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MARSCHNER REVIEW

Plant allelochemicals: agronomic, nutritional and ecological relevance in the soil system

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Abstract
Background Allelopathy is an ecological phenomenon consisting of both positive and negative effects between organisms determined by the release of secondary metabolites into the environment. Root exudation represents the most important pathway of releasing allelochemicals. Once released into the soil, allelochemicals interact with the organic and inorganic soil phases, as well as with soil microorganisms. The set of these interactions fix allelochemicals bioavailability and phytotoxic level.
Scope Here we critically review the interactions between plant allelochemicals and physical, chemical and biological soil characteristics by reporting the literature available and pointing out both positive and negative relationships affecting allelochemicals phytotoxicity and nutrient availability. In addition, we have reported a qualitative balance of allelochemicals in the soil. Thirdly, we reviewed the exudation process of allelochemicals and the transport mechanisms across plasma membranes.
Conclusions A two-way relationship exists between soil characteristics and allelochemicals. The level of phytotoxicity is not affected only by a single soil characteristic, but they are closely linked to each other and exert a multiple-effect on retention, transport and transformation processes of allelochemicals in soil. Further efforts are needed to better understand the interactions involved in soil allelopathy and to create new opportunities for a sustainable control of agroecosystems.

Keywords Allelopathy · Secondary metabolites · Rhizosphere · Root exudation · Soil characteristics · Soil microorganisms

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Introduction

In recent years, agriculture has had to deal with increasing environmental pollution mainly arising from two aspects linked by a common goal: the maximization of yields. On one hand, the improper utilization of synthetic chemicals for weed and pest control in agroecosystems; on the other, the mismanagement of fertilization, principally for nitrogen. Allelopathy has offered a new alternative for the development of eco-friendly agricultural practices, with the dual purpose of enhancing crop productivity and maintaining ecosystem stability (Scavo et al. 2018a). Allelopathy involves the positive or negative effects of a plant (donor), including microorganisms, on neighbouring plants (targets) through the release of chemical compounds into the environment, mostly in the soil. According to Inderjit and Weiner (2001), it is possible to distinguish between direct plant-plant allelopathic interference (allelopathy in the narrow sense) and indirect allelopathy. The former refers to the direct action of an allelochemical produced and released by a donor plant on receiver plants; the latter represents the effects of allelochemicals on abiotic and biotic soil processes that affect other plants. Aldrich (1984) described these two kinds of allelopathy as *true* and *functional* allelopathy. Indeed, allelochemicals released into the soil can (i) directly affect the target organisms, (ii) be degraded or transformed by soil microorganisms, (iii) induce a third species to produce another compound which interferes with donor plants and (iv) cause changes to soil abiotic factors that affect target plants. Most have focused on the *in vitro* direct allelopathy and the identification of potential allelochemicals. However, it is impossible to separate direct from indirect allelopathic effects in field conditions and to assert that direct allelopathy is solely responsible for an observed phenomenon in the field, because many abiotic and biotic soil factors influence the fate of allelochemicals. Therefore, indirect allelopathic interactions, from an ecological point of view, are probably more important in plant communities than direct ones (Inderjit and Weiner 2001). For this reason, we believe that they should be further investigated by the scientific community under a soil chemical ecology context.

How allelochemicals must reach the root system of the target plant through the soil in order to exert a phytotoxic effect, has been well documented (Inderjit 2001). However, establishing an allelopathic interference depends on several factors such as the concentration, the movement and the persistence of allelopathic compounds. In fact, allelochemicals are subjected to transformations by the complex of chemical, physical and biological characteristics of the soil environment that determine their phytotoxic level (Blum 2006; Cheng 1992; Dao 1987). Soil characteristics, especially biological ones, may vice versa be affected by allelochemicals. Thus, there is a two-way relationship between them. However, these relationships have been little investigated by the scientific community. Finding a linkage may help researches in studying and increasing the knowledge on the allelopathic behaviour of plants. Allelochemicals released into the rhizosphere exert a significant impact on nutrient availability, dynamics and uptake by the plant. A broader knowledge of the effects of plant allelochemicals on mineral nutrient soil cycles, heavy metal detoxification and nutrient solubility can enhance the nutrient use efficiency through a reduction of their losses and the development of a more efficient and sustainable fertilization technique.

This review focuses on the interactions between plant allelochemicals and physical, chemical and biological soil characteristics from an agronomic and ecological point of view, by reporting the literature available on this topic and pointing out both the positive and negative relationships affecting allelochemicals phytotoxicity. Moreover, a qualitative balance of allelochemicals inputs and outputs in soil was developed. Furthermore, we also discuss the exudation process of allelochemicals and the transport mechanisms across plasma membranes. The influence of plant allelochemicals on mineral nutrition and the most important plant-soil-microorganism interactions are also discussed.

Balance of allelochemicals in soil

Donor plants release allelochemicals into the environment through volatilization from living parts of the plant, leaching from plant foliage, decomposition of plant material and root exudation (Scavo et al. 2018a). Except for volatilization, the other pathways release allelopathic compounds into the soil. Once released by the donor plant, allelochemicals enter into a complex plant-soil system in which different factors affect their availability and, consequently, their effective influence on target plants (Blum et al. 1999; Kruse et al. 2000). This plant-soil system, is in turn influenced by several meteorological factors, demonstrating the complexity of this phenomenon. As shown in Fig. 1, in addition to the chemical nature of the allelochemical produced, the phytotoxic activity of allelochemicals in the soil is affected by climatic conditions (e.g. solar radiation, temperature, rainfall), soil factors (e.g. texture, pH, ion-exchange capacity, organic matter content, nutrient dynamics, moisture content and microbial ecology) and plant factors of both the donor and target plants (e.g. species, botanical variety, growth stages, plant parts, etc.). Since the pathways of release of allelochemicals into the environment, as well as plant and meteorological factors affecting their production, have already been reviewed in depth (de Albuquerque et al. 2011; Rice 1984; Scavo et al. 2018a), this article addresses root exudation, which is the most important pathway of release of such secondary metabolites into the soil, and soil factors (physical, chemical and biological) interacting with allelochemicals.

In order to be adsorbed by the roots of the target plant, allelochemicals may be present in the soil solution (Kobayashi 2004). Therefore, the key factor determining the phytotoxic activity of allelochemicals is their concentration in soil water. However, similar to herbicides, in the soil environment these compounds are subjected to retention, transformation and transport processes (Cheng 1992; Weidenhamer 1996). Retention is a physical process consisting in the interaction (frequently described as adsorption or sorption) between allelochemicals and soil particles (e.g. clays, Fe-, Al-, and Mn-sesquioxides, organic matter), water and/or air (Bezuidenhout and Laing 2006; Cheng and Koskinen 2010). In many cases, it is a dynamic and reversible process implying the mobility of allelochemicals in soil. Transformation is a positive or negative biochemical process, mainly operated by soil microorganisms, involving the conversion of allelochemicals into more active, less active or entirely inactive compounds. This process leads to a reduction of the amount of the original allelochemical available for transport (Cheng 1992). Transport represents the movement of allelochemicals in the soil, and it is closely affected by the retention and transformation processes. The interaction of these processes is governed by the chemical nature of the allelopathic compound, the organisms involved, the properties of the soil and the environmental conditions.

Understanding the available concentration of allelochemicals in the soil solution is of central importance. As commonly found in weed science for herbicides, we have developed a conceptual framework (Fig. 2) representing a qualitative balance of allelochemicals inputs and outputs in soil, in which is possible to observe their dynamicity. In addition to the direct release by plants, allelochemicals can enter into the soil through faunal and microbial exudation (from both living microorganisms and decomposed microbial biomass), decomposition of organic matter and mineral weathering. Similar to herbicides, allelochemicals are continually removed and/or immobilised from the soil solution by leaching, microbial breakdown, adsorption to soil particles and plant uptake (Cheng 1995; Inderjit et al. 2001; Weidenhamer 1996). However, the behaviour of allelochemicals in the soil is more complicated than herbicides, as the former are continuously released from the donor plant with significant differences in relation to plant organs (Abu-Romman 2016; Iqbal et al. 2002; Suksungworn et al. 2016) and growth stages (Aslam et al. 2016). The knowledge of allelochemicals dynamicity in the soil is an important aspect for the better understanding of their interactions with plants, microorganisms and insects and for the possible future application of allelochemical-based bioherbicides, living and dead mulches.

