.12.009

2096 Löbmann MT, Vetukuri RR, de Zinger L, et al (2016) The occurrence of pathogen suppressive soils in Sweden

2097   in relation to soil biota, soil properties, and farming practices. Appl Soil Ecol 107:57–65. doi:

2098   10.1016/j.apsoil.2016.05.011

2099 Louda SM, Collinge SK (1992) Plant resistance to insect herbivores: a field test of the environmental stress

2100   hypothesis. Ecology 73:153–169. doi: 10.2307/1938728

2101 Love CJ, Zhang S, Mershin A (2008) Source of sustained voltage difference between the xylem of a potted ficus
2102   benjamina tree and its soil. PLoS One 3:1–5. doi: 10.1371/journal.pone.0002963

2103 Lu H, McClung CR, Zhang C (2017) Tick tock: Circadian regulation of plant innate immunity. Annu Rev
2104   Phytopathol 55:287–311. doi: 10.1146/annurev-phyto-080516-035451

2105 Lu Y, Yao J (2018) Chloroplasts at the crossroad of photosynthesis, pathogen infection and plant defense. Int J
2106   Mol Sci 19:1–37. doi: 10.3390/ijms19123900

2107 Lushchak VI (2014) Free radicals, reactive oxygen species, oxidative stress and its classification. Chem Biol
2108   Interact 224:164–175. doi: 10.1016/j.cbi.2014.10.016

2109 Maai E, Nishimura K, Takisawa R, Nakazaki T (2019) Light stress-induced chloroplast movement and midday
2110   depression of photosynthesis in sorghum leaves. Plant Prod Sci 00:1–10. doi:
2111   10.1080/1343943X.2019.1673666

2112 Mackenzie JS, Jeggo M (2019) The one health approach-why is it so important? Trop Med Infect Dis 4:5–8. doi:
2113   10.3390/tropicalmed4020088

2114 Madigan AP, Egidi E, Bedon F, et al (2019) Bacterial and fungal communities are differentially modified by
2115   melatonin in agricultural soils under abiotic stress. Front Microbiol 10:. doi: 10.3389/fmicb.2019.02616

2116 Manivannan A, Soundararajan P, Cho YS, et al (2018) Sources of silicon influence photosystem and redox
2117   homeostasis-related proteins during the axillary shoot multiplication of *Dianthus caryophyllus*. Plant
2118   Biosyst 152:704–710. doi: 10.1080/11263504.2017.1320312

2119 Marschner H (1995) Mineral nutrition of higher plants, Second edi. Academic press Publishing

2120 Marschner H, Römheld V, Horst WJ, Martin P (1986) Root- induced changes in the rhizosphere: Importance for
2121   the mineral nutrition of plants. Zeitschrift für Pflanzenernährung und Bodenkd 149:441–456. doi:
2122   10.1002/jpln.19861490408

2123 Marschner P (2011) Rhizosphere biology. In: Marschner's Mineral Nutrition of Higher Plants: Third Edition.
2124   Elsevier, pp 369-388 doi:10.1016/B978-0-12-384905-2.00015-7

2125 Martínez M, Arata AF, Lázaro L, et al (2019) Effects of waterlogging stress on plant-pathogen interaction
2126   between *Fusarium poae* and wheat/ barley. Acta Sci - Agron 41:1–9. doi:
2127   10.4025/actasciagron.v41i1.42629

2128 Masiello CA, Gallagher ME, Randerson JT, et al (2008) Evaluating two experimental approaches for measuring
2129   ecosystem carbon oxidation state and oxidative ratio. J Geophys Res Biogeosciences 113:1–9. doi:
2130   10.1029/2007JG000534

2131 Masoero G, Cugnetto A (2018) The Raw pH in plants: A multifaceted parameter. J Agron Res 1:18–34. doi:
2132   10.14302/issn.2639-3166.jar-18-2397

2133 Matthysse AG (2006) The genus Agrobacterium. In: Dworkin M, Falkow S, Rosenberg E, et al. (eds) The
2134   Prokaryotes. Springer New York, New York, NY, pp 91–114

2135 Mbengue M, Navaud O, Peyraud R, et al (2016) Emerging trends in molecular interactions between plants and
2136   the broad host range fungal pathogens *Botrytis cinerea* and *Sclerotinia sclerotiorum*. Front Plant Sci 7:1–9.
2137   doi: 10.3389/fpls.2016.00422

2138 McCall AC, Fordyce JA (2010) Can optimal defense theory be used to predict the distribution of plant chemical
2139   defenses ? J Ecol 98:985–992. doi: 10.1111/j.1365-2745.2010.01693.x

Mehdy MC (1994) Active oxygen species in plant defense against pathogens. Plant Physiol 105:467–472

Meisner A, De Boer W (2018) Strategies to maintain natural biocontrol of soil-borne crop diseases during severe drought and rainfall events. Front Microbiol 9:1–8. doi: 10.3389/fmicb.2018.02279

Melakerberhan H, Jones AL, Hanson E, Bird GW (1995) Effect of low soil pH on aluminum availability and on mortality of cherry seedlings. Plant Dis 79:886–892

Méthot PO, Alizon S (2014) What is a pathogen? Toward a process view of host-parasite interactions. Virulence 5:775–785. doi: 10.4161/21505594.2014.960726

Mhlongo MI, Piater LA, Madala NE, et al (2018) The chemistry of plant–microbe interactions in the rhizosphere and the potential for metabolomics to reveal signaling related to defense priming and induced systemic resistance. Front Plant Sci 9:1–17. doi: 10.3389/fpls.2018.00112

Miles PW, Oertli JJ (1993) The significance of antioxidants in the aphid-plant interaction. The redox hypothesis. Entomol Exp Appl 67:275–283

Miyara I, Shnaiderman C, Meng X, et al (2012) Role of nitrogen-metabolism genes expressed during pathogenicity of the alkalinizing *Colletotrichum gloeosporioides* and their differential expression in acidifying pathogens. Mol Plant-Microbe Interact 25:1251–1263. doi: 10.1094/MPMI-01-12-0017-R

