SOIL SICKNESS AND NEGATIVE PLANT-SOIL FEEDBACK: A REAPPRAISAL OF HYPOTHESES*

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SUMMARY

Soil sickness (SS) is the rise of negative conditions for plant vegetative and reproductive performances induced into the soil by the plant itself. In natural ecosystems, plant ecologists refer to SS as negative plant-soil feedback (NPSF). Scope of this review is to provide an updated picture of the current SS understanding by an explicit comparison between agro-ecosystems and natural plant communities. By an extensive analysis of literature we found that SS is pervasive in agro-ecosystems, occurring in 111 cultivated plants belonging to 41 taxonomic families. Concerning NPSF in natural plant communities, we found evidence of this phenomenon for a total of 411 vascular plants belonging to 72 plant families. NPSF occurs in most of the terrestrial ecosystems, including tropical and temperate forests, coastal sand dunes, old fields and grassland, deserts, as well as heathland and tundra. Three main hypotheses have been proposed to explain SS: (i) soil nutrient depletion or imbalance; (ii) build-up of soilborne pathogen and parasite populations, coupled with a shift in soil microbial community composition; (iii) release of phytotoxic and autotoxic compounds during decomposition of crop residues. Evidences from both agro-ecosystems and natural plant communities undoubtedly ruled out the nutrient deficiency as a primary causal factor. Moreover, the massive use of mineral fertilizers, especially under intensive cultivation systems, appears an incorrect strategy that only exacerbates the decline of soil quality by inducing acidification and salinization. Soilborne pathogens are often isolated from symptomatic plants and many autotoxic compounds have been identified and quantified from sick soil. However, both the pathogenic and autotoxicity hypotheses are still unable to fully explain the species-specificity, as well as the long durability of SS observed in field conditions. The recent discovery that extracellular DNA (exDNA) has self-inhibitory effects, support the autotoxicity hypothesis, nevertheless this is a totally new topic, and more solid and systematic field investigations are needed. A better understanding of the causes of SS is a necessary step to develop eco-friendly solutions to overcome this problem.

INTRODUCTION

Soil quality is one of the central factors that control yield and crop health in an agro-ecosystem (Larkin, 2015). Soil quality is defined as the disposition of the soil to function within ecosystem boundaries to sustain biological productivity, maintain environmental quality, and promote plant and animal health (Doran and Parkin, 1994). Agricultural practices like crop rotations, application of mineral fertilizers and organic amendment, tillage regime and the use of agrochemicals largely affect soil quality (Bastida *et al.*, 2008; Parr *et al.*, 1992; Wang *et al.*, 2014). Indeed, soil quality derives from the interaction among physical, chemical and microbiological factors that, in turn, control water retention capacity, soil structure and stability of aggregates, organic matter dynamics, nutrient mineralization and suppression of soilborne pathogens (Abiven *et al.*, 2009; Janvier *et al.*, 2007).

In the last decades, the spread of intensive agriculture caused a significant decrease in the primary productivity worldwide, and this has been linked to soil deterioration (Bennett *et al.*, 2012). Soil erosion, salinity, sodicity (Naidu *et al.*, 1995), soil compaction (Drewry *et al.*, 2008; Kukal *et al.*, 2008), pollution by heavy metals and xenobiotics (Shen *et al.*, 2005), decrease of soil organic carbon (Johnston, 1986), and the loss of beneficial microbiomes (Ibekwe *et al.*, 2001), are all factors that reduce soil quality. In this broad context, a special case of soil quality decline is soil sickness.

Soil sickness (SS) is defined as the rise of negative conditions for plant vegetative and reproductive performances induced into the soil by the plant itself (Bennett *et al.*, 2012; Huang *et al.*, 2013; Mazzoleni *et al.*, 2007). This phenomenon is known in agronomy as "soil fatigue"

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(Schreiner and Sullivan, 1908), or "replant disease problem" (Mai and Abawi, 1978). SS has been demonstrated to be strongly species-specific, i.e. mainly affecting individuals of the same species. In particular, sensitivity to SS declines with the increase of the phylogenetic distance among species (Zucconi, 2003). Moreover, in the last three decades, researchers recognized the importance of SS in shaping the structure of natural plant communities and for the maintenance of their species diversity (Van der Putten *et al.*, 2013). Plant ecologists refer to SS as Negative Plant-Soil Feedback (NPSF), stressing the mutual, although negative interactions between plant and soil. In ecology, NPSF is often referred as 'Soil Carry-over Effects' (Bartelt-Ryser *et al.*, 2005), 'Legacy Effects', or 'Historical Contingencies' (Kardol *et al.*, 2007). However, despite the decadal research efforts addressed to SS and NPSF topics, the underlying causative mechanisms are still poorly understood, yet highly debated.

The general scope of this review is to provide an updated picture of the current SS understanding. After an historical overview, a comprehensive analysis that includes studies on SS and NPSF has been discussed, thus providing a complete description of the mechanisms behind this complex phenomenon. Moreover, an explicit comparison between agro-ecosystems and natural plant communities has been likewise included in order to promote new approaches to the understanding of this phenomenon. The review specifically aims to:

i. Assess the occurrence of SS and NPSF in agro-ecosystem and natural plant communities;

ii. Explore the underlying causative mechanisms, by comparing the main hypotheses proposed to explain this phenomenon;

iii. Describe the methodological approaches, highlighting their strength and weakness.