Root exudation

Root systems have a multitude of functions including the anchorage of the plant and the absorption of water and nutrients. In addition to these main functions, roots are a site of photoassimilates storage and carbon reserves, synthesis of phytohormones (e.g. auxins, cytokinins, abscisic acid, gibberellic acid, ethylene), synthetic activities (e.g. nitrogen fixation, synthesis of organic acids, etc.), and exudation of metabolites (Blum 2006; Osmont et al. 2007). It has been estimated that over 10.000 allelochemicals are produced by higher plants, with a significant variability in their activity and mode of action in target plants (Weston et al. 2012). Living roots of many weed and crop species continuously produce and secrete both low- and high-molecular weight compounds into the rhizosphere in response to biotic and abiotic stresses (Bertin et al. 2003). The chemicals secreted into the soil by roots are broadly referred to as root exudates (Walker et al. 2003). Their quantity and quality are related to the plant species, cultivar, plant development stage, and environmental stress factors (Badri and Vivanco 2009; Uren 2000). These variables are widely reported in literature for several allelopathic plants. Aulakh et al. (2001), for example, found that rice exudation rates, in general, are the lowest at the seedling stage, increase until flowering and then decrease at maturity. Sorghum and wheat root exudations decrease with plant age and increase when the soil is stressed by compaction, drought, and low nutrient supply (Weil and Brady 2017). Generally, actively growing root systems secrete more exudates, indicating a positive correlation between root exudation and root growth (Lucas Garcia et al. 2001). In addition, the nature of root surface morphology (e.g. suberized or unsuberized, with or without mycorrhizal hyphae, thickness of periderm, quantity and location of root hairs, etc.) as well as the root system architecture

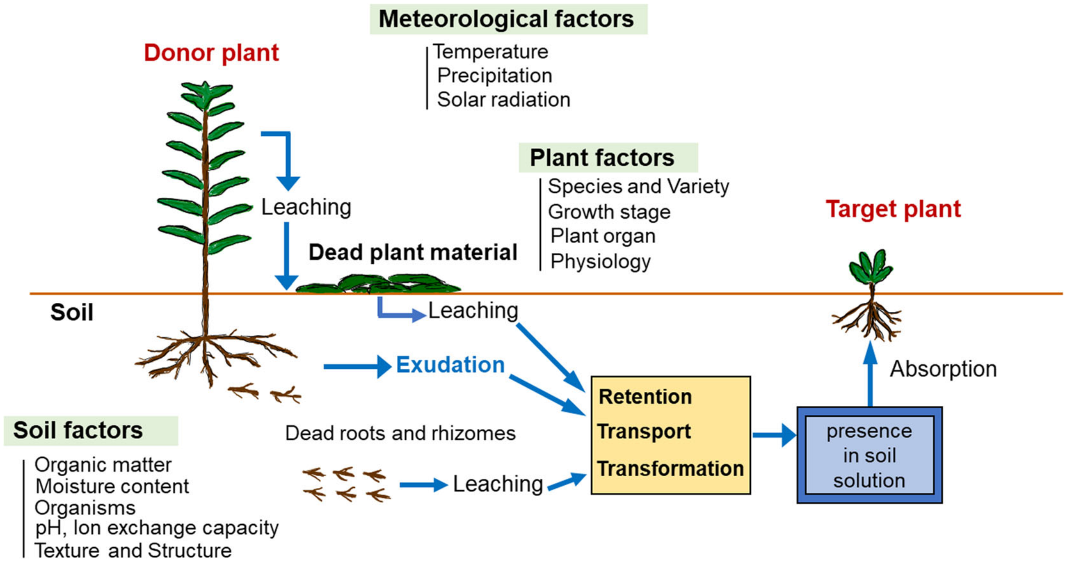

Fig. 1 Influence of meteorological, soil and plant factors on the phytotoxicity of allelochemicals in soil (modified from Kobayashi 2004). Different kinds of both meteorological and plant factors affect the quantity and quality of allelochemicals released by the donor plant. Once released into the soil system, several soil factors influence the retention, transport and transformation processes of allelochemicals in the soil and, thus, their presence in the soil solution in order to be absorbed by the target plant

(tap root system of dicotyledonous species or fibrous one of monocotyledonous plants, amount of root branching, number of lateral roots, etc.) are all factors involved in determinating the quantitative and qualitative composition of exudates (Badri and Vivanco 2009; Blum 2006). Nevertheless, root exudation also depends on the root zone. The zone immediately behind the root tip is considered the major site of exudation (Pearson and Parkinson 1961). The root cap (Curlango-Rivera et al. 2013; Hawes et al. 2012; Pina et al. 2016) and root hair cells (Czarnota et al. 2003a) are the root cells chiefly involved in root exudation, followed by cortex and stellar cells (Pineros et al. 2002). All these factors are closely correlated with each other, because the type of roots depends on plant age, season and soil conditions (e.g. texture, structure, temperature, water content, pH, etc.).

The rhizosphere and the importance of root exudates

The narrow region of soil matrix immediately surrounding the root and in which living roots secrete an enormous range of compounds is called "rhizosphere". This term was coined by Lorentz Hiltner (Hartmann et al. 2008) to describe the portion of soil where microorganism-mediated processes are controlled by the root system (Berg and Smalla 2009). Since then, many definitions of rhizosphere have been suggested

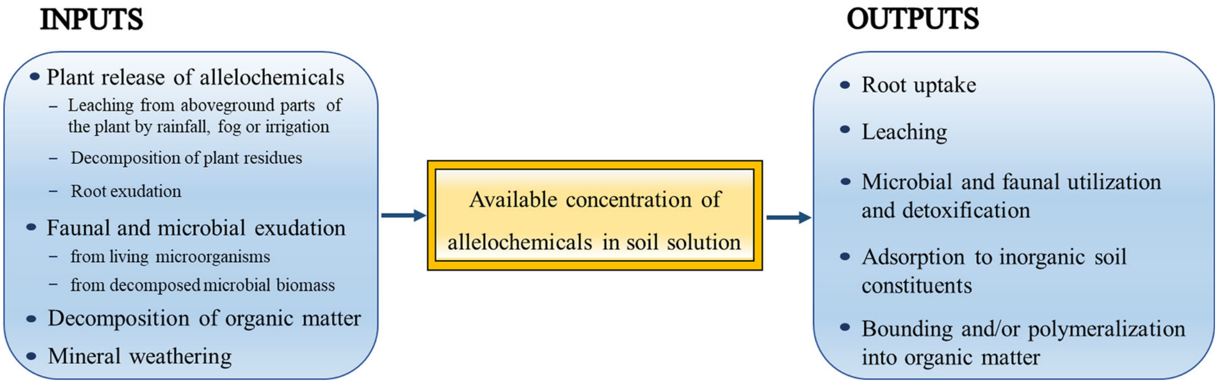

Fig. 2 Balance of allelochemicals inputs and outputs in soil affecting their bioavailability in the soil solution and phytotoxic activity

(Kennedy 1998; McNear Jr 2013; Rovira and Davey 1974; Uren 2000). The rhizosphere can ranges from about 0 to 2 mm or more (depending on the plant type, soil moisture and texture, and presence of mycorrhizae) away from the root surface and includes three zones (Lynch 1987) (Fig. 3): endorhizosphere, rhizoplane and ectorhizosphere. The endorhizosphere refers to the internal zone and includes the apoplastic space between the root cortex and endodermis and is colonisable by microorganisms. Since the rhizosphere is defined as external to the root, Kloepper et al. (1992) and York et al. (2016) consider the term endorhizosphere improper. The rhizoplane, first defined by Clark (1949), represents the root surface, including epidermis and mucilage, closely adhering to the ectorhizosphere. It is the most active site of microorganism-plant interactions and plays a key role on the fate of allelochemicals in soil. The ectorhizosphere is the soil layer surrounding the root. The rhizosphere is a biologically active zone, influenced by root metabolic activities, densely populated by microorganisms. For these reasons, its chemical, biological and physical characteristics drastically differ from bulk soil. In particular, it has higher levels of cation exchange capacity, exchangeable base cations, base saturation, organic matter and carbon dioxide than bulk soil (Gobran et al. 1998). The rhizosphere is characterized by gradients of its properties that change in both time and space.

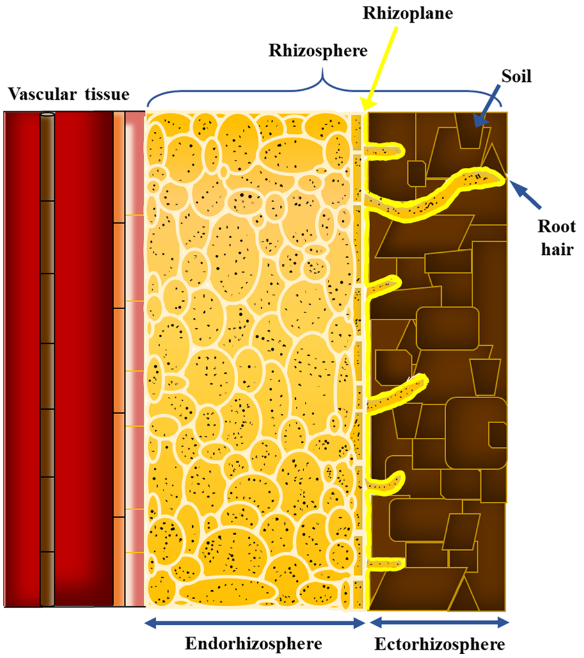

Fig. 3 Scheme of the rhizosphere showing its three sections: the endorhizosphere, the rhizoplane and the ectorhizosphere (modified from McNear Jr 2013)

The ubiquitous phenomenon consisting in the loss of carbon-containing compounds from plant roots into the rhizosphere is referred to as rhizodeposition (Doornbos et al. 2012; Jones et al. 2004). Root-derived compounds, generally called rhizodeposits, have been classified according to their mode of excretion and chemical composition into five predominate categories (Rovira 1969):

1) root exudates: sugars, amino acids, organic acids, vitamins and hormones;
2) secretions: polymeric carbohydrates, enzymes and secondary metabolites secreted with the involvement of energy;
3) mucigel: newly removed cells of cellulose, pectin, starch, and lignin, secreted by the root cap as result of abrasive forces of the root movement through the soil;
4) lysates: shedding, wall and contents of sloughed-off cells as well as whole roots;
5) gases: carbon dioxide, ethylene, etc.