Moebius-Clune BN, D.J. M-C, Gugino BK, et al (2017) Comprehensive assessment of soil health - The Cornell framework manual, Edition3.2. New York

Molki B, Thi Ha P, Mohamed A, et al (2019) Physiochemical changes mediated by "*Candidatus Liberibacter asiaticus*" in Asian citrus psyllids. Sci Rep 9:1–9. doi: 10.1038/s41598-019-52692-7

Morabito D, Guerrier G (2000) The free oxygen radical scavenging enzymes and redox status in roots and leaves of *Populus x Euramericana* in response to osmotic stress, desiccation and rehydration. J Plant Physiol 157:74–80. doi: 10.1016/S0176-1617(00)80138-8

Morris BM, Reid B, Gow NAR (1995) Tactic response of zoospores of the fungus *Phytophthora palmivora* to solutions of different pH in relation to plant infection. Microbiology 141:1231–1237. doi: 10.1099/13500872-141-5-1231

Morris CE, Lamichhane JR, Nikolić I, et al (2019) The overlapping continuum of host range among strains in the *Pseudomonas syringae* complex. Phytopathol Res 1:1–16. doi: 10.1186/s42483-018-0010-6

Mühling KH, Plieth C, Hansen UP, Sattelmacher B (1995) Apoplastic ph of intact leaves of *Vicia faba* as influenced by light. J Exp Bot 46:377–382. doi: 10.1093/jxb/46.4.377

Müller-Schüssele SJ, Wang R, Gütle DD, et al (2020) Chloroplasts require glutathione reductase to balance reactive oxygen species and maintain efficient photosynthesis. Plant J 103:1140–1154. doi: 10.1111/tpj.14791

Mullineaux P, Rausch T (2005) Glutathione, photosynthesis and the redox regulation of stress-responsive gene expression. Photosynth Res 86:459–474

Murdock LL, Brookhart G, Dunn PE, et al (1987) Cysteine digestive proteinases in Coleoptera. Comp Biochem Physiol -- Part B Biochem 87:783–787. doi: 10.1016/0305-0491(87)90388-9

Nachin L, Barras F (2000) External pH: An environmental signal that helps to rationalize pel gene duplication in *Erwinia chrysanthemi*. Mol Plant-Microbe Interact 13:882–886. doi: 10.1094/MPMI.2000.13.8.882

Nagel M, Seal CE, Colville L, et al (2019) Wheat seed ageing viewed through the cellular redox environment and changes in pH. Free Radic Res 53:641–654. doi: 10.1080/10715762.2019.1620226

Napoleão TA, Soares G, Vital CE, et al (2017) Methyl jasmonate and salicylic acid are able to modify cell wall but only salicylic acid alters biomass digestibility in the model grass *Brachypodium distachyon*. Plant Sci 263:46–54. doi: 10.1016/j.plantsci.2017.06.014

Nelson EB (2018) The seed microbiome: Origins, interactions, and impacts. Plant Soil 422:7–34. doi: 10.1007/s11104-017-3289-7

Newland PL, Hunt E, Sharkh SM, et al (2008) Static electric field detection and behavioural avoidance in cockroaches. J Exp Biol 211:3682–3690. doi: 10.1242/jeb.019901

Nguyen D, D'Agostino N, Tytgat TOG, et al (2016) Drought and flooding have distinct effects on herbivore-induced responses and resistance in *Solanum dulcamara*. Plant Cell Environ 39:1485–1499. doi: 10.1111/pce.12708

Njenga KW, Nyaboga E, Wagacha JM, Mwaura FB (2017) Silicon induces resistance to bacterial blight by altering the physiology and antioxidant enzyme activities in cassava. World J Agric Res 5:42–51. doi: 10.12691/wjar-5-1-6

Nobori T, Tsuda K (2019) The plant immune system in heterogeneous environments. Curr Opin Plant Biol 50:58–66. doi: 10.1016/j.pbi.2019.02.003

Noctor G (2006) Metabolic signalling in defense and stress: the central roles of soluble redox couples. Plant Cell Environ 29:409–425

Noctor G, De Paepe R, Foyer CH (2007) Mitochondrial redox biology and homeostasis in plants. Trends Plant Sci 12:125–34. doi: 10.1016/j.tplants.2007.01.005

Noctor G, Queval G, Mhamdi A, et al (2011) Glutathione. Arab B 9:e0142. doi: 10.1199/tab.0142

Norton JM, Harman GE (1985) Responses of soil microorganisms to volatile exudates from germinating pea seeds. Can J Bot 63:1040–1045. doi: 10.1139/b85-142

Ntarlagiannis D, Atekwana EA, Hill EA, Gorby Y (2007) Microbial nanowires: Is the subsurface "hardwired"? Geophys Res Lett 34:3–7. doi: 10.1029/2007GL030426

Oka Y (2010) Mechanisms of nematode suppression by organic soil amendments-A review. Appl Soil Ecol 44:101–115. doi: 10.1016/j.apsoil.2009.11.003

Ongena M, Jourdan E, Schäfer M, et al (2005) Isolation of an N-alkylated benzylamine derivative from *Pseudomonas putida* BTP1 as elicitor of induced systemic resistance in bean. Mol Plant-Microbe Interact 18:562–569. doi: 10.1094/MPMI-18-0562

Opalka N, Brugidou C, Bonneau C, et al (1998) Movement of rice yellow mottle virus between xylem cells through pit membranes. Proc Natl Acad Sci U S A 95:3323–8. doi: 10.1073/pnas.95.6.3323

Ort DR (2001) When there is too much light. Plant Physiol 125:29–32. doi: 10.1104/pp.125.1.29

Ortega A, Garrido I, Casimiro I, Espinosa F (2017) Effects of antimony on redox activities and antioxidant defense systems in sunflower (*Helianthus annuus* L.) plants. PLoS One 12:1–21. doi: 10.1371/journal.pone.0183991

Padan E, Bibi E, Ito M, Krulwich TA (2005) Alkaline pH homeostasis in bacteria: New insights. Biochim Biophys Acta - Biomembr 1717:67–88. doi: 10.1016/j.bbamem.2005.09.010

Padmanabhan SY, Ganguly D (1954) Relation between the age of rice plant and its susceptibility to *Helminthosporium* and blast diseases. Proc Indian Acad Sci - Sect B 39:44–50. doi: 10.1007/BF03050372

Pandey P, Irulappan V, Bagavathiannan M V., Senthil-Kumar M (2017) Impact of combined abiotic and biotic

2220   stresses on plant growth and avenues for crop improvement by exploiting physio-morphological traits.