HISTORICAL OVERVIEW

During the Holocene, the human beings changed their lifestyle, switching from nomadic (i.e. moving from one place to another in response to variations in the season and climate) to sedentary (i.e. living for a prolonged period in the same place) (Gupta, 2004). Thus, animal hunting and natural fruit gathering were replaced by sedentary agriculture, with a consequent impact on the interactions between plant and soil.

The first evidence of soil sickness dates back to the time of ancient Greeks and Romans. In his botanical works, Theophrastus (*ca.* 371-287 BC) reported that chickpea (*Cicer arietinum*) does not reinvigorate the soil in which dwells but "exhausts" it (Rice, 1984). In the Roman Empire, Columella (4-70 AD) in his epic poem *De Rerum Rusticarum*, pointed out that the practice of planting a single crop year after year on the same land, such as barley, leads to SS. To

overcome this problem, he suggested the use of manure or other organic materials as soil amendment, or the practice of crop rotation and fallow instead of monoculture. In the same period, Pliny the Elder (23-79 AD) wrote in his encyclopedic work "*Natural History*" that the plants grown near and below the shade of black walnut (*Juglans nigra*) are damaged by its own residues. To explain this phenomenon, later known as *allelopathy*, he hypothesized that plant roots or leaf litter could release phytotoxic substances in the surrounding environment which affect the growth of other plants (Rice, 1984).

In the following centuries agronomists, horticulturists and foresters investigated the phenomenon of SS, but only in the 20th century a significant increase of scientific knowledge was achieved thanks to the development of new analytical techniques and scientific instruments. Pioneering works in the early 1900s reported evidences that phytotoxic compounds are involved in SS (Benedict, 1941; Proebsting and Gilmore, 1941; Russell and Petherbridge, 1912; Schreiner and Shorey, 1909). The attention on phytotoxic compounds derived from root exudates, decaying plant debris and sick soil reached the peak in the 1960s and 1970s (Börner, 1960; Collina and Zucconi, 1967; Patrick, 1971). The role of phytotoxic compounds in SS was recently challenged by the discovery that extracellular DNA had species-specific inhibitory effect on plants (Mazzoleni *et al.*, 2015a).

In the 1960s, several studies demonstrated that soil sterilization reduces or avoid the rise of SS, suggesting that detrimental microbes are involved (Hoestra, 1968; Savory, 1966). Since that time, a large number of soilborne pathogens and plant parasitic nematodes have been isolated from soils or diseased plant roots. Patrick *et al.* (1963) firstly proposed the hypothesis that phytotoxic compounds, either released by roots during exudation or during decomposing of plant residues, indirectly promote the activity of soilborne pathogens by weakening the plant and, consequently, reducing its resistance.

Plant ecologists, in contrast, did not recognise the importance of SS in shaping natural ecosystem until the 1990s. SS probably was unnoticed because in natural ecosystems plants live in mixed communities, with monospecific stand occurring only under specific ecological conditions (Mazzoleni *et al.*, 2007). Because the impact of SS on conspecifics is the reduction of individual's vigour and dominance in favour of other species, in mixed communities it is difficult to observe and isolate SS effects. This can be detected only in long-term field studies that monitor population dynamics at an individual scale. In this regard, Watt (1947) for the first time described species alternation in time and space in heathland dominated by the shrub *Calluna vulgaris*. Here, this species was unable to regenerate over the same physical place, driving to a sort of a natural rotation with other species. Few years later, in USA and Australia it was noticed that after clear-cutting several tree species, including *Sequoia sempervirens* (Florence, 1965),

Eucalyptus pilularis (Florence and Crocker, 1962), and *Grevillea robusta* (Webb *et al.*, 1967), were unable to regenerate in stand previously occupied by conspecifics. The authors proposed that regeneration failure was caused by the accumulation of unidentified, autotoxic factors (Webb *et al.*, 1967). However, these scattered observations were considered by ecologists as a "noise" and the SS process was ignored as important in ecological frameworks. In the 1990s, thanks to some key studies, SS gained consideration to fully understand natural plant communities. Van der Putten *et al.* (1993) demonstrated that soilborne pathogens and plant-parasitic nematodes are responsible for the successional replacement of Marram grass (*Ammophila arenaria*) in sand dune communities. Bever (1994) reported that herbaceous species from old-field suffer when cultivated in soil previously used by conspecific, and coined the term "negative plant-soil feedback" (NPSF). Later, the same author proposed a conceptual framework where NPSF process was mechanistically linked to species coexistence, successional dynamics and the maintenance of plant diversity (Bever *et al.*, 1997). Since then, the research interest on NPSF rose exponentially driving to a burst of publications on this topic (Fig. 1).