Root exudation is therefore part of the rhizodeposition process. In addition to carbon-containing compounds derived from products of photosynthesis, plant roots release non-carbon-containing compounds such as the ion H^+, inorganic ions, water and electrons, albeit in lower quantities (Uren 2000). However, the most dramatic changes on the physical, biological and chemical nature of the soil is produced by the release of organic carbon (Jones et al. 2009). On average, 30 to 60% of photosynthesized C is allocated by plants to the roots (Marschner 1995). It is estimated that about 60% of photosynthesized C is transferred by annual plants to the roots, while up to 70% is allocated by woody plants. According to Marschner (1995), nearly 5 to 21% of all photosynthetically fixed carbon is released into the rhizosphere through root exudates by higher plants.

Root exudation involves two different active processes: excretion and secretion (Bais et al. 2004a). The former consists in the release of metabolic wastes and mixtures of small compounds with unknown functions, while the latter refers to molecules with known functions. Root secretions are probably involved in external processes (e.g. nutrient acquisition) and have a direct ecological role in the rhizosphere. Most allelochemicals released via exudation are secretions. Excretions, on the

Table 1 List of major plant allelochemicals released into the rhizosphere through root exudation

Chemical class	Allelochemicals	Donor plants	References
Alkaloids	α-tomatine	*Solanum lycopersicum* L.	1
	Hordenine, gramine	*Hordeum vulgare* L.	2
	Emetine	*Cephaelis ipecacuanha* (Brot.) L. Andersson	3
	Nicotine	*Nicotiana tabacum* L.	4
	8-hydroxyquinoline	*Centaurea diffusa* Lam.	5
Amino acids	Mugineic acid phytosiderophores	*Triticum aestivum* L., *T. durum*,	6
Benzoquinones	Sorgoleone, 5-ethoxysorgoleone, 2,5-dimethoxysorgoleone	*Sorghum halepense* (L.) Pers., *S. sudanense*, *S. vulgare*, *S. bicolor*, *S. bicolor* x S. *sudanense*	7
Benzoxazinoids	DIBOA (2,4-dihydroxy-(2*H*)-1,4-benzoxazin-3(4*H*)-one), DIMBOA (2,4-dihydroxy-7-methoxy-(2*H*)-1,4-benzoxazin-3(4*H*)-one), MBOA (6-methoxybenzoxazolin-2-one), BOA (benzoxazolin-2(3*H*)-one)	*Secale cereale* L., *T. aestivum*, T. *durum*, *T. spelta*, *Zea mays* L., × *Triticosecale* Wittm.	8
Coumarins	Cinnamic acid	*Cucumis sativus* L.	9
	Scopoletin, esculetin, coumarin	*Avena sativa* L.	10
	Umbelliferone	*A. sativa, Medicago sativa* L.	10, 11
Diterpenes	Esulone A, kansuinine B, 3,3′,4-tri-*O*-methylellagic acid	*Euphorbia esula* L.	12
	Momilactone A, momilactone B	*Oryza sativa* L.	13
Flavonoids	Quercetin	*Fagopyrum esculentum* Moench, *Miscanthus x giganteus*, *Lotus pedunculatus* Cav., *Glycine max* (L.) Merr., *M. sativa*, *Z. mays*	11, 14, 15, 16, 17, 21
	Luteolin, apigenin, luteolin- and apigenin derivatives	*M. sativa*, *L. pedunculatus*, *Pisum sativum* L., *Miscanthus x giganteus*	11, 15, 16, 18
	Kaempferol	*L. pedunculatus*, *M. sativa*	11, 16
	Naringenin	*L. pedunculatus, P. sativum*, *M. sativa*	11, 16, 18
	(±)-catechin	*Centarurea maculosa* Lam., *C. stoebe*, *C. diffusa*, *L. pedunculatus*, *Z. mays*	16, 19, 20, 21
Hydroxycinnamic acids and simple phenols	*p*-hydroxybenzoic, vanillic, *p*-coumaric, syringic, ferulic, caffeic	*A. sativa*, *O. sativa*, *T. aestivum*, *T. durum*,	10, 22
Isoflavonoids	(6a*R*,11a*R*)-maackiain, (6a*R*,11a*R*)- trifolirhizin, barbacarpan, formononetin, irilone	*Trifolium pratense* L.	23
Napthoquinones	Juglone	*Juglans nigra* L., *J. cinerea*, *J. regia*	24
Lignans	Pinoresinol	Several woody species (e.g. *Fraxinus excelsior* L.)	25
Quassinoids	Ailanthone, 2-dihydroailanthone	*Ailanthus altissima* (Mill.) Swingle	26
	Quassin, neoquassin	*Quassia amara* L., *A. altissima*	26
Sesquiterpene lactones	Artemisinin	*Artemisia annua* L.	27
	Dehydrocostus lactone, custunolide, tomentosin	*Helianthus annuus* L.	28

Table 1 (continued)

Chemical class	Allelochemicals	Donor plants	References
	Cnicin	*C. maculosa*	29
Sterols	Campesterol	*Arachis hypogaea* L.	30
	Stigmasterol	*A. hypogea*, *L. esculentum*,	30, 1
	β-sitosterol	*Sedum alfredii* Hance	31
Tannins	Ellagic acid	*E. esula*	12,
	Gallic acid	*C. sativus*, *F. esculentum*, *O. sativa*, *Aegiceras corniculatum* (L.) Blanco, *Miscanthus x giganteus*	9, 14, 15

1: Rial et al. 2018; **2**: Bouhaouel et al. 2018; **3**: Itoh et al. 1999; **4**: Zhao et al. 2013; **5**: Tharayil et al. 2009; **6**: Sugiura and Nomoto 1984; **7**: Czarnota et al. 2003b; **8**: Belz and Hurle 2005; **9**: Yu et al. 2003; **10**: Pérez and Ormeño-Nuñez 1991; **11**: Peters and Long 1988; **12**: Qin et al. 2006; **13**: Kato-Noguchi et al. 2010; **14**: Kalinova et al. 2007; **15**: Téchér et al. 2011; **16**: Steele et al. 1999; **17**: Graham 1991; **18**: Makarova et al. 2016; **19**: Tharayil and Triebwasser 2010; **20**: Tharayil et al. 2009; **21**: Kidd et al. 2001; **22**: Wu et al. 2001; **23**: Liu et al. 2013; **24**: Bertin et al. 2003; **25**: Caligiani et al. 2013; **26**: Heisey 1996; **27**: Li et al. 2014; **28**: Raupp and Spring 2013; **29**: Kelsey and Locken 1987; **30**: Thompson and Hale 1983; **31**: Luo et al. 2017.

contrary, influence internal metabolic processes (Uren 2000). Root exudates, which are a part of rhizodeposits, are also classified into low- and high-molecular weight compounds. Low-M_r compounds include amino acids, organic acids, sugars, phenolics, and other secondary metabolites and represent the majority of root exudates, whereas high-M_r compounds are represented by proteins, terpenoids, vitamins and polysaccharides (primarily mucilage) (Badri and Vivanco 2009; Bais et al. 2006). A list of root exudates has been exhaustively reviewed in previous works (Bertin et al. 2003; Rovira 1969; Uren 2000). In literature, many evidences have been reported on the root exudation of allelochemicals, suggesting how this pathway of release represents the largest source of plant allelochemicals into the rhizosphere. Major allelochemicals released by plants through root exudation are listed in Table 1.

Cellular transport of root exudates and allelochemicals

For a long time, root exudation has been considered solely a passive process. Nowadays, we know that plants are able to actively secrete metabolites into the environment. The three passive pathways by which plant living roots release secondary metabolites out of the cells are diffusion, ion channels and vesicle transport (Bertin et al. 2003; Neumann and Romheld 2001), while the active secretion process involves the utilization of specific membrane-bound transport proteins embedded in the plasma membrane (Fig. 4). Since most allelochemicals are large charged molecules and ions, they are too polar to directly diffuse through the cell membrane. Therefore, they need other transport pathways such as subcellular vesicles, channels and transporters, also known as carriers (Taiz and Zeiger 2002; Walker et al. 2003).