2221   Front Plant Sci 8:1–15. doi: 10.3389/fpls.2017.00537

2222   Pandit TK, Mukkherjee D (2016) Cadmium enrichment in soil:plant physiological manifestation. In:

2223   Hemantarajan A (ed) Advances in plant physiology vol.17. Development and mechanisms underlying

2224   plant resilience to changing environment. Scientific Publishers (India), pp 141–185

2225   Paradiso A, Caretto S, Leone A, et al (2016) ROS production and scavenging under anoxia and re-oxygenation

2226   in Arabidopsis cells: A balance between redox signaling and impairment. Front Plant Sci 7:1–11. doi:

2227   10.3389/fpls.2016.01803

2228   Pastor V, Luna E, Ton J, et al (2013) Fine tuning of reactive oxygen species homeostasis regulates primed

2229   immune responses in Arabidopsis. Mol Plant-Microbe Interact 26:1334–1344. doi: 10.1094/MPMI-04-13-

2230   0117-R

2231   Pastori GM, Foyer CH (2002) Common components, networks, and pathways of cross- tolerance to stress. The

2232   central role of "Redox" and abscisic acid-mediated controls. Plant Physiol 129:460–468. doi:

2233   10.1104/pp.011021.460

2234   Paszkowski U (2006) Mutualism and parasitism: the yin and yang of plant symbioses. Curr Opin Plant Biol

2235   9:364–370. doi: 10.1016/j.pbi.2006.05.008

2236   Paungfoo-Lonhienne C, Rentsch D, Robatzek S, et al (2010) Turning the table: Plants consume microbes as a

2237   source of nutrients. PLoS One 5:1–11. doi: 10.1371/journal.pone.0011915

2238   Payne PA, Asher MJCC, Kershaw CD (1994) The incidence of *Pythium spp*. and *Aphanomyces cochlioides*

2239   associated with the sugar- beet growing soils of Britain. Plant Pathol 43:300–308. doi: 10.1111/j.1365-

2240   3059.1994.tb02688.x

2241   Pedersen P, Tylka GL, Mallarino A, et al (2010) Correlation between soil pH, *Heterodera glycines* population

2242   densities, and soybean yield. Crop Sci 50:1458–1464. doi: 10.2135/cropsci2009.08.0432

2243   Perazzolli M, Roatti B, Bozza E, Pertot I (2011) *Trichoderma harzianum* T39 induces resistance against downy

2244   mildew by priming for defense without costs for grapevine. Biol Control 58:74–82. doi:

2245   10.1016/j.biocontrol.2011.04.006

2246   Pett-Ridge J, Firestone MK (2005) Redox fluctuation structures microbial communities in a wet tropical soil.

2247   Appl Environ Microbiol 71:6998–7007. doi: 10.1128/AEM.71.11.6998

2248   Pidello A (2014) Principes de chimie redox en écologie microbienne, QUAE. CIRAD, IFREMER, INRA,

2249   IRSTEA, Paris, France

2250   Pisoschi AM, Pop A (2015) The role of antioxidants in the chemistry of oxidative stress: A review. Eur J Med

2251   Chem 97:55–74. doi: 10.1016/j.ejmech.2015.04.040

2252   Pitann B, Schubert S, Mühling KH (2009) Decline in leaf growth under salt stress is due to an inhibition of H^+-

2253   pumping activity and increase in apoplastic pH of maize leaves. J Plant Nutr Soil Sci 172:535–543. doi:

2254   10.1002/jpln.200800349

2255   Podgórska A, Burian M, Szal B (2017) Extra-cellular but extra-ordinarily important for cells: Apoplastic reactive

2256   oxygen species metabolism. Front Plant Sci 8:1–20. doi: 10.3389/fpls.2017.01353

2257   Pollard M, Beisson F, Li Y, Ohlrogge JB (2008) Building lipid barriers: biosynthesis of cutin and suberin.

2258   Trends Plant Sci 13:236–246. doi: 10.1016/j.tplants.2008.03.003

2259   Ponnamperuma FN (1972) The chemistry of submerged soils. Adv Agron 24:29–96

2260   Pörtner HO (1987) Contributions of anaerobic metabolism to pH regulation in animal tissues: theory. J Exp Biol

2261   131:69–87

2262   Potters G, Horemans N, Jansen MAKK (2010) The cellular redox state in plant stress biology - A charging

2263   concept. Plant Physiol Biochem 48:292–300. doi: 10.1016/j.plaphy.2009.12.007

2264   Prasch CM, Sonnewald U (2015) Signaling events in plants: Stress factors in combination change the picture.

2265   Environ Exp Bot 114:4–14. doi: 10.1016/J.ENVEXPBOT.2014.06.020

2266   Prusky D, Yakoby N (2003) Pathogenic fungi: Leading or led by ambient pH? Mol Plant Pathol 4:509–516. doi:

2267   10.1046/j.1364-3703.2003.00196.x

2268   Purdy LH (1979) *Sclerotinia sclerotiorum* : History, diseases and symptomatology, host range, geographic

2269   distribution, and impact. Phytopathology 69:875. doi: 10.1094/phyto-69-875