OCCURRENCE OF SOIL SICKNESS AND NEGATIVE PLANT-SOIL FEEDBACK

SS is pervasive in agro-ecosystems, and Table 1 provides an updated list of cultivated plants susceptible to SS. We found scientific evidence for the occurrences of SS in 111 species, belonging to 41 taxonomic families. In addition, SS has been observed by farmers in many other cultivated plants, but these data are mostly unpublished. SS is a severe problem for field crop cultivations, in horticulture and floriculture as well as for orchard trees (Table 1). In fact, it is very difficult to find any herbaceous plantations or orchards that do not experience the consequences of SS when cultivated in monoculture and monosuccession. As Table 1 highlights, major crops and trees are affected by SS including wheat, corn, rice, sugarcane, alfalfa, soybean, grape, and, among trees, peach, apple, olive, citrus, tea and coffee. The length of plant life cycle correlates with the susceptibility to SS, with short-living plants (annuals) being the most sensitive, followed by perennial forb, tree, vine, shrub and perennial grass (Fig. 2b). Interestingly, in 21.6% of the cases, SS was found for plants belonging to the Poaceae and Fabaceae families (Fig. 2a). Members of the Fabaceae are especially sensitive to SS, with many species severely affected (e.g. alfalfa, cicer, clover, soybean, bean, etc.; Table 1). SS has been also reported for other plant families, including Apiaceae, Asteraceae, Brassicaceae, Cucurbitaceae, Liliaceae, Rosaceae and Solanaceae (Table 1). Another evidence that SS is a global phenomenon is that its cases have been observed and described for agroecosystems in various regions of the world, characterized
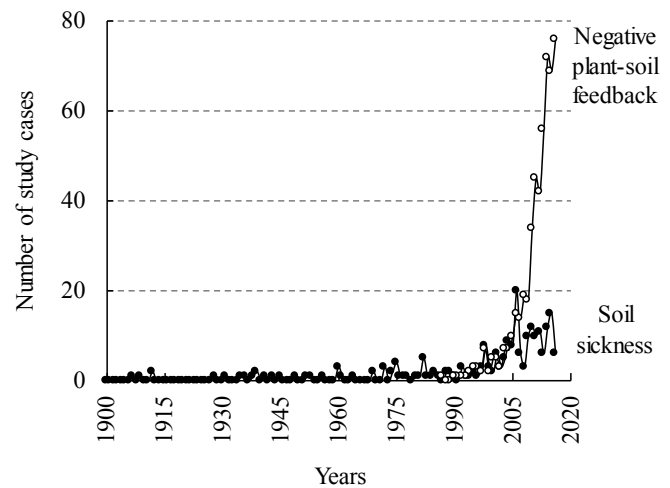

Fig. 1. Number of papers published in the last 117 years on soil sickness in agro-ecosystems, and negative plant-soil feedback in natural plant communities (data from Scopus accessed on March, 2017).
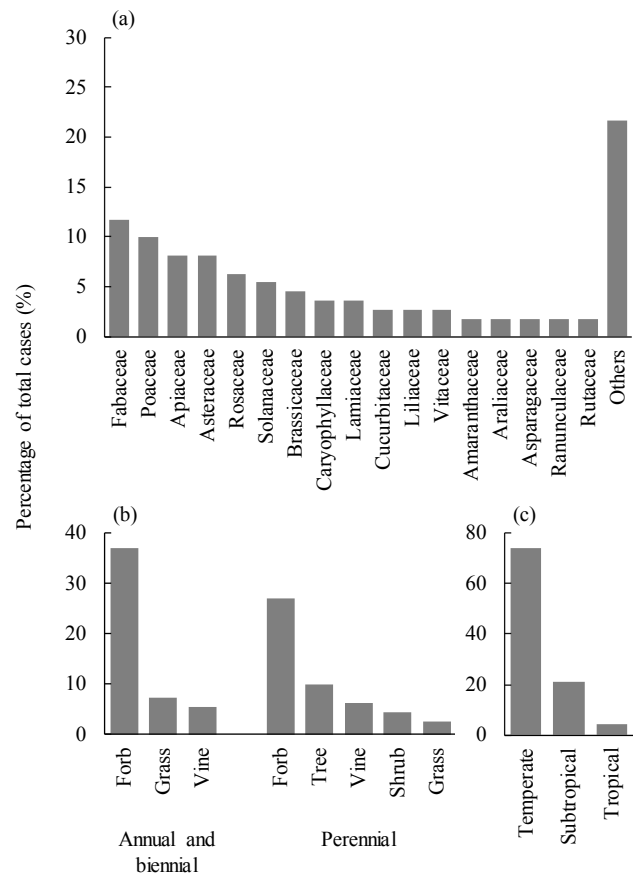

Fig. 2. Relative occurrence of soil sickness cases (complete list reported in Table 1) for plant families (a), life forms (b) and climate zones (c).

by different climatic conditions and soil types (Fig. 2c). Examples of less common, yet recurring, SS cases in tropical and sub-tropical environments include *Coffea arabica*, *Musa* sp., *Oryza sativa* and *Saccharum officinarum* (Table 1).
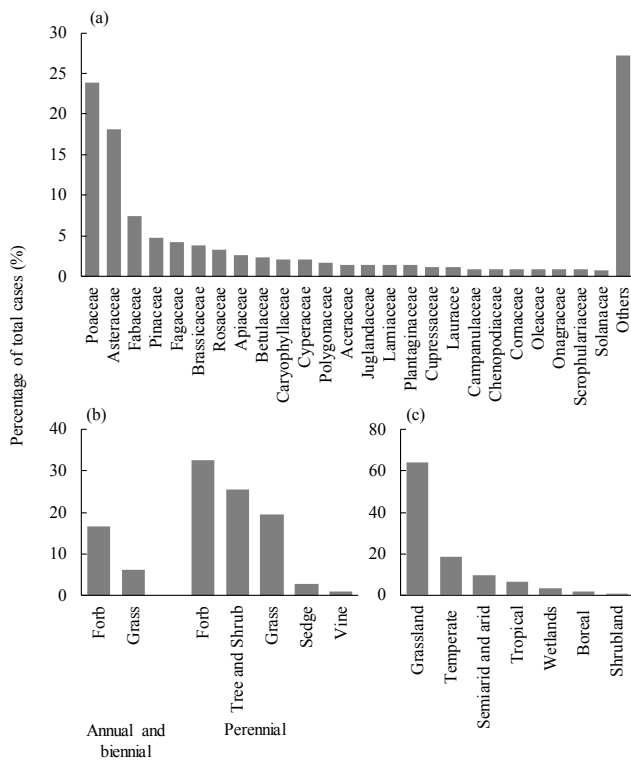
Fig. 3. Relative occurrence of negative plant-soil feedback cases (complete list reported in Supplementary Table S1 for plant families (a), life forms (b), and climate zones (c).