Among plant carriers there are the ATP-binding cassette (ABC) transporters, the multidrug and toxic compound extrusion (MATE) transporters, the aluminium-activate malate transporter (ALMT), and the major facilitator superfamily (MFS) (Weston et al. 2012). Membrane-protein transporters are the most important secretion process involving the exudation of plant allelochemicals from the root into the rhizosphere. Some examples are provided by benzoxazinoids from the Poaceae family, artemisinin, juglone and several phenolics and alkaloids. The intracellular transport of flavonoids, one of the most important chemical class comprising allelochemicals, and their exudation into the rhizosphere can occur via transporters of the ABC (Buer et al. 2007) or MATE (Zhao and Dixon 2009) families. The ABC transporters are an ancient superfamily of proteins, classified into 13 subfamilies, which can be found in all phyla (Higgins 1992). They use the hydrolysis of ATP to power the transport of a broad range of compounds across cell membranes. Most of them are localized in the vacuolar membrane and play a wide variety of physiological roles such as root exudation (Badri et al. 2008; Sugiyama et al. 2007). Sugiyama et al. (2007) indicated an ATP-dependent manner transport for the isoflavonoid ginestenin from soybean root vesicles. Many poaceae species utilize YS1 (yellow stripe 1) and YS1-like (YSL) protein transporters to secrete and transport mugineic acid family phytosiderophores under Fe-deficiency (Senoura et al. 2017). MATE transporters, which are widely distributed in all kingdoms of living organisms, use an electrochemical gradient of H^+ or Na^+ to transport secondary metabolites from cells (Omote et al. 2006). They are responsible for multidrug resistance (e.g. aluminium or tetramethylammonium tolerance) through the exudation of toxic metabolites and xenobiotics from cells. The ALMT genes are typical of plants and confer aluminium resistance by facilitating the efflux of malate anions (Ryan et al. 1995). Sasaki et al. (2004) found that the wheat gene ALMT1 and heterologous expression of ALMT1 in *Xenopus* oocytes, rice and cultured tobacco cells, encode a membrane protein for the efflux of malate from the root apices, avoiding aluminium toxicity in acid soils. The MFS proteins are the largest family of secondary transporters found in all phyla (Yan 2013). They transport a wide spectrum of compounds (e.g. ions, carbohydrates, lipids, amino acids and peptides, nucleosides, etc.) across membranes.

The transport of high-M_r compounds via root cells can also be mediated by vesicles or specialized organelles (Battey and Blackbourn 1993). Vesicle transport of secondary metabolites such as allelochemicals from the site of synthesis to storage compartments and to cell membrane for efflux, has been described in detail (Field et al. 2006; Robatzek 2007). Most likely, it is related to the necessity of separating from the cytoplasm and safely transporting allelochemicals, most of which are cytotoxic for the host cells (Weston et al. 2012). Flavonoids (e.g. luteonin, catechin, etc.), synthesized on the surface of endoplasmatic reticulum (ER), are separate from the ER and transported by ER-originating vesicles that fuse to the cell membrane and release their contents (Walker et al. 2003). Bock et al. (2002) suggested a vesicle-mediated mechanism for the transport of the alkaloid berberine in different *Berberis* species and *Papaver somniferum* L. Moreover, it is thought that sorgoleone, the toxic benzoquinone produced by *Sorghum* spp., is synthesized on ER and Golgi bodies, transported through subcellular trafficking or to

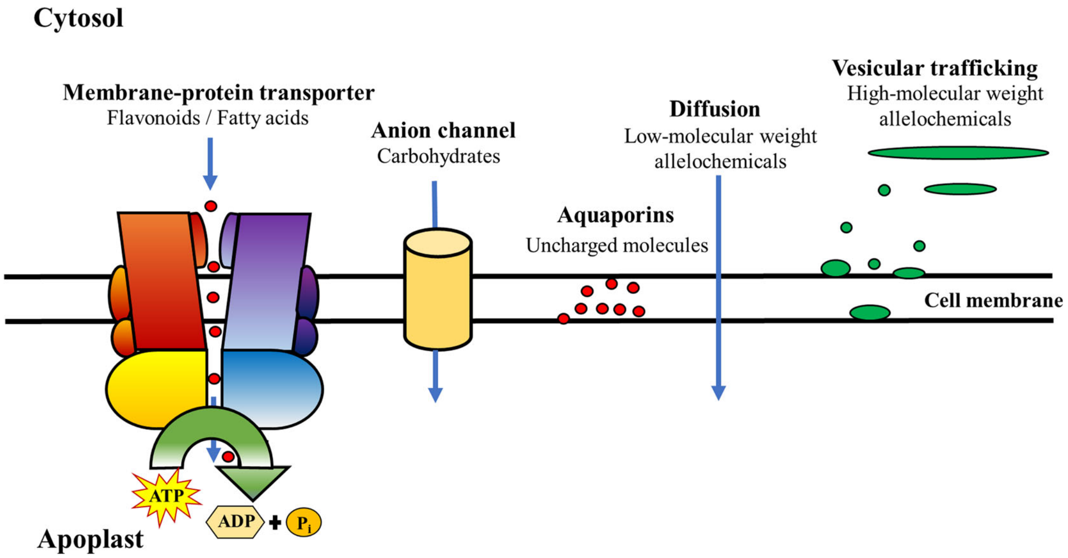

Fig. 4 Pathways of release of root exudates into the rhizosphere through the plant cell membrane. Living plant roots can release secondary metabolites out of the cell primarily through three passive processes (diffusion, ion channels and vesicle transport) and an active secretion pathway involving the utilization of specific membrane-bound transport proteins (modified from Badri and Vivanco 2009)

the plasma membrane for efflux, and exuded from living root hairs (Czarnota et al. 2003a; Grotewold 2001; Weston et al. 2012). Besides, vesicle transport is a defence mechanism for plants, which react to pathogen infection by trafficking antimicrobial compounds to the site of infection through subcellular-membrane vesicles and organelles such as the Golgi or ER-vesicles.

Membrane-protein transporters and subcellular vesicles are the most important mechanisms involved in the translocation of allelochemicals across cell membranes into the rhizosphere. In addition to these processes, plants possess other passive pathways for the release of root exudates and secondary metabolites, even if little used because most of allelochemicals are complex-charged molecules. Diffusion involves electrochemical positive concentration gradients between the cytoplasm of root cells and the soil which support the release of low-M_r compounds such as sugars, amino acids and phenolics that, in the cytoplasmic pH of root cells, are negatively charged, and the uptake of cations from the outside of the cell (Bertin et al. 2003). Another diffusion process is by aquaporins, also known as water channels. They are integral membrane proteins that facilitate the transport of water, and in some cases, small neutral molecules such as glycerol and urea (aquaglyceroporins) across cell membranes. Aquaporin permeability is regulated by phosphorylation (Assmann and Haubrick 1996).

Ion channels are membrane protein complexes allowing the diffusion of ions and charged molecules across the cell membrane. This pathway of release does not need the input of ATP, but works through an electrochemical gradient. Ion channels are ion selective because they are able to discriminate between size and charge of molecules. Anion channels are involved in the released of carbohydrates, specifically organic acids such as citrate, malate or oxalate into the rhizosphere (Jones and Darrah 1995; Walker et al. 2003). For example, maize (*Zea mays* L.), wheat (*Triticum aestivum* L.) and other plant species exudate citric, malic, and related organic acids through ion channels in response to high Al^{3+} concentrations (Ma et al. 2001).

Interactions between allelochemicals and soil characteristics

The behaviour of allelochemicals in the soil is fundamental for the determination of their phytotoxic effects, particularly the adsorption-desorption balance, which influences the concentration of allelochemicals in soil water (Kobayashi 2004). This balance is very dynamic and reversible. It is closely influenced by soil physical (texture, structure, organic matter content, moisture and aeration), chemical (reaction, ion exchange capacity, nutrient dynamics, O_2 and CO_2 concentrations), and biological characteristics (soil microorganisms). Likewise, plants can modify their rhizosphere characteristics through ion, H_2O and O_2 uptake and rhizodeposition (Darrah 1991). A summary on the effects of soil characteristics on allelochemicals phytotoxicity is reported in Table 2. It is important to underline that the level of phytotoxicity is not affected only by a single soil characteristic. On the contrary, these are closely linked to each other and exert a multiple-effect on retention, transport and transformation processes of allelochemicals in soil.

Soil texture

Soil texture refers to the size of particles making up a soil and to the particle-size distribution into textural classes. It has considerable influence on water holding capacity, soil moisture, aeration and temperature, soil reaction, soil microbial communities, ion exchange capacity, nutrient retention and soil porosity, etc. Clay minerals such as kaolinites, vermiculites, smectites, etc. are the active portion of a soil, because chemical reactions occur on their surface. Soil texture closely affects allelochemicals leaching and, consequently, their phytotoxic effects (de Albuquerque et al. 2011). Besides, since clay minerals differ greatly from each other, also the typology of clay influences the availability of allelochemicals. For example, smectite-dominated soil such as Vertisols, very rich in montmorillonites (expanding 2:1 silicate clays), have the highest specific surface area, ion exchange capacity, water retention capacity and, thus, the strongest retention power towards allelochemicals. On the contrary, in soils dominated by nonexpanding 1:1 silicate clays such as kaolinites, which exhibit opposite characteristics compared to montmorillonites, the retention of allelochemicals is very low. Inderjit and Dakshini (1994) reported different amounts of *Pluchea lanceolata* (DC.) Oliv. & Hiern leaf leachates in four soil types (sandy loam, clay loam, silty loam, and sand). Jennings and Nelson (1998), studying in columns the influence of soil texture on alfalfa autotoxicity, found that chemicals moved through the

Table 2 Positive (+) and negative (–) effects of soil characteristics on the allelochemicals phytotoxicity in soil