2270   Qi PF, Balcerzak M, Rocheleau H, et al (2016) Jasmonic acid and abscisic acid play important roles in host-

2271   pathogen interaction between *Fusarium graminearum* and wheat during the early stages of fusarium head

2272   blight. Physiol Mol Plant Pathol 93:39–48. doi: 10.1016/j.pmpp.2015.12.004

2273   Raaijmakers JM, Paulitz TC, Steinberg C, et al (2009) The rhizosphere: A playground and battlefield for

2274   soilborne pathogens and beneficial microorganisms. Plant Soil 321:341–361. doi: 10.1007/s11104-008-

2275   9568-6

2276   Rabotnova IL, Schwartz W (1962) The importance of physical-chemical factors (pH and rH_2) for the life activity

2277   of microorganisms. VEB Gustav Fisher Verlag, Jena

2278   Raghavendra AS, Yin ZH, Heber U (1993) Light-dependent pH changes in leaves of C4 plants Comparison of

2279   the pH response to carbon dioxide and oxygen with that of C3 plants. Planta 189:278–287. doi:

2280   10.1007/BF00195087

2281   Ramegowda V, Senthil-Kumar M (2015) The interactive effects of simultaneous biotic and abiotic stresses on

2282   plants: Mechanistic understanding from drought and pathogen combination. J Plant Physiol 176:47–54.

2283   doi: 10.1016/j.jplph.2014.11.008

2284   Ranieri A, Castagna A, Baldan B, Soldatini GF (2001) Iron deficiency differently affects peroxidase isoforms in

2285   sunflower. J Exp Bot 52:25–35. doi: 10.1093/jxb/52.354.25

2286   Ranjit SL, Manish P, Penna S (2016) Early osmotic, antioxidant, ionic, and redox responses to salinity in leaves

2287   and roots of Indian mustard (*Brassica juncea* L.). Protoplasma 253:101–110. doi: 10.1007/s00709-015-

2288   0792-7

2289   Rasool B, McGowan J, Pastok D, et al (2017) Redox control of aphid resistance through altered cell wall

2290   composition and nutritional quality. Plant Physiol 175:259–271. doi: 10.1104/pp.17.00625

2291   Ratnadass A, Deguine J-P (2021) Crop protection practices and viral zoonotic risks within a One Health

2292   framework. Sci Total Environ 774:145172. doi: 10.1016/j.scitotenv.2021.145172

2293   Reicosky DC, Dugas WA, Torbert HA (1997) Tillage-induced soil carbon dioxide loss from different cropping

2294   systems. Soil Tillage Res 41:105–118. doi: 10.1016/S0167-1987(96)01080-X

2295   Rempelos L, Almuayrifi MSB, Baranski M, et al (2020) The effect of agronomic factors on crop health and

2296   performance of winter wheat varieties bred for the conventional and the low input farming sector. F Crop

2297   Res 254:. doi: 10.1016/j.fcr.2020.107822

2298   Rengel Z (2002) Handbook of plant growth. pH as the master variable. Marcel Dekker, New York

2299   Reniere ML (2018) Reduce, induce, thrive: Bacterial redox sensing during pathogenesis. J Bacteriol 200:1–12.

doi: 10.1128/jb.00128-18

Rocher F, Chollet J-F, Jousse C, Bonnemain J (2006) Salicylic acid , an ambimobile molecule exhibiting a high ability to accumulate in the phloem. Plant Physiol 141:1684–1693. doi: 10.1104/pp.106.082537.upper

Rolfe SA, Griffiths J, Ton J (2019) Crying out for help with root exudates: adaptive mechanisms by which stressed plants assemble health-promoting soil microbiomes. Curr Opin Microbiol 49:73–82. doi: 10.1016/j.mib.2019.10.003

Rouxel T, Balesdent MH (2005) The stem canker (blackleg) fungus, *Leptosphaeria maculans*, enters the genomic era. Mol Plant Pathol 6:225–241. doi: 10.1111/j.1364-3703.2005.00282.x

Saharan GS, Mehta N, Saharan, G. S.; Mehta N (2007) Sclerotinia Diseases of Crop Plants: Biology, Ecology and Disease Management

Sakr N (2016) Silicon control of bacterial and viral diseases in plants. J Plant Prot Res 56:331–336. doi: 10.1515/jppr-2016-0052

Salazar C, Hernández C, Pino MT (2015) Plant water stress: Associations between ethylene and abscisic acid response. Chil J Agric Res 75:71–79. doi: 10.4067/S0718-58392015000300008

Samuels L, Kunst L, Jetter R (2008) Sealing plant surfaces: Cuticular wax formation by epidermal cells. Annu Rev Plant Biol 59:683–707. doi: 10.1146/annurev.arplant.59.103006.093219

Santo-Domingo J, Demaurex N (2012) Perspectives on: SGP Symposium on mitochondrial physiology and medicine: The renaissance of mitochondrial pH. J Gen Physiol 139:415–423. doi: 10.1085/jgp.201110767

Schimel J, Balser TC, Wallenstein M (2007) Microbial stress response physiology and its implications for ecosystem function. Ecology 88:1386–1394

Schimel JP, Schaeffer SM (2012) Microbial control over carbon cycling in soil. Front Microbiol 3:1–11. doi: 10.3389/fmicb.2012.00348

Schlatter D, Kinkel L, Thomashow L, et al (2017) Disease suppressive soils: New insights from the soil microbiome. Phytopathology 107:1284–1297. doi: 10.1094/PHYTO-03-17-0111-RVW

Schmidke I, Krüger C, Frömmichen R, et al (1999) Phloem loading and transport characteristics of iron in interaction with plant-endogenous ligands in castor bean seedlings. Physiol Plant 106:82–89. doi: 10.1034/j.1399-3054.1999.106112.x

Schneider R (ed) (1982) Suppressive soils and plant disease. The American phytopathological society, St Paul, Minnesota, USA

Schoeneweiss DF (1975) Predisposition, stress, and plant disease. Annu Rev Phytopathol 13:193–211