Concerning NPSF in natural plant communities, from an extensive review of the literature we found evidence of this phenomenon for a total of 411 vascular plants belonging to 72 plant families (Supplementary Table S1; Fig. 3a). NPSF has been reported in most of the terrestrial ecosystems, including tropical and temperate forests (Bennett *et al.*, 2017; Mangan *et al.*, 2010), coastal sand dunes (Oremus and Otten, 1981), old fields and grassland (Bezemer *et al.*, 2006; Olff *et al.*, 2000), deserts (Rutten *et al.*, 2016), salt marshes (Castellanos *et al.*, 1994), as well as heathland and tundra (Bonanomi *et al.*, 2005a). In our data set, NPSF occurrences were higher in temperate grassland followed by temperate forest, arid ecosystems and tropical forest (Fig. 3c). Few cases have been reported from wetlands and shrubland (Fig. 3c). These data, however, are partially influenced by the American and North European works, as they carried out most of the studies reported so far. Moreover, grasslands have been often selected as model system because plants are small, short-lived and easy to manipulate compared to shrubland and forest ecosystems. Therefore, the lower occurrence of NPSF studies in ecosystems such as the Mediterranean shrublands or the boreal forest, does not necessarily indicate that these ecosystems are less subjected to the NPSF.

NPSF affects plants of different life forms including annual (Kardol *et al.*, 2007), perennial herbs and sedge (Jordan *et al.*, 2008), shrubs (Sigüenza *et al.*, 2006), and trees (Reinhart *et al.*, 2005). However, annual plants occur more

frequently than shrubs and trees, with some cases reported for vine and sedge (Fig. 3b; Supplementary Table S1). This observation is consistent with the meta-analysis by Kulmatiski *et al.* (2008), reporting that annual and biennial plants experience more intense NPSF than perennials, and particularly woody species. The higher susceptibility of annual species toward negative feedback can be explained with the absence of storage organs (e.g. rhizomes, tubers, bulbs, twigs), which make these plants less capable of facing environmental stresses (Pastor and Durkee Walker, 2006). By the taxonomic point of view, Poaceae, Asteraceae and Fabaceae are the families with the highest number of reported cases of NPSF (Supplementary Table S1). In natural ecosystems, nitrogen-fixing Fabaceae are a key step in successions where they play an important role in the accumulation of nitrogen stocks into the soil (Bellingham *et al.*, 2001; Walker *et al.*, 2003). However, these species, after a peak of dominance that lasts few years, rapidly disappear (Chapin *et al.*, 1994; Stinca *et al.*, 2015). This can be explained by NPSF that exacerbates the competitive interaction with later successional species. For example, Teste *et al.* (2017) reported that nitrogen-fixing species from Mediterranean shrublands of Southwest Australia suffer a stronger negative feedback compared to other woody species in the same environment. The high susceptibility of Fabaceae to NPSF is consistent with evidences from agro-ecosystems, where plants belonging to this family suffer intense and long-lasting SS (Table 1).

In agro-ecosystems, where plants are cultivated in even-aged and pure monoculture stands, SS is easily detected as poor seed emergence or poorly developed patches (Fig. 4a). For perennial plants and orchard trees, a common but generic symptom of SS is the stunted growth and reduction of yield. In natural ecosystems, instead, plants generally grow in mixed communities and, therefore, the impact of NPSF depends on the growth form. For instance, a number of empirical and modelling studies demonstrated that the acquisition of different propagation modes provide a way to escape NPSF that develops in the "home" soil (Bever, 1994). Thus, different spatial patterns emerge from the interaction between NPSF and growth forms with different life spans, as it occurs for annual herbs and trees (Vincenot *et al.*, 2017). For trees and shrubs NPSF is spatially localized under their canopy, and so these plants escape the detrimental effects of "home soil" via seed dispersal (Packer and Clay, 2000). In other words, plants with a single rooting point, exhibit a distance-dependent inhibition, a sort of seedling repellence from their mother plant (Fig. 4b). Seedling establishment is reduced or even completely absent under the canopy of the mother plant due to NPSF despite the high abundance of seeds, thus producing the so-called Janzen-Connell recruitment distribution (Fig. 4b; Janzen, 1970). This distribution has been described for shrubs (Bonanomi *et al.*, 2008; Lambers and Clark, 2003) and, most commonly, for trees in both temperate and tropical forests (Augspurger, 1984; Mangan *et*

Table 1. List of experimental studies reporting soil sickness in agro-ecosystems. Taxonomic family, life form and life cycle, experimental conditions and the putative mechanism/s causing soil sickness as proposed by the authors are reported. Studies are ordered alphabetically by plant name.