Soil characteristic		Allelochemicals phytotoxicity	Type of interaction	References
Ion exchange capacity	High Low	– +	A high ion exchange capacity means higher retention of allelochemicals and, thus, less bioavailability.	Belz et al. 2009; Inderjt and Bhowmik 2004
Organic matter content	High	–	Soil organic matter bonds allelochemicals and decreases their bioavailability and phytotoxicity. Moreover, it regulates soil pH, increase soil temperature and facilitates the chemical degradation carried out by microorganisms.	Dalton et al. 1989; Hess et al. 1992; Horrie et al. 1989
Reaction as pH	> 7	+	The different behaviour of plant allelochemicals in response to soil pH is explained by their different chemical structure and protonation status. Soil reaction strongly affects the chemical transformation of allelochemicals into more or less toxic compounds.	Batish et al. 2007
	< 7	+		Norouzi et al. 2015
Structure	Well-structured	+	A well-structured soil presents a high porosity, an equilibrium between soil liquid and gaseous phases, and a high soil organic matter content, thus increasing the transformation process operated by microorganisms and decreasing allelochemicals leaching. Soil structure allows contact between allelochemicals and target plant roots due to the major spatial movement of roots.	Schmidt and Ley 1999
Texture	Clay	+	Clays, by decreasing water infiltration and increasing cation exchange capacity, reduce allelochemicals leaching. In sandy soils, aerobic microorganisms rapidly degrade allelochemicals.	del Moral and Muller 1970; Goslee et al. 2001; Noy-Meir 1973; Rietveld et al. 1983
	Sandy	+	Commons nutrient deficiencies characterising sandy-aerated soils stimulate allelochemicals production.	Inderjit and Asakawa 2001

Sarpy fine sandy loam (mixed, mesic Typic Udipsamments) faster than through the Carlow silty clay loam (fine, smectitic, mesic Vertic Endoaquulls). According to del Moral and Muller (1970), *Eucalyptus camaldulensis* Dehnh. is more toxic on fine than on coarse soils. This is probably due to the high evaporation that concentrates allelochemicals near the soil surface, and to the low infiltration that prevents allelochemicals from leaching out of the rooting zone (Noy-Meir 1973). Moreover, Rietveld et al. (1983) stated that in well-aerated and drained sandy soils, the microbial degradation of toxic compounds operated by aerobic microorganisms is accelerated. Goslee et al. (2001) reported that *Acroptilon repens* (L.) DC. became dominant faster and reached a higher proportion of the total biomass on fine- than on coarse-textured soils. El-Darier et al. (2014) found that *Medicago sativa* L. crude powder reduced the accumulation of total stem, leaf and root dry matter of *Vicia faba* L. more so in clay than in sandy soils. On the contrary, Bouhaouel et al. (2018) pointed out that *Hordeum vulgare* L. subsp. *vulgare* allelochemicals exuded by roots were more toxic in a sandy substrate. Also Shaukat et al. (2003) reported higher phytotoxic effects of *Conyza canadensis* L. shoot aqueous extracts in amendment sandy soils, followed by loamy sand and sandy loam soils, probably to the minimal adsorption on soil particles and to the low microbial and chemical degradation. According to Inderjit and Asakawa (2001), the higher inhibitory activity of plants in sandy soil is due to the nutrient deficiency characterizing these kinds of substrates, which stimulates the production and release of allelochemicals.

Results on the influence of soil texture on allelochemicals phytotoxicity contradict each other, since some authors found higher inhibitory activity in clay soils while others in sandy substrates. We consider the former hypothesis more realistic. In fact, clays, thanks to their high surface area and negative surface charges decrease water infiltration, increase cation exchange capacity and, thus, reduce allelochemicals leaching, which is the most important factor affecting their phytotoxic behaviour. Moreover, in clay soils the aeration is lower than in sandy ones, and therefore aerobic microorganisms slowly degrade allelochemicals. However, most experiments in literature were carried out in artificial substrates under laboratory conditions. The setup of long-term field experiments plays a key role for a better understanding on the effects of soil texture on allelochemicals phytotoxic potential.

Soil structure

Soil structure is the arrangement and organization of soil particles in the unit of soil particle density. Pagliai and Vignozzi (2002) defined soil structure as "the combination of different types of pores". Soil particles, particularly silicate clay, tend to bind together in aggregates. Soil aggregation generates porosity variability and regulates the ratios between solid, liquid and gaseous soil phases. Many agronomic functions depend on pore size distribution and shape (Ringrose-Voase and Bullock 1984). Rhizodeposition promotes the formation of aggregates both directly and indirectly. Directly thanks to the adsorption of rhizodeposits (e.g. ions such as Ca^{2+}, Fe^{2+}, Al^{3+}, K^{+}, as well as mucillages and several organic acids) with colloids, and indirectly since root exudates are used as food by microorganisms, which play a key role in the aggregation process. Likewise, the availability of allelochemicals in the soil is affected by soil structure (Schmidt and Ley 1999), mainly the retention process. A well-structured soil, for example, has a high cation exchange capacity, which decreases the leaching of allelochemicals operated by water. The size and shape of soil pores affect allelochemicals adsorption considerably. Indeed, Jardine et al. (1990), stated that solute concentrations in general are correlated to pore size. In particular, micropores have a greater retention capacity than meso- and macropores (Blum 2006). Soil structure can also affect the transformation process carried out by microbial communities since it regulates soil porosity, the equilibrium between soil liquid and gaseous phases, as well as soil organic matter content. The oxidation/reduction potential too, also known as redox potential, depends closely on the oxygen level in soil (Weil and Brady 2017). Furthermore, soil structure affects the release and spatial disposition of allelochemicals in soil by influencing the explorable depth by roots.

Although soil structure is a key soil characteristic, its interactions with allelochemicals have been little investigated by the scientific community. Therefore, major efforts are needed to investigate the relationship between size and distribution of pores and channels with retention and transport processes of allelochemicals in the soil.

Soil organic matter content

Soil organic matter (SOM) represents the organic fraction of the soil solid phase and comprises about 2-3% of the total weight. SOM includes a complex mixture of many substances that, for simplicity, can be classified into five main classes: 1) *edaphon* (all the living organisms), 2) "fresh" organic matter, (e.g. plant litter and residues, root and leaf exudates, remains of soil organisms), 3) "*labile*" (= easily altered) humus (SOM with a carbon/ nitrogen ratio (C/N) of 15-20, 4) humus (SOM in which the humification process completely occurred and characterised by a C/N≈10) and 5) DOM (dissolved organic matter in solution that passes through a 0.45 μm filter.)

There is a quite lot evidence on the influence of SOM on the availability of allelochemicals in soil, particularly on the adsorption-desorption process (Fageria 2012; Inderjit 2001; Vogel and Dawson 1985). SOM, thanks to its high surface area and negative surface charges, contributes to enhance the cation exchange capacity in the same way as clays. Humin, humic and fulvic acids are estimated to account from 20 to 80% of the cation exchange capacity (Wagner and Wolf 1998). On one hand, SOM can bond allelochemicals making them inactive and/or decreasing their bioavailability and phytotoxicity (Dalton et al. 1989). For example, Horrie et al. (1989) observed that *Cytisus scoparius* (L.) Link allelochemicals concentration was higher in soils with low SOM, inhibiting lettuce seedling emergence, while decreasing in soils with high SOM. In hot-semiarid soils, which generally have a low SOM (<1%), allelochemicals adsorption is low, promoting the spread and diffusion of allelopathic plants such as *Rhaponticum repens* (L.) Hidalgo and *Centaurea* *maculosa* Lam. (Grossl 2008). Kulmatiski and Beard (2006) indicated that *C. maculosa* diffusion in the field was lowered by adding activated carbon into the soil thanks to the sequestration of (±)-catechin. The activity of sorgoleone was reported to be decreased due to the high retention to SOM (Hess et al. 1992). On the other hand, allelochemicals, as well as heavy metals and cations such as Fe^{3+}, Al^{3+}, Mn^{2+} and Ca^{2+}, can be chelated by SOM in order to prevent their oxidation and increase their efficiency (Cheng 1989; Jabran et al. 2013; Marschner 1995). Moreover SOM, particularly humus, tends to give a darker color to O and A horizons, which allows increasing the solar radiation absorption and, thus, the soil temperature (Blum 2006; Fang et al. 2005). A higher soil temperature means a greater microbial activity and, consequentially, more rapid transformation processes of allelochemicals. SOM also exerts a buffer power on soil pH by avoiding excesses of acidity or alkalinity (Jansen van Rensburg et al. 2009; McCauley et al. 2009).