Schwarzländer M, Fricker MD, Müller C, et al (2008) Confocal imaging of glutathione redox potential in living plant cells. J Microsc 231:299–316. doi: 10.1111/j.1365-2818.2008.02030.x

Seabloom EW, Borer ET, Gross K, et al (2015) The community ecology of pathogens: Coinfection, coexistence and community composition. Ecol Lett 18:401–415. doi: 10.1111/ele.12418

Secchi F, Zwieniecki MA (2016) Accumulation of sugars in the xylem apoplast observed under water stress conditions is controlled by xylem pH. Plant Cell Environ 39:2350–2360. doi: 10.1111/pce.12767

Segal LM, Wilson RA (2018) Reactive oxygen species metabolism and plant-fungal interactions. Fungal Genet Biol 110:1–9. doi: 10.1016/j.fgb.2017.12.003

Sen Y, van der Wolf J, Visser R, van Heusden S (2015) Bacterial canker of tomato: current knowledge of detection, management, resistance, and interactions. Plant Dis 99:4–13

2340 Serrano I, Audran C, Rivas S (2016) Chloroplasts at work during plant innate immunity. J Exp Bot 67:3845–
2341   3854. doi: 10.1093/jxb/erw088

2342 Sewelam N, Kazan K, Schenk PM (2016) Global plant stress signaling : Reactive oxygen species at the cross
2343   road. Front Plant Sci 7:1–21. doi: 10.3389/fpls.2016.00187

2344 Shah SRA, Tao L, Haijuan C, et al (2015) Age-related resistance and the defense signaling pathway of Ph-3
2345   gene against *Phytophthora infestans* in tomatoes. Hortic Plant J 1:70–76. doi: 10.16420/j.issn.2095-
2346   9885.2015-0019

2347 Shah TH (2017) Plant nutrients and insects development. Int J Entomol Res 2:54–57

2348 Shao HB, Chy LY, Shao MA, et al (2008) Higher plant antioxidants and redox signaling under environmental
2349   stresses. C R Biol 331:433–41. doi: 10.1016/j.crvi.2008.03.011

2350 Shapiro-Ilan DI, Lewis EE, Campbell JF, Kim-Shapiro DB (2012) Directional movement of entomopathogenic
2351   nematodes in response to electrical field: Effects of species, magnitude of voltage, and infective juvenile
2352   age. J Invertebr Pathol 109:34–40. doi: 10.1016/j.jip.2011.09.004

2353 Shi S, Richardson AE, O'Callaghan M, et al (2011) Effects of selected root exudate components on soil bacterial
2354   communities. FEMS Microbiol Ecol 77:600–610. doi: 10.1111/j.1574-6941.2011.01150.x

2355 Shikano I, Ericsson JD, Cory JS, Myers JH (2010) Indirect plant-mediated effects on insect immunity and
2356   disease resistance in a tritrophic system. Basic Appl Ecol 11:15–22. doi: 10.1016/j.baae.2009.06.008

2357 Shrestha R, Lee SH, Hur JH, Lim CK (2005) The effects of temperature, pH, and bactericides on the growth of
2358   *Erwinia pyrifoliae* and *Erwinia amylovora*. Plant Pathol J 21:127–131. doi: 10.5423/PPJ.2005.21.2.127

2359 Sierla M, Rahikainen M, Salojärvi J, et al (2013) Apoplastic and chloroplastic redox signaling networks in plant
2360   stress responses. Antioxid Redox Signal 18:2220–39. doi: 10.1089/ars.2012.5016

2361 Simpfendorfer S, Harden TJ, Murray GM (2001) Effect of temperature and pH on the growth and sporulation of
2362   *Phytophthora clandestina*. Australas Plant Pathol 30:1–5. doi: 10.1071/AP00054

2363 Singh A, Jain A, Sarma BK, et al (2013) Rhizosphere microbes facilitate redox homeostasis in *Cicer arietinum*
2364   against biotic stress. Ann Appl Biol 163:33–46. doi: 10.1111/aab.12030

2365 Singh B, Schulze DG (2015) Soil minerals and plant nutrition. Nat Educ Knowl 6:1–6

2366 Singh JS, Kumar A, Rai AN, Singh DP (2016) Cyanobacteria: A precious bio-resource in agriculture, ecosystem,
2367   and environmental sustainability. Front Microbiol 7:1–19. doi: 10.3389/fmicb.2016.00529

2368 Smiley R, Cook R (1972) Relationship between take-all of wheat and rhizosphere pH in soils fertilized with
2369   ammonium vs. nitrate-nitrogen. Phytopathology 63:882–890

2370 Sobrino-plata J, Meyssen D, Cuypers A, et al (2014) Glutathione is a key antioxidant metabolite to cope with
2371   mercury and cadmium stress. Plant Soil 377:369–381. doi: 10.1007/s11104-013-2006-4

2372 Soengas P, Rodríguez VM, Velasco P, Cartea ME (2018) Effect of temperature stress on antioxidant defenses in
2373   *Brassica oleracea*. ACS Omega 3:5237–5243. doi: 10.1021/acsomega.8b00242

2374 Song Y, Deng SP, Acosta-Martinez V, et al (2008) Characterization of redox-related soil microbial communities
2375   along a river floodplain continuum by fatty acid methyl ester (FAME) and 16S rRNA genes. Appl Soil
2376   Ecol 40:499–509. doi: 10.1016/j.apsoil.2008.07.005

2377 Sorauer P (1974) Handbuch der Pflanzenkrankheiten. Hempel und Parey, Wiegandt, Berlin

2378 Soundararajan P, Manivannan A, Ko CH, Jeong BR (2018) Silicon enhanced redox homeostasis and protein
2379   expression to mitigate the salinity stress in *Rosa hybrida* 'Rock Fire.' J Plant Growth Regul 37:16–34. doi:

2380   10.1007/s00344-017-9705-7

2381   Spann TM, Schumann AW (2010) Mineral nutrition contributes to plant disease and pest resistance. Univ
2382   Florida IFAS Ext HS1181:1–5