N°	Species	Family	Life form	Life cycle	Ecosystem	Experimental condition	Putative mechanisms	References
1	*Agrostemma githago*	Caryophyllaceae	Forb	Annual	Temperate	Greenhouse – Hydroponic and pot	Autotoxicity	Asao *et al.*, 2007
2	*Ammi majus*	Apiaceae	Forb	Annual	Temperate	Greenhouse – Hydroponic and pot	Autotoxicity	Asao *et al.*, 2007
3	*Angelica sinensis*	Apiaceae	Forb	Perennial	Temperate	Field – Pot	Autotoxicity and soilborne pathogens	Zhang *et al.*, 2015
					Temperate	Growth chamber – *In vitro* and pot	Autotoxicity	Zhang *et al.*, 2010a
4	*Antirrhinum majus*	Plantaginaceae	Forb	Perennial	Temperate	Greenhouse – Hydroponic and pot	Autotoxicity	Asao *et al.*, 2007
5	*Apium graveolens*	Apiaceae	Forb	Perennial	Temperate	Growth chamber – *In vitro*	Autotoxicity	Asao *et al.*, 2004
6	*Aquilegia flabellata*	Ranunculaceae	Forb	Perennial	Temperate	Greenhouse – Hydroponic and pot	Autotoxicity	Asao *et al.*, 2007
7	*Arachis hypogaea*	Fabaceae	Forb	Annual	Temperate	Growth chamber – *In vitro*	Autotoxicity	Huang *et al.*, 2013
					Temperate	Growth chamber – Pot	Microbial shift and soilborne pathogens	Li *et al.*, 2014a
					Temperate		Autotoxicity and soilborne pathogens	Li *et al.*, 2010a
8	*Asparagus officinalis*	Asparagaceae	Forb	Perennial	Temperate	Growth chamber – *In vitro* / Greenhouse – Pot	Autotoxicity	Miller *et al.*, 1991
					Subtropical	Field – Plot	Soilborne pathogens	Nigh, 1990
					Temperate	Growth chamber – *In vitro* / Greenhouse – Pot	Autotoxicity and soilborne pathogens	Hartung and Stephens, 1983
9	*Avena sativa*	Poaceae	Grass	Annual	Temperate	Growth chamber – Pot	Autotoxicity	Nielsen *et al.*, 1960
10	*Beta vulgaris*	Chenopodiaceae	Forb	Biennial	Temperate	Field – Pot	Soilborne pathogens and nematodes	Crump and Kerry, 1987
11	*Brassica campestris*	Brassicaceae	Forb	Biennial	Temperate	Growth chamber – *In vitro*	Autotoxicity	Asao *et al.*, 2004
12	*Brassica napus*	Brassicaceae	Forb	Annual	Temperate	Greenhouse – Pot / Field – Plot	Microbial shift and soilborne pathogens	Hilton *et al.*, 2013
13	*Brassica oleracea*	Brassicaceae	Forb	Biennial	Temperate	Growth chamber – *In vitro*	Autotoxicity	Asao *et al.*, 2004
14	*Brassica rapa*	Brassicaceae	Forb	Biennial	Temperate	Greenhouse – Hydroponic and pot	Autotoxicity	Asao *et al.*, 2007
15	*Calendula officinalis*	Asteraceae	Forb	Perennial	Temperate	Greenhouse – Hydroponic and pot	Autotoxicity	Asao *et al.*, 2007
16	*Callistephus chinensis*	Asteraceae	Forb	Annual	Temperate	Greenhouse – Hydroponic and pot	Autotoxicity	Asao *et al.*, 2007
17	*Camellia sinensis*	Theaceae	Shrub	Perennial	Tropical	Growth chamber – *In vitro*	Autotoxicity	Owuor, 2016
18	*Capsicum annuum*	Solanaceae	Forb	Perennial	Temperate	Greenhouse – Plot	Soilborne pathogens	Martínez *et al.*, 2011
19	*Carthamus tinctorius*	Asteraceae	Forb	Annual	Temperate	Greenhouse – Hydroponic and pot	Autotoxicity	Asao *et al.*, 2007
20	*Carum copticum*	Apiaceae	Forb	Annual	Subtropical	Growth chamber – *In vitro*	Autotoxicity	Chaturvedi and Muralia, 1975
21	*Celosia argentea*	Amaranthaceae	Forb	Annual	Temperate	Greenhouse – Hydroponic and pot	Autotoxicity	Asao *et al.*, 2007
22	*Chrysanthemum coronarium*	Asteraceae	Forb	Annual	Temperate	Growth chamber – *In vitro*	Autotoxicity	Asao *et al.*, 2004
23	*Chrysanthemum morifolium*	Asteraceae	Forb	Annual	Temperate		Autotoxicity	Zhou *et al.*, 2009
24	*Cicer arietinum*	Fabaceae	Forb	Annual			Not reported	Rice, 1984
25	*Citrullus lanatus*	Cucurbitaceae	Annual vine	Annual	Temperate	Growth chamber – *In vitro* / Greenhouse – Hydroponic	Autotoxicity	Hao *et al.*, 2007
					Temperate	Growth chamber – *In vitro* and pot	Autotoxicity	Yu *et al.*, 2000
26	*Citrus aurantium*	Rutaceae	Tree	Perennial	Subtropical	Growth chamber – *In vitro* / Greenhouse – Pot	Autotoxicity and soilborne pathogens	Hassan *et al.*, 1989
27	*Citrus jambhiri*	Rutaceae	Tree	Perennial	Subtropical	Greenhouse – Hydroponic	Autotoxicity	Burger and Small, 1983
28	*Coffea arabica*	Rubiaceae	Shrub	Perennial	Tropical	Growth chamber – *In vitro*	Autotoxicity	Waller *et al.*, 1990
					Tropical		Nematodes	Serracin *et al.*, 1999
29	*Colocasia esculenta*	Araceae	Forb	Perennial	Temperate	Greenhouse – Hydroponic	Autotoxicity	Asao *et al.*, 2003
30	*Coriandrum sativum*	Apiaceae	Forb	Annual	Subtropical	Growth chamber – *In vitro*	Autotoxicity	Chaturvedi and Muralia, 1975
31	*Crocus sativus*	Iridaceae	Forb	Perennial	Temperate	Field – Plot	Not reported	Gresta *et al.*, 2016
32	*Cucumis melo*	Cucurbitaceae	Annual vine	Annual	Temperate	Growth chamber – *In vitro* and pot	Autotoxicity	Yu *et al.*, 2000
					Temperate	Growth chamber – *In vitro* and pot / Field – Plot	Autotoxicity and soilborne pathogens	Yang *et al.*, 2014