Soil reaction

Soil reaction represents the degree of acidity, alkalinity or neutrality of the soil aqueous extract and it is expressed as pH. Soil reaction can affect the growth of both crop plants and weeds (Joe and Allen 1980), the life of microorganisms (Rousk et al. 2009) and, chiefly, the availability of nutrients (Härdtle et al. 2004). The influence of soil pH on allelochemicals is widely reported in literature (Batish et al. 2007; Borek et al. 1994; Norouzi et al. 2015). Soil reaction is closely involved in the chemical transformation of allelochemicals into more or less toxic compounds. Borek et al. (1994) found that the enzymatic decomposition of sinigrin, a well know glucosinate produced by *Brassica* spp., operated by the enzyme myrosinase (β-thioglucoside glucohydrolase) was highly dependent on soil reaction. In particular, allylnitrile production was highest at pH 3.0, while at higher pH values (≈6.0) allyl isothiocyanate was the only sinigrin decomposition product. Also, the degradation processes of benzoxazinoids in soil are governed by the pH level. Niemeyer et al. (1982) documented an asymmetric bell-shaped curve of DIMBOA decomposition rates under a pH range, with a maximum around pH 9.0. Dayan (2006) reported a higher production of sorgoleone in *Sorghum bicolor* (L.) Moench seedlings grown in buffers as the pH decreased. Batish et al. (2007), studying the effect of *Chenopodium murale* L. residues on growth, nodulation and macromolecule content of chickpea (*Cicer arietinum* L.) and pea (*Pisum sativum* L.), pointed out that the pH of the residue-amended soil changed from neutral (6.85) to slightly alkaline (7.47) with 5-40 g residue kg^{-1} soil. The observed reduction in root, shoot length and dry matter accumulation in amended soils was accompanied by an increase in the SOM, electrical conductivity and available nitrogen. Norouzi et al. (2015) reported that the allelopathic effects of powdered below- and aboveground organs of alfalfa (*M. sativa*), sorghum (*S. bicolor*) and tobacco (*Nicotiana tabacum* L.) on several weeds increased in response to lower soil pH levels. Likewise, plants are able to modify rihizosphere pH through the exudation of allelochemicals, principally with the aim of increasing nutrient availability.

Ion exchange capacity

In soil, both mineral (e.g. clay minerals as well as Fe-, Al- and Mn-oxides) and organic (humus) colloids have negative or positive surface charges allowing the attraction with cations and anions (Lavelle and Spain 2001). The ion exchange capacity represents the measurement of the total absorbed/desorbed ions per unit mass of soil. It is highly influenced by soil texture, type of clays, SOM, soil reaction, the kind and concentration of ions and the presence of ions of opposite charge. For example, the negative charges are more abundant in alkaline or sub-alkaline soil of semiarid regions, rich in 2:1 silicate clays, while positive charges predominate acid soils rich in 1:1 clays and Al- and Fe-oxides (Weil and Brady 2017). In the former, there is a prevalence of cation adsorption, in the latter that of anion. The ion exchange capacity includes the cation exchange capacity (CEC) and the anion exchange capacity (AEC). CEC is the number of readily exchangeable cations (e.g. Na^+, H^+, K^+, NH_4^+, Ca^{2+}, Mg^{2+}, Mn^{2+}, Al^{3+}, Fe^{3+}) neutralizing negative charges on soil surfaces (Rhoades 1982). Soils can have CEC values between 6 and >40 meq 100 g^{-1}. Generally, CEC is higher with high pH levels and clay soils. AEC is the same of CEC, expressed in terms of anions (e.g. $H_2PO_4^-$, NO_3^-, Cl^-, HPO_4^{--}, SO_4^{--}, PO_4^{---}), principally operated by Fe- and Al-oxides. AEC and CEC are inversely proportional. They are very important for the adsorption/desorption balance and, thus, for the retention and transport processes by affecting allelochemicals leaching and availability. Inderjit and Bhowmik (2004), evaluating the growth of cucumber

Table 3 The role of soil allelochemicals in plant nutrition.

Nutrient soil condition	Allelochemicals role	References
Fe-deficiency	Phytosiderophores exudation from poaceae plant roots, formation of Fe^{3+}-phytosiderophores complexes, transport with YS1/YSL protein transporters across plasma membranes and improve available Fe^{2+} for plant.	Meda et al. 2007; Senoura et al. 2017; Ueno et al. 2007
Micronutrients deficiency	Exudation of mugineic acid family phytosiderophores to chelate metallic micronutrient and increase their solubility, availability and transport.	Suzuki et al. 2016; Tsai and Schmidt 2017
P-deficiency	Organic acids secretion to acidified rhizosphere, block phosphate from Ca^{2+}, Fe^{3+} and Al^{3+}, and improve available P for plant.	Dakora and Phillips 2002; Wang et al. 2014
Al^{3+} toxicity	Organic acids (e.g. citrate, malate, oxalate, etc.) and flavonoids exudation to chelate and detoxify soil aluminium.	Kochian et al. 2004; Valentinuzzi et al. 2016
High nitrification rate	Exudation of biological nitrification inhibition substances (BNIS) such as phenolics and terpenoids to inhibit the ammonium-oxiding bacteria enzymes.	Rice 1984; Subbarao et al. 2009
	Allelochemicals exudation to inhibit soil N mineralization.	Dietz et al. 2013
High N volatilization losses	Allelochemicals exudation to inhibit the denitrification process of NO_3^- into N_2O and NO.	Ma 2005
Nutrient availability and uptake by plant	Allelochemicals exudation to depolarize of cell membrane electrical potential, inhibit mitochondrial oxidative phosphorylation and electron transport, and alter membrane permeability.	Balke 1985

(*Cucumis sativus* L.) and radish (*Raphanus sativus* L.) in two soils amended with different amounts of benzoic acid, reported a higher sorption of benzoic acid in the soil with higher clay content, SOM and CEC. Belz et al. (2009) found that parthenin degradation, which is the allelochemical responsible for the invasive success of *Parthenium hysterophorus* L., is favoured in clay soils with high CEC. These two examples showed a lower allelopathic potential correlated to high CEC, probably due to the strong retention forces that prevent allelochemicals from making contact with target plants.

Mineral nutrients availability

Root exudation of allelochemicals into the rhizosphere exerts a strong influence on nutrient release, solubilization, mobilization and uptake by plants (Jabran et al. 2013; Yu and Matsui 1997) (Table 3). It is known that mineral availability not only depends on its concentration, but also on mineral form. In the soil, although a mineral is relatively abundant, it can be present in an unavailable form for the plant. This phenomenon is mainly correlated to the soil reaction. For example, P and Fe become insoluble in high pH levels in presence of calcium carbonate ($CaCO_3$), while Al^{3+} and Mn^{2+} precipitate in highly acid soils, often becoming toxic. Under nutrient deficiency, many plant species exudate allelochemicals in order to increase their availability (Jones and Darrah 1994). One of the most important tools utilized by plants to increase their nutrition efficacy is the alteration of rhizosphere pH levels. According to Bais et al. (2006), root exudates can increase or decrease soil nutrient availability through two mechanisms: phytosiderophores (PS) and organic acid secretion. Although these secondary metabolites are not allelochemicals *sensu stricto*, most authors suggest that in addition to the phytotoxic effects to the target plants, allelochemicals could induce a stimulatory effect on the donor plant in terms of resource acquisition (Rice 1984; Tharayil et al. 2009). For this reason, such PS and organic acids are considered putative allelochemicals within the so-called "allelopathy-paradigm".

Several poaceae plants, such as wheat, sorghum, oat and barley, under metallic micronutrient deficiency (mainly Zn^{2+}, Mn^{2+}, Fe^{3+} and Cu^{2+}) exudates metal-chelating amino acids called phytosiderophores (Sugiura and Nomoto 1984). The most common example of plant PS utilization refers to Fe-deficiency. PS act as chelators by forming organic complexes with Fe^{3+}, which is precipitated and insoluble in soils, and taking up the Fe^{3+}-phytosiderophore complex by Fe deficiency-inducible transporters of the YS1/YSL protein family, thus increasing its solubility and transport (Curie et al. 2001; Meda et al. 2007; Ueno et al. 2007). PS release and FePS uptake are under different genetic control among poaceae species (Römheld and Marschner 1990). Recently, Suzuki et al. (2016) reported the detection of 2'-deoxymugineic acid (DMA), a compound belonging to the mugineic acid family phytosiderophores (MAs) in the olive (*Olea europaea* L.) xylem sap, indicating for the first time the presence of PS in a non-graminaceous dicot plant. Nozoye et al. (2017) found that the biomass-energy crop *Erianthus ravennae* (L.) Beauv. secreted mugineic acid (MA) and deoxymugineic acid (DMA) under soil Fe-deficiency. Apart from PS in poaceae plants, dicots are also able to exudates phenolics compounds such as coumarins that work as metallic micronutrient chelators (mainly Al^{3+}, Fe^{3+} and Mn^{2+}) to avoid their deficiency in soil (Dakora and Phillips 2002; Tsai and Schmidt 2017).