2383   Spoel SH, Loake GJ (2011) Redox-based protein modifications: The missing link in plant immune signalling.
2384   Curr Opin Plant Biol 14:358–364. doi: 10.1016/j.pbi.2011.03.007

2385   Srivastava A, Atomic B, Redij T (2017) Crosstalk of plant hormone and redox oxidation states signal
2386   transduction in plant interaction of other components with phytohormones. In: Pandey G (ed) Mechanism
2387   of Plant Hormone Signaling under Stress, First. John Wiley & Sons, pp 3–22

2388   Stacy A, Fleming D, Lamont RJ, et al (2016) A commensal bacterium promotes virulence of an opportunistic
2389   pathogen via cross-respiration. MBio 7:e00782. doi: 10.1128/mBio.00782-16

2390   Steinberg C, Edel-Hermann V, Alabouvette C, Lemanceau P (2019) Soil suppressiveness to plant diseases. In:
2391   Van Elsas JD, Jansson J TJ (ed) Modern Soil Microbiology. Press Taylor & Francis Group, New York, pp
2392   345–361

2393   Steinmetz NF, Lomonossoff GP, Evans DJ (2006) Decoration of cowpea mosaic virus with multiple, redox-
2394   active, organometallic complexes. Small 2:530–533. doi: 10.1002/smll.200500453

2395   Su PH, Lai YH (2017) A reliable and non-destructive method for monitoring the stromal pH in isolated
2396   chloroplasts using a fluorescent pH probe. Front Plant Sci 8:1–10. doi: 10.3389/fpls.2017.02079

2397   Sun Y, Li Y, Wang B, et al (2020) Leaf nitrate accumulation influences the photorespiration of rice (*Oryza*
2398   *sativa* L.) seedlings. Plant Soil 323–338. doi: 10.1007/s11104-020-04710-1

2399   Šustr V, Stingl U, Brune A (2014) Microprofiles of oxygen, redox potential, and pH, and microbial fermentation
2400   products in the highly alkaline gut of the saprophagous larva of *Penthetria holosericea* (Diptera:
2401   Bibionidae). J Insect Physiol 67:64–69. doi: 10.1016/j.jinsphys.2014.06.007

2402   Suzuki T, Shinogi T, Narusaka Y, Park P (2003) Infection behavior of *Alternaria alternata* Japanese pear
2403   pathotype and localization of 1,3-β- d -glucan in compatible and incompatible interactions between the
2404   pathogen and host plants. J Gen Plant Pathol 69:91–100. doi: 10.1007/s10327-002-0001-3

2405   Tano BF, Brou CY, Dossou-yovo ER, et al (2020) Spatial and temporal variability of soil redox potential , pH
2406   and electrical conductivity across a toposequence in the savanna of West Africa. Agronomy 10:1787. doi:
2407   doi:10.3390/agronomy10111787

2408   Teixeira PJP, Colaianni NR, Fitzpatrick CR, Dangl JL (2019) Beyond pathogens: microbiota interactions with
2409   the plant immune system. Curr Opin Microbiol 49:7–17. doi: 10.1016/j.mib.2019.08.003

2410   Thivierge K, Prado A, Driscoll BT, et al (2010) Caterpillar- and salivary-specific modification of plant proteins.
2411   J Proteome Res 5887–5895

2412   Thomma BPHJ, Nürnberger T, Joosten MHAJ (2011) Of PAMPs and effectors: The blurred PTI-ETI dichotomy.
2413   Plant Cell 23:4–15. doi: 10.1105/tpc.110.082602

2414   Thompson IA, Huber DM (2007) Manganese and plant disease. In: Datnoff LE, Elmer WH, Huber DM (eds)
2415   Mineral nutrition and plant diseases. The American Phytopathology Society, pp 139–153

2416   Thomson CJ, Greenway H (1991) Metabolic evidence for stelar anoxia in maize roots exposed to low O_2
2417   concentrations. Plant Physiol 96:1294–1301. doi: 10.1104/pp.96.4.1294

2418   Tollenaere C, Lacombe S, Wonni I, et al (2017) Virus-bacteria rice co-infection in Africa: field estimation,
2419   reciprocal effects, molecular mechanisms, and evolutionary implications. Front plant Sci 8:. doi:

2420   10.3389/fpls.2017.00645

2421   Torres MA, Jones JDG, Dangl JL (2006) Reactive oxygen species signaling in response to pathogens. Plant
2422   Physiol 141:373–378. doi: 10.1104/pp.106.079467

2423   Toyota K, Shirai S (2018) Growing interest in microbiome research unraveling disease suppressive soils against
2424   plant pathogens. Microbes Environ 33:345–347. doi: 10.1264/jsme2.ME3304rh

2425   Tsang EWT, Bowler C, Herouart D, et al (1991) Differential regulation of superoxide dismutases in plants
2426   exposed to environmental stress. Plant Cell 3:783–792

2427   Ursini F, Maiorino M, Forman HJ (2016) Redox homeostasis: The Golden Mean of healthy living. Redox Biol
2428   8:205–215. doi: 10.1016/j.redox.2016.01.010

2429   Usha Rani P, Pratyusha S (2013) Defensive role of *Gossypium hirsutum* L. anti-oxidative enzymes and phenolic
2430   acids in response to *Spodoptera litura* F. feeding. J Asia Pac Entomol 16:131–136. doi:
2431   10.1016/j.aspen.2013.01.001

2432   Van Baarlen P, Van Belkum A, Summerbell RC, et al (2007) Molecular mechanisms of pathogenicity: How do
2433   pathogenic microorganisms develop cross-kingdom host jumps? FEMS Microbiol Rev 31:239–277. doi:
2434   10.1111/j.1574-6976.2007.00065.x

2435   Van Bel AJE, Gaupels F (2004) Pathogen-induced resistance and alarm signals in the phloem. Mol Plant Pathol
2436   5:495–504. doi: 10.1111/J.1364-3703.2004.00243.X