Table 1 (continued). List of experimental studies reporting soil sickness in agro-ecosystems. Taxonomic family, life form and life cycle, experimental conditions and the putative mechanism/s causing soil sickness as proposed by the authors are reported. Studies are ordered alphabetically by plant name.

N°	Species	Family	Life form	Life cycle	Ecosystem	Experimental condition	Putative mechanisms	References
33	*Cucumis sativus*	Cucurbitaceae	Annual vine	Annual	Temperate	Greenhouse – Hydroponic	Autotoxicity	Yu and Matsui, 1994
					Temperate	Greenhouse – Pot	Soilborne pathogens	Zhou and Wu, 2012
					Temperate	Greenhouse – Hydroponic	Autotoxicity and soilborne pathogens	Ye *et al.*, 2004
					Temperate	Greenhouse – Pot	Microbial shift	Zhou *et al.*, 2014
34	*Cuminum cyminum*	Apiaceae	Forb	Annual	Subtropical	Growth chamber – *In vitro*	Autotoxicity	Chaturvedi and Muralia, 1975
35	*Daucus carota*	Apiaceae	Forb	Biennial	Subtropical	Growth chamber – *In vitro*	Autotoxicity	Chaturvedi and Muralia, 1975
36	*Delphinium ajacis*	Ranunculaceae	Forb	Annual	Temperate	Greenhouse – Hydroponic and pot	Autotoxicity	Asao *et al.*, 2007
37	*Dianthus caryophyllus*	Caryophyllaceae	Forb	Perennial	Temperate	Greenhouse – Hydroponic and pot	Autotoxicity	Asao *et al.*, 2007
38	*Eustoma grandiflorum*	Gentianaceae	Forb	Perennial	Temperate	Greenhouse – Hydroponic and pot	Autotoxicity	Asao *et al.*, 2007
39	*Ficus carica*	Moraceae	Tree	Perennial	Temperate	Greenhouse – Pot	Soilborne pathogens	Hosomi and Uchiyama, 1998
40	*Foeniculum vulgare*	Apiaceae	Forb	Annual	Subtropical	Growth chamber – *In vitro*	Autotoxicity	Chaturvedi and Muralia, 1975
41	*Fragaria × ananassa*	Rosaceae	Forb	Perennial	Temperate	Greenhouse – Hydroponic	Autotoxicity	Asaduzzaman *et al.*, 2012
42	*Glycine max*	Fabaceae	Forb	Annual	Temperate		Autotoxicity	Han *et al.*, 2002
					Temperate	Field – Plot	Microbial shift	Li *et al.*, 2010b
43	*Godetia amoena*	Onagraceae	Forb	Annual	Temperate	Greenhouse – Hydroponic and pot	Autotoxicity	Asao *et al.*, 2007
44	*Gomphrena globosa*	Amaranthaceae	Forb	Annual	Temperate	Greenhouse – Hydroponic and pot	Autotoxicity	Asao *et al.*, 2007
45	*Gossypium* spp.	Malvaceae	Shrub	Perennial	Temperate		Autotoxicity	Jiang *et al.*, 2013
					Temperate	Growth chamber – *In vitro* / Greenhouse – Pot	Microbial shift and soilborne pathogens	Li *et al.*, 2015
46	*Gypsophila elegans*	Caryophyllaceae	Forb	Annual	Temperate	Greenhouse – Hydroponic and pot	Autotoxicity	Asao *et al.*, 2007
47	*Helianthus annuus*	Asteraceae	Forb	Annual	Subtropical	Greenhouse – Pot	Autotoxicity	Wilson and Rice, 1968
48	*Hordeum vulgare*	Poaceae	Grass	Annual	Subtropical	Growth chamber – *In vitro*	Autotoxicity	Ben-Hammouda *et al.*, 2002
					Temperate	Greenhouse – Pot	Microbial shift	Alström, 1992
					Temperate	Field – Plot	Soilborne pathogens	Delogu *et al.*, 2003
49	*Humulus lupulus*	Cannabaceaae	Perennial vine	Perennial	Temperate	Greenhouse – Pot	Autotoxicity	Zhang *et al.*, 2011
50	*Ipomea batatas*	Convolvulaceae	Perennial vine	Perennial	Tropical	Field – Plot	Nematodes	Hartemink *et al.*, 2000
51	*Juglans nigra*	Juglandaceae	Tree	Perennial			Soilborne pathogens	Grente, 1963
52	*Lactuca sativa*	Asteraceae	Forb	Annual	Temperate	Growth chamber – *In vitro*	Autotoxicity	Asao *et al.*, 2004
53	*Lathyrus odoratus*	Fabaceae	Annual vine	Annual	Temperate	Greenhouse – Hydroponic and pot	Autotoxicity	Asao *et al.*, 2007
54	*Lilium davidii*	Liliaceae	Forb	Perennial	Temperate	Growth chamber – *In vitro*	Autotoxicity	Wu *et al.*, 2015
55	*Lilium × elegans*	Liliaceae	Forb	Perennial	Temperate	Greenhouse – Hydroponic and pot	Autotoxicity	Asao *et al.*, 2007
56	*Lilium × formolongi*	Liliaceae	Forb	Perennial	Temperate	Greenhouse – Hydroponic and pot	Autotoxicity	Asao *et al.*, 2007
57	*Limonium sinuatum*	Plumbaginaceae	Forb	Perennial	Temperate	Greenhouse – Hydroponic and pot	Autotoxicity	Asao *et al.*, 2007
58	*Linum usitatissimum*	Linaceae	Forb	Annual			Autotoxicity	Börner, 1960
59	*Lolium rigidum*	Poaceae	Grass	Annual	Temperate	Growth chamber – *In vitro* / Greenhouse – Pot	Autotoxicity	Canals *et al.*, 2005
60	*Malus domestica*	Rosaceae	Tree	Perennial	Subtropical	Field – Plot	Microbial shift	Rumberger *et al.*, 2007
					Temperate	Greenhouse – Pot	Soilborne pathogens and nematodes	Utkhede *et al.*, 1992
					Subtropical	Field – Plot	Soilborne pathogens	Mazzola, 1998
61	*Malus* spp.	Rosaceae	Tree	Perennial			Autotoxicity	Börner, 1959 in Singh *et al.*, 1999
62	*Manihot esculenta*	Euphorbiaceae	Forb	Perennial	Subtropical	Field – Plot	Nutrient imbalance or depletion	Howeler and Cadavid, 1990
63	*Matthiola incana*	Brassicaceae	Forb	Annual	Temperate	Greenhouse – Hydroponic and pot	Autotoxicity	Asao *et al.*, 2007