Another important tool enabling many plants to improve mineral nutrient acquisition is organic acid secretion. This mechanism, contrary to PS secretion, is more importance for P availability than for micronutrients (Dakora and Phillips 2002). In soils, P availability depends on pH level (it is very low in alkaline soils), concentrations of anions that compete with P ions for ligand exchange reactions and concentrations of metals Ca^{2+}, Fe^{3+} and Al^{3+} that can co-precipitate with P ions (Hinsinger 2001). However, in the rhizosphere P availability is higher thanks to the localized acidification caused by CO_2 or HCO_3^- secretion and to the exudation of organic acids such as malic or citric acids (Hoffland et al. 1989). Plant roots, under P- or Fe-deficiency, release citrate and other dicarboxylates to block phosphate from Ca^{2+}, Fe^{3+}, or Al^{3+} precipitates and release available P into the soil (Bais et al. 2006; Meda et al. 2007). The most widely known example of rhizosphere acidification due to allelochemicals exudation is provided by *Lupinus albus* L., which forms proteoid roots under P-deficiency in order to exudate a large amount of citrate and increase P solubilization (Johnson et al. 1996; Wang et al. 2014). Nevertheless, organic acid secretion by plant root is helpful in response to elevated Al^{3+} concentrations in the soil solution and as protection from Al^{3+} toxicity (Kochian et al. 2004). The Al-induced organic acid secretion is species-specific, however citrate was found to be the most effective Al-detoxifying compound among different species (Kochian et al. 2004). Valentinuzzi et al. (2016) reported that *L. albus* exudes citrate and flavonoids in response to Al^{3+} toxicity. The mechanisms of Al^{3+} tolerance and P acquisition due to organic acid secretion into the rhizosphere are often linked because citrate, malate, oxalate, etc. chelate aluminium and mobilize phosphates (Chen et al. 2017).

Allelochemicals released by plants into the soil affect several phases of soil nitrogen cycle. One of the most important problems associated with intensive agriculture is related to the environmental pollution caused by nitrogen leaching in groundwater. N leaching losses are estimated in a range of 20-100 kg ha^{-1} $year^{-1}$, depending on season and rainfall regime as well as on soil texture. The nitrification process consists in transforming ammoniacal N (NH_4^+) into nitric N (NO_3^-) through two phases:

1) NH_4^+ oxidation to nitrite (NO_2^-) carried out by the bacteria genera *Nitrosomonas*, *Nitrosococcus* and *Nistrosospira* (Teske et al. 1994);
2) NO_2^- oxidation to nitrate (NO_3^-) operated by the *Nitrobacter* genus (Both et al. 1992).

The regulation of nitrification, therefore, plays a key role in improving N-use efficiency in sustainable agriculture. It has been observed how different kinds of plant allelochemicals such as phenolics or terpenoids act as biological nitrification inhibition substances (BNIS) through the inhibition of the activities of enzymes (e.g. ammonium mono-oxygenase, hydroxylamine oxidoreductase, etc.) of ammonium-oxiding bacteria (Rice 1984; Subbarao et al. 2009). Dietz et al. (2013) indicated that *Plantago lanceolata* L. allelochemicals such as aucubin, catalpol, and verbascoside, suppressed soil N mineralization due to the incorporation of leaf material into the soil. The utilization of BNIS could be an important tool in improving N-use efficiency of N fertilizers in agroecosystems by decreasing the nitrification rate (Jabran et al. 2013). Moreover, allelochemicals can reduce N volatilization losses by affecting the denitrification process of NO_3^- into N_2O, as reported by Ma (2005) for wheat allelochemicals.

In addition to the increase of nutrient solubilization, availability and use efficiency, allelochemicals generally decrease or inhibit mineral uptake by plants (Jabran et al. 2013). Several experiments demonstrated the inhibition of nutrient absorption in plants grown in association with other plants, due to the addition of specific allelochemicals in the nutrient solution (Abenavoli et al. 2010) or with plant residues and mulches leachates (Babu et al. 2013). Three main physiological processes are involved in reducing the mineral nutrient uptake (Balke 1985): 1) the depolarization of cell membrane electrical potential; 2) the inhibition of mitochondrial oxidative phosphorylation and electron transport, which means a decrease of the ATP content; 3) the alteration of membrane permeability. The inhibition of nutrient uptake is manifested through a reduction in mineral concentrations of plant tissues or a decrease of seedlings growth.

Interaction between allelochemicals and soil microorganisms

Allelopathy involves many kinds of interactions including plant-plant, plant-insect and plant-microorganism interactions, in which the allelopathic agent may be either the plant or the microorganism. Here we discuss only the plant-microorganism interactions with the plants as donors of allelochemicals. Plants affect and communicate with their microbial community, mainly at rhizoplane level, through the release of specific root exudates, including allelochemicals, which are an important C-source for microorganisms, determining an increasing of microbial biomass around the roots. Nevertheless, plants are able to modify the chemical composition of their root exudates once in contact with microorganisms (De-la-Peña et al. 2008), in order to either recruit beneficial bacteria or repress pathogenic microorganisms (Doornbos et al. 2012).

Many studies have been conducted on the *in vitro* antimicrobial activity of plant allelochemicals (Mazzaglia et al. 2018; Scavo et al. 2019a). However, the mere presence of allelochemicals in the donor plant and their antimicrobial activities in artificial medium (e.g. agar) do not demonstrate an allelopathic activity in natural conditions (Romeo 2000), because soil microorganisms consume a high quantity of organic molecules and, thus, inhibitory compounds may not accumulate at toxic levels. The microbial degradation of allelochemicals depends on the chemical nature of the considered compound, on soil texture, structure, aeration, temperature, SOM and pH, as well as on the microbial species involved. For example, among different species of *Cephalosporium* genus (e.g. *C. furcatum*, *C. khandalense*, *C. nordinii* and *C. roseum*), *C. furcatum* presents the highest degrading capacity of ferulic acid (Rice 1984). Nevertheless, the seasonal variation in the microbial population may influence the availability of allelochemicals. Abbate et al. (2005), for example, studying the bacterial communities in the rhizosphere of transgenic rolABC citrange Troyer by using phenotypical testing (BIOLOG) and 16S rDNA gene-based molecular analysis (ARDRA; DGGE), found that, on one hand, the structure of such rhizosphere communities was minimally altered and, on the other, the eubacterial DGGE (denaturing gradient-gel electrophoresis) profiles reflected marked seasonal population shifts. Gyamfi et al. (2002) reported minor differences in the DGGE patterns of the eubacterial population associated with transgenic canola due to the seasonal variation. Dunfield and Germida (2003), studying the variation in the microbial community of a transgenic canola variety, found differences during the plant growing season while remaining stable after winter, concluding that the observed changes were temporary and did not persist in the next field season. Moreover, the structure of soil bacteria communities is often related to the spatial location. In particular, bacterial abundance in the rhizosphere is reported to be higher than in root-free soil (Gamalero et al. 2004; Watt et al. 2006), and rhizosphere bacterial density follows the trend: basal region>bulk soil>apical region (Dennis et al. 2008). The amount of microbial species and their relative abundance within specific root zones is a poorly investigated aspect in the rhizosphere microbial ecology. This could be explained by the high heterogeneity of both abundance and distribution of rhizosphere microorganisms, which vary considerably in relation to the position along longitudinal root axes (Dennis et al. 2008). At the root base, in fact, bacterial communities have been observed to partially cover the rhizoplane, while in root apices they are present as clusters that occupy a relatively small proportion of the available root surface (Chin-A-Woeng et al. 1997). Nevertheless, each plant species cultivates a specific microbial rhizosphere community, both bacteria (Smalla et al. 2001) and fungi (Broeckling et al. 2008), and both in natural and agroecosystems (Broz et al. 2007), as reported by numerous studies carried out with the DGGE method.

The nature of plant-microorganism interaction can be either beneficial or deleterious. Positive interactions affected by plant allelochemicals are represented by symbiotic associations with mycorrhizae, rhizobia and plant growth-promoting bacteria (PGPB), while negative

Table 4 The positive and negative role of allelochemicals in plant-soil-microorganism interactions.

Type of interaction	Allelochemicals role	References
Positive interactions		
Legume-*Rhizobium* symbiosis	Isoflavonoids exuded by legume roots enhance the growth of rhizobial cells, their chemotaxis and the transcription of *nod* genes.	Peters et al. 1986; Sugiyama et al. 2007
Arbuscular mycorrhizal associations	Under P-deficiency, different plant species exude strigolactones into the rhizosphere to stimulate the hyphal branching of mycorrhizal fungi.	Akiyama et al. 2005; Buee et al. 2000
Plant growth-promoting bacteria (PGPB)	Under stress conditions, plant allelochemicals exuded into the rhizosphere promote and attract PGPB chemotaxis on root surface.	Somers et al. 2004
Induced systematic resistance (ISR)	Several PGPB species, thanks to a chemical communication with plant via allelochemicals exuded into the rhizosphere, induce the creation of a protective biofilm on plant roots with the aim of restricting pathogen access.	Bais et al. 2004b; Bakker et al. 2003
Plant (semi-)volatile organic compounds (VOCs) – herbivore insects	When insect herbivores attack a plant, their roots produce different kinds of VOCs as cues for natural enemies of root herbivores.	Hiltpold et al. 2015; Vaughan et al. 2013; van Dam and Bouwmeester 2016
Negative interactions		
Parasitic plant associations	Under P-deficiency, mycorrhizal fungi induce the secretion of strigolactones from donor plant roots. These compounds stimulate the colonization of host plant roots by promoting hyphal branching. Strigolactones, however, at the same time promote the parasitic plant infection by stimulating their seed germination through an increase of mitochondrial activity.	Bouwmeester et al. 2003, 2007
	Strigolactone and its derivatives, at certain concentrations, inhibit arbuscular mycorrhizal shoot branching.	Gomez-Roldan et al. 2008
Plant VOCs – herbivore insects	Certain soil insect herbivores use VOCs released by plants into the rhizosphere to localize their host.	van Dam and Bouwmeester 2016
Quorum sensing inhibitors	Plants can exude chemical compounds into the rhizosphere to interfere and take advantage of the quorum sensing capacity of bacteria.	Bais et al. 2006; Fuqua et al. 2001

ones include the associations with parasitic plants, herbivores and pathogenic microorganisms (Badri and Vivanco 2009) (Table 4).