2437   Van Bruggen AHC, Semenov AM (2000) In search of biological indicators for soil health and disease
2438   suppression. Appl Soil Ecol 15:13–24. doi: 10.1016/S0929-1393(00)00068-8

2439   Van Buyten E, Höfte M (2013) Pythium species from rice roots differ in virulence, host colonization and
2440   nutritional profile. BMC Plant Biol 13:. doi: 10.1186/1471-2229-13-203

2441   Van Dongen JT, Schurr U, Pfister M, Geigenberger P (2003) Phloem metabolism and function have to cope with
2442   low internal oxygen. Plant Physiol 131:1529–1543. doi: 10.1104/pp.102.017202

2443   van Haperen P, Voorrips RE, van Loon JJA, Vosman B (2019) The effect of plant development on thrips
2444   resistance in Capsicum. Arthropod Plant Interact 13:11–18. doi: 10.1007/s11829-018-9645-6

2445   Van West P, Appiah AA, Gow NAR (2003) Advances in research on oomycete root pathogens. Physiol Mol
2446   Plant Pathol 62:99–113. doi: 10.1016/S0885-5765(03)00044-4

2447   van West P, Morris BM, Reid B, et al (2002) Oomycete plant pathogens use electric fields to target roots. Mol
2448   Plant Microbe Interact 15:790–798. doi: 10.1094/MPMI.2002.15.8.790

2449   Vartoukian SR, Palmer RM, Wade WG (2010) Strategies for culture of "unculturable" bacteria. FEMS
2450   Microbiol Lett 309:1–7. doi: 10.1111/j.1574-6968.2010.02000.x

2451   Veivers PC, O'Brien RW, Slaytor M (1980) The redox state of the gut of termites. J Insect Physiol 26:75–77

2452   Venard C, Vaillancourt L (2007) Colonization of fiber cells by *Colletotrichum graminicola* in wounded maize
2453   stalks. Phytopathology 97:438–447. doi: 10.1094/PHYTO-97-4-0438

2454   Visnovitz T, Touati M, Miller AJ, Fricke W (2013) Apoplast acidification in growing barley (*Hordeum vulgare*
2455   L.) leaves. J Plant Growth Regul 32:131–139. doi: 10.1007/s00344-012-9282-8

2456   Voges MJEEE, Bai Y, Schulze-Lefert P, Sattely ES (2019) Plant-derived coumarins shape the composition of an
2457   Arabidopsis synthetic root microbiome. Proc Natl Acad Sci U S A 116:12558–12565. doi:
2458   10.1073/pnas.1820691116

2459   Vozáry E, Jócsák I, Droppa M, Bóka K (2008) Connection between structural changes and electrical parameters

2460   of pea root tissue under anoxia. In: Pamella Padilla (ed) Anoxia. InTech, pp 131–146

2461 Wagner E, Abrechtová JTP, Normann J, Greppin H (2000) Redox state and phosphorylation potential as

2462   macroparameters in rhythmic control of metabolism — a molecular basis for seasonal adaptation of

2463   development BT - The Redox State and Circadian Rhythms. In: Driessche T Vanden, Guisset J-L, Petiau-

2464   de Vries GM (eds). Springer Netherlands, Dordrecht, pp 257–277

2465 Wang C yu, Zhou X, Guo D, et al (2019) Soil pH is the primary factor driving the distribution and function of

2466   microorganisms in farmland soils in northeastern China. Ann Microbiol 69:1461–1473. doi:

2467   10.1007/s13213-019-01529-9

2468 Wang JP, Xu YP, Zang XP, et al (2016) *Sclerotinia sclerotiorum* virulence is affected by mycelial age via

2469   reduction in oxalate biosynthesis. J Integr Agric 15:1034–1045. doi: 10.1016/S2095-3119(15)61199-6

2470 Wang M, Chen S, Chen L, Wang D (2020) Microbial mechanisms responsible for the variation of soil Cd

2471   availability under different pe+pH environments. Ecotoxicol Environ Saf 206:111057. doi:

2472   10.1016/j.ecoenv.2020.111057

2473 Wang YC, Yu M, Shih PY, et al (2018) Stable pH suppresses defense signaling and is the key to enhance

2474   Agrobacterium-mediated transient expression in Arabidopsis seedlings. Sci Rep 8:1–9. doi:

2475   10.1038/s41598-018-34949-9

2476 War AR, Paulraj MG, Ahmad T, et al (2012) Mechanisms of plant defense against insect herbivores. Plant

2477   Signal Behav 7:1306–1320. doi: 10.4161/psb.21663

2478 Ward GM (1960) Potassium in plant metabolism. III. Some carbohydratre changes in the wheat seedling

2479   associated with varying rates of potassium supply. Can J Plant Sci 40:729–735

2480 Webb RW (1921) Studies in the physiology of the fungi . XV . Germination of the spores of certain fungi in

2481   relation to Hydrogen-ion concentration. Ann Missouri Bot Gard 8:283–341

2482 Wei J, Loon JJA Van, Gols R, et al (2014) Reciprocal crosstalk between jasmonate and salicylate defense-

2483   signalling pathways modulates plant volatile emission and herbivore host-selection behaviour. J Exp Bot

2484   65:3289–3298. doi: 10.1093/jxb/eru181

2485 Weller DM, Raaijmakers JM, Gardener BBM, Thomashow LS (2002) Microbial populations responsible for

2486   specific soil suppressiveness to plant pathogens. Annu Rev Phytopathol 40:309–48. doi:

2487   10.1146/annurev.phyto.40.030402.110010

2488 Wells JM, Raju BC, Hung H, et al (1987) *Xylella fastidiosa* gen. nov. , sp. nov: Gram-Negative, Xylem-

2489   Limited, Fastidious Plant Bacteria Related to *Xanthomonas spp*. Int J Syst Bacteriol 37:136–143

2490 Wezel A, Casagrande M, Celette F, et al (2014) Agroecological practices for sustainable agriculture. A review.

2491   Agron Sustain Dev 34:1–20. doi: 10.1007/s13593-013-0180-7

2492 White JF, Kingsley KL, Zhang Q, et al (2019) Review: Endophytic microbes and their potential applications in

2493   crop management. Pest Manag Sci 75:2558–2565. doi: 10.1002/ps.5527

2494 Wicklow DT, Jordan AM, Gloer JB (2009) Antifungal metabolites (monorden, monocillins I, II, III) from

2495   *Colletotrichum graminicola*, a systemic vascular pathogen of maize. Mycol Res 113:1433–1442. doi:

2496   10.1016/j.mycres.2009.10.001

2497 Wielkopolan B, Obre A (2016) Three-way interaction among plants , bacteria , and coleopteran insects. Planta

2498   244:313–332. doi: 10.1007/s00425-016-2543-1

2499 Wilkinson S (1999) PH as a stress signal. Plant Growth Regul 29:87–99. doi: 10.1023/A:1006203715640

2500   Wilkinson S, Davies WJ (1997) Xylem sap pH increase: A drought signal received at the apoplastic face of the
2501   guard cell that involves the suppression of saturable abscisic acid uptake by the epidermal symplast. Plant
2502   Physiol 113:559–573. doi: 10.1104/pp.113.2.559

2503   Williams A, de Vries FT (2019) Plant root exudation under drought: implications for ecosystem functioning.
2504   New Phytol. doi: 10.1111/nph.16223

2505   Williams B, Kabbage M, Kim HJ, et al (2011) Tipping the balance : *Sclerotinia sclerotiorum* secreted oxalic acid
2506   suppresses host defenses by manipulating the host redox environment. PLOS Pathog 7:e1002107. doi:
2507   10.1371/journal.ppat.1002107

2508   Wilts BD, Schaap IAT, Schmidt CF (2015) Swelling and softening of the cowpea chlorotic mottle virus in
2509   response to pH shifts. Biophys J 108:2541–2549. doi: 10.1016/j.bpj.2015.04.019

2510   Wissenschafts B, Issn B, Physiology P, et al (1999) The role of extracellular pH homeostasis in potato resistance
2511   to ring rot pathogen. J Phytopathol 147:679–686

2512   Worrall JJ, Adams GC, Tharp SC (2010) Summer heat and an epidemic of cytospora canker of Alnus. Can J
2513   Plant Pathol 32:376–386. doi: 10.1080/07060661.2010.499265

2514   Wright JP, Fisher DB (1981) Measurement of the sieve tube membrane potential. Plant Physiol 67:845–848. doi:
2515   10.1104/pp.67.4.845

2516   Xi B, Zhao X, He X, et al (2016) Successions and diversity of humic-reducing microorganisms and their
2517   association with physical-chemical parameters during composting. Bioresour Technol 219:204–211. doi:
2518   10.1016/j.biortech.2016.07.120

2519   Xie L, Zhang JZ, Cai L, Hyde KD (2010) Biology of *Colletotrichum horii*, the causal agent of persimmon
2520   anthracnose. Mycology 1:242–253. doi: 10.1080/21501203.2010.526644

2521   Yadeta KA, Thomma BPHJ (2013) The xylem as battleground for plant hosts and vascular wilt pathogens. Front
2522   Plant Sci 4:1–12. doi: 10.3389/fpls.2013.00097

2523   Yamamoto Y, Kobayashi Y, Devi SR, et al (2003) Oxidative stress triggered by aluminum in plant roots. In: J. A
2524   (ed) Roots: The Dynamic Interface between Plants and the Earth.Developments in Plant and Soil Sciences,
2525   vol 101. Springer, Dordrecht, The Netherlands, pp 239–243

2526   Yang JW, Yi HS, Kim H, et al (2011) Whitefly infestation of pepper plants elicits defense responses against
2527   bacterial pathogens in leaves and roots and changes the below-ground microflora. J Ecol 99:46–56. doi:
2528   10.1111/j.1365-2745.2010.01756.x

2529   Yoder JI (2001) Host-plant recognition by parasitic *Scrophulariaceae.* Curr Opin Plant Biol 4:359–365

2530   Yruela I (2013) Transition metals in plant photosynthesis. Metallomics 5:1090–1109. doi: 10.1039/c3mt00086a

2531   Yu K, Pieterse CMJ, Bakker PAHM, Berendsen RL (2019) Beneficial microbes going underground of root
2532   immunity. Plant Cell Environ 42:2860–2870. doi: 10.1111/pce.13632

2533   Yuan J, Zhao J, Wen T, et al (2018) Root exudates drive the soil-borne legacy of aboveground pathogen
2534   infection. Microbiome 6:1–12. doi: 10.1186/s40168-018-0537-x

2535   Zebelo SA, Maffei ME (2015) Role of early signalling events in plant – insect interactions. J Exp Bot 66:435–
2536   448. doi: 10.1093/jxb/eru480

2537   Zechmann B, Zellnig G, Urbanek-Krajnc A, Müller M (2007) Artificial elevation of glutathione affects symptom
2538   development in ZYMV-infected *Cucurbita pepo* L. plants. Arch Virol 152:747–762. doi: 10.1007/s00705-
2539   006-0880-2

2540   Zhang J, Yan H, Xia M, et al (2020) Wheat root transcriptional responses against *Gaeumannomyces graminis*

2541   var. tritici. Phytopathol Res 2:23. doi: 10.1186/s42483-020-00071-w

2542   Zhang J, Zeng B, Mao Y, et al (2017) Melatonin alleviates aluminium toxicity through modulating antioxidative

2543   enzymes and enhancing organic acid anion exudation in soybean. Funct Plant Biol 44:961–968

2544   Zou C, Zhang F (2003) Ammonium improves iron nutrition by decreasing leaf apoplastic pH of sunflower plants

2545   (*Helianthus annuus* L. cv. Frankasol). Chinese Sci Bull 48:2216–2221. doi: 10.1007/BF03182855

2546