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64	*Medicago sativa*	Fabaceae	Forb	Perennial	Temperate	Growth chamber – *In vitro*	Autotoxicity	Chon *et al.*, 2002
					Temperate	Growth chamber – *In vitro*	Autotoxicity and soilborne pathogens	Bonanomi *et al.*, 2011
65	*Musa* sp.	Musaceae	Forb	Perennial	Tropical	Field – Plot	Nutrient imbalance or depletion	Bekunda, 1999
66	*Narcissus tazetta*	Amaryllidaceae	Forb	Perennial	Temperate	Greenhouse – Hydroponic and pot	Autotoxicity	Asao *et al.*, 2007
67	*Nicotiana tabacum*	Solanaceae	Forb	Annual	Subtropical	Growth chamber – *In vitro*	Autotoxicity	Ren *et al.*, 2015
68	*Ocimum basilicum*	Lamiaceae	Forb	Annual	Temperate	Greenhouse – Plot	Not reported	Minuto *et al.*, 2002
69	*Olea europaea*	Oleaceae	Tree	Perennial	Temperate	Greenhouse – Pot	Autotoxicity	Endeshaw *et al.*, 2015
70	*Oryza sativa*	Poaceae	Grass	Annual	Subtropical	Field – Plot	Nutrient imbalance or depletion	Olk *et al.*, 2009
					Subtropical	Growth chamber – *In vitro* / Field – Plot	Autotoxicity	Chou and Lin, 1976
					Subtropical	Greenhouse – Pot	Nematodes and nutrient imbalance or depletion	Kreye *et al.*, 2009
					Subtropical	Greenhouse – Pot	Nutrient imbalance or depletion	Nie *et al.*, 2009
71	*Panax notoginseng*	Araliaceae	Forb	Perennial	Subtropical	Growth chamber – *In vitro* / Greenhouse – Hydroponic	Autotoxicity	Yang *et al.*, 2015
72	*Panax quinquefolium*	Araliaceae	Forb	Perennial	Temperate	Growth chamber – In vitro	Autotoxicity	He *et al.*, 2009
73	*Papaver rhoeas*	Papaveraceae	Forb	Annual	Temperate	Greenhouse – Hydroponic and pot	Autotoxicity	Asao *et al.*, 2007
74	*Parthenium argentatum*	Asteraceae	Shrub	Perennial	Subtropical	Greenhouse – Pot	Autotoxicity	Bonner and Galston, 1944
75	*Petroselinum crispum*	Apiaceae	Forb	Biennial	Temperate	Growth chamber – *In vitro*	Autotoxicity	Asao *et al.*, 2004
76	*Phaseolus vulgaris*	Fabaceae	Forb	Annual	Temperate	Growth chamber – *In vitro* / Greenhouse – Hydroponic	Autotoxicity	Asaduzzaman and Asao, 2012
77	*Phleum pratense*	Poaceae	Grass	Perennial	Temperate	Growth chamber – Pot	Autotoxicity	Nielsen *et al.*, 1960
78	*Physalis alkekengi*	Solanaceae	Forb	Perennial	Temperate	Greenhouse – Hydroponic and pot	Autotoxicity	Asao *et al.*, 2007
79	*Piper nigrum*	Piperaceae	Perennial vine	Perennial	Subtropical	Greenhouse – Pot	Microbial shift	Xiong *et al.*, 2015
80	*Pisum sativum*	Fabaceae	Annual vine	Annual	Temperate	Growth chamber – *In vitro* / Greenhouse – Hydroponic	Autotoxicity	Asaduzzaman and Asao, 2012
					Temperate	Greenhouse – Pot	Soilborne pathogens	Bodker and Leroul, 1993
					Temperate	Field – Plot	Microbial shift	Nayyar *et al.*, 2009
81	*Platycodon grandiflorum*	Campanulaceae	Forb	Perennial	Temperate	Greenhouse – Hydroponic and pot	Autotoxicity	Asao *et al.*, 2007
82	*Pogostemon cablin*	Lamiaceae	Forb	Annual	Subtropical	Greenhouse – Hydroponic / Field – Pot	Autotoxicity	Xu *et al.*, 2015
83	*Prunus avium*	Rosaceae	Tree	Perennial	Temperate	Greenhouse – Pot	Soilborne pathogens	Hoestra, 1965
84	*Prunus dulcis*	Rosaceae	Tree	Perennial	Subtropical	Greenhouse – Pot	Soilborne pathogens	Fatemi, 1980
85	*Prunus persica*	Rosaceae	Tree	Perennial	Temperate	Greenhouse – Pot	Autotoxicity	Tagliavini and Marangoni, 1992
					Subtropical	Greenhouse – Pot	Soilborne pathogens	Yang *et al.*, 2012
					Temperate	Growth chamber – Pot	Microbial shift	Benizri *et al.*, 2005
86	*Prunus serotina*	Rosaceae	Tree	Perennial	Temperate	Field – Pot	Soilborne pathogens	Reinhart *et al.*, 2005
87	*Pseudostellaria heterophylla*	Caryophyllaceae	Forb	Perennial	Subtropical	Field – Plot	Microbial shift	Wu *et al.*, 2016
88	*Rehmannia glutinosa*	Orobanchaceae	Forb	Perennial	Temperate	Growth chamber – *In vitro*	Soilborne pathogens	Bu *et al.*, 2014
					Temperate	Growth chamber – *In vitro*	Autotoxicity	Li *et al.*, 2012
89	*Rudbeckia hirta*	Asteraceae	Forb	Biennial	Temperate	Greenhouse – Hydroponic and pot	Autotoxicity	Asao *et al.*, 2007
90	*Saccharum officinarum*	Poaceae	Grass	Perennial	Tropical	Greenhouse – Pot / Field – Plot	Soilborne pathogens and nematodes	Pankhurst *et al.*, 2005
91	*Saccharum* spp.	Poaceae	Grass	Perennial	Subtropical	Greenhouse – Pot	Autotoxicity	Viator *et al.*, 2006
92	*Salvia miltiorrhiza*	Lamiaceae	Shrub	Perennial	Subtropical	Field – Plot	Microbial shift	Tang *et al.*, 2015
93	*Scutellaria baicalensis*	Lamiaceae	Forb	Perennial	Temperate	Growth chamber – *In vitro* and pot	Autotoxicity and soilborne pathogens	Zhang *et al.*, 2010b
94	*Setaria italica*	Poaceae	Grass	Annual			Autotoxicity	Lee *et al.*, 1967 in Singh *et al.*, 1999
95	*Solanum lycopersicum*	Solanaceae	Forb	Annual	Temperate	Greenhouse – Plot	Microbial shift	Li *et al.*, 2014b
					Temperate	Growth chamber – *In vitro* and hydroponic	Autotoxicity	Yu and Matsui, 1993

Table 1 (continued). List of experimental studies reporting soil sickness in agro-ecosystems. Taxonomic family, life form and life cycle, experimental conditions and the putative mechanism/s causing soil sickness as proposed by the authors are reported. Studies are ordered alphabetically by plant name.

N°	Species	Family	Life form	Life cycle	Ecosystem	Experimental condition	Putative mechanisms	References
					Temperate	Growth chamber – *In vitro* / Greenhouse – Pot	Autotoxicity and soilborne pathogens	Bonanomi *et al.*, 2007
96	*Solanum melongena*	Solanaceae	Forb	Annual	Temperate	Growth chamber – *In vitro*	Autotoxicity	Wang and Wang, 2005
97	*Solanum tuberosum*	Solanaceae	Forb	Perennial	Temperate	Field – Plot	Microbial shift	Larkin and Honeycutt, 2006
98	*Sorghum bicolor*	Poaceae	Grass	Annual			Not reported	Rice, 1984
99	*Trifolium alexandrinum*	Fabaceae	