The role of allelochemicals in positive and negative plant-microorganism interactions

Positive plant-microorganism interactions include those with beneficial effects for the plant. The most important positive interaction is through mycorrhizal symbiosis. Arbuscular mycorrhizal fungi colonize the roots of a very wide range of plants in order to increase nutrient uptake, especially that of P, and enhance the plant health. Once a chemical signal is perceived from the host plant, mycorrhizal fungi extensively invade its root tissues. P-availability is a key factor regulating the hyphal branching (Nagahashi and Douds 1999). The hyphal branching of arbuscular mycorrhizal fungi is induced and stimulated by flavonoids (Buee et al. 2000) and, mainly, strigolactones such as sorgolactone, 5-deoxy-strigol and strigol (Akiyama et al. 2005). These compounds act at very low concentrations. Sorgolactone, for example, induces branching at a concentration as low as 10^{-13} M (Besserer et al. 2006). Different plant species are reported to exude strigolactones: tomato (*Solanum lycopersicum* L.), sorghum (*S. bicolor*), maize (*Z. mays*), pearl millet (*Pennisetum glaucum* (L.) R.Br.), red clover (*Trifolium pretense* L.), cotton (*Gossypium hirsutum* L.), etc. (Awad et al. 2006; Cook et al. 1972; Rial et al. 2018).

The legume-*Rhizobium* symbiosis represents another important positive plant-microorganism interaction. This kind of association is very specific and each rhizobial strain nodulates a specific host legume. Chemical compounds responsible for this interaction are isoflavonoids such as daidzein, genistenin and luteolin (Perret et al. 2000; Peters et al. 1986; Sugiyama et al. 2007), whereas rhizobia produce lipochitooligosaccharides, called *nod*D, to communicate with the host plant (Phillips and Tsai 1992). These compounds exuded by legume roots govern the growth of rhizobial cells, their chemotaxis as well as the transcription of *nod* genes.

PGPB are the rhizosphere bacteria involved in the promotion of plant growth (Compant et al. 2005). Only 1-2% of rhizosphere bacteria promote plant growth (Antoun and Kloepper 2001). The most important bacteria genera identified as PGPR are *Bacillus* and *Pseudomonas* spp. (Podile and Kishore 2006). PGPB chemotaxis on root surface is influenced by root allelochemicals in order to attract these positive rhizoacteria when the plant is under stress condition (Somers et al. 2004). PGPB can affect plant growth both indirectly and directly. The direct promotion is through the supply of nutrients and phytohormones such as auxins, cytokinins and gibberellins. The diazotroph *Azospirillum*, for example, aside from fixing nitrogen, secretes the above mentioned phytohormones for the host plant (Steenhoudt and Vanderleyden 2000). The indirect promotion is achieved by increasing plant defensive capacity to phytopathogenic organisms (Van Loon 2007) and tolerance to abiotic stresses. Many PGPB species cause the induced systemic resistance (ISR) in different plant species (Bakker et al. 2003), namely the creation of a protective biofilm on plant roots with the aim of restricting pathogen access (Bais et al. 2004b). ISR is an important defensive mechanism for plants not only against soilborne pathogens, but also towards aboveground pathogenic microorganisms. In certain situations, above- and belowground parts of plants communicate to respond to pathogenic attack. When insect herbivores attack a plant, their roots produce (semi-)volatile organic compounds (VOCs) belonging to terpenoids or thiophenes chemical classes (Vaughan et al. 2013) as cues for natural enemies of root herbivores (van Dam and Bouwmeester 2016). Western corn rootworm (WRC) larvae induce maize roots to secrete *(E)*-β-caryophyllene in order to attract an entomopathogenic nematode after feeding on maize's leaves (Rasmann et al. 2005). Hiltpold et al. (2015) indicated that the water exudates secreted by *P. sativum* attract, at low concentrations, beneficial entomopathogenic nematodes and stimulate their activity, while inducing reversible quiescence at high concentrations.

Given the wide scientific literature on the *in vitro* antimicrobial effects of plant allelochemicals, it appears reasonable that allelochemicals exuded into the rhizosphere could play inhibitory effects against pathogenic soil microorganisms. However, the role of allelochemicals in pathogenesis of root-infecting bacteria and fungi has not been fully appreciated, probably due to the inadequate methods available for analysis (Bais et al. 2006).

The association with parasitic plants such as *Striga* spp. and *Orobanche* spp. represents the most important example of negative plant-microorganism interaction. This type of interaction is mediated by the same mechanism and chemical compounds involved in the association with arbuscular mycorrhizal fungi (Badri and Vivanco 2009). The latter process is stimulated under P-deficiency, inducing the secretion of strigolactones from donor plant roots. These compounds stimulate the colonization of host plant roots by promoting hyphal branching (Akiyama et al. 2005). At the same time however, strigolactone and its derivatives promote the parasitic plant infection by stimulating their seed germination through an increase of mitochondrial activity (Bouwmeester et al. 2007). In addition to strigolactones, also other compounds such as isoflavonoids, sorgoleone and the sesquiterpene lactones parthenolide and 3,5-dihydroxydehydrocostus-lactone have been reported to stimulate parasitic plant seed germination (Bouwmeester et al. 2003; de Luque et al. 2000). Moreover, strigolactone inhibition of arbuscular mycorrhizal shoot branching was reported (Gomez-Roldan et al. 2008).

The secretion of VOCs from plant roots can have a negative aspect. Indeed, soil herbivores seem to use VOCs to localize their host (van Dam and Bouwmeester 2016). Eilers et al. (2016) reported that *Melolontha melolontha* L. larvae use VOCs exuded by *Taraxacum* sect. *Ruderalia* Kirschner & al. to found it over a distance of several centimetres. A similar behaviour was observed on other insect herbivores such as *Diabrotica virgifera virgifera* LeConte involving the volatile compound *(E)*-β-caryophyllene (Robert et al. 2012).

Certain bacteria quench pathogen quorum-sensing capacity by degrading autoinducer signals, thereby blocking the expression of numerous virulence genes (Morello et al. 2004). Examples of this inhibition have been found to exist in nature. Many Gram-negative bacteria utilize autoinducers such as N-acyl homoserine lactones (AHLs) to coordinate gene expression in a population density-dependent way. At low population densities, cells produce a basal level of AHL via the activity of AHL synthase. As cell density increases, AHLs accumulate in the growth environment. When a critical threshold concentration is reached, the AHL molecule diffuses into the cell and binds to its cognate receptor, which in turn activates or represses the coordinated expression of particular sets of genes that enhance the ecological competence of the bacterium (Fuqua et al. 2001). It is possible that plants can exude chemical compounds into the rhizosphere to take advantage of this bacterial communication system (Bais et al. 2006).

Future perspectives

Plants release a wide variety of chemical compounds into the environment both as a defense mechanism against biotic or abiotic stress factors and as a tool to communicate with other plants, soil microorganisms and within the plant itself. The progress in the analysis methodologies and technical instrumentations in recent years has enabled acquiring new knowledge on this topic. A better understanding of allelochemicals behaviour in soil could positively be applied in agroecosystems for weed and pest control and applied to traditional agricultural practices under Integrated Pest and Weed Management Systems (IPMS, IWMS). Allelopathic mechanisms can be effectively exploited for agroecosystem control in different modes. The most important concern (1) the selection of smothering crops, their breeding and inclusion in crop rotations (Scavo et al. 2019b); (2) the use of their residues as living mulches, dead mulches or green manure; and (3) the selection of the most active allelopathic compounds and their use as bioherbicides (Scavo et al. 2018b, 2019c, d, e). Nevertheless, allelopathy could be applied to manage nutrient soil dynamics, enhance plant nutrient use efficiency and avoid heavy metal-toxicity phenomena. However, many aspects of these interactions are unknown. A major challenge for the scientific community is to investigate the influence of soil physical and chemical characteristics in field conditions over long-term experiments, particularly the role of soil texture and structure on allelochemicals phytotoxicity. The complex of plant-microorganism interactions in the rhizosphere represents the area requiring major studies to better understand the aboveground chemical communication and the physiological processes involved in both positive and negative interactions with microorganisms. Moreover, the knowledge on root exudates chemistry is currently high, with hundreds of allelochemicals identified in the last decades. Their transport processes through plasma membrane need more attention though, with the aim of clarifying the behaviour of allelopathic plants and controlling the genes involved for breeding programs. Given the complexity of the soil system and the considerable heterogeneity of soils in different environments, the challenge for researchers appear more tasking than in other scientific areas, and requires involving multidisciplinary research groups, with skills belonging to botany, agronomy, biology, chemistry, ecology and soil chemistry.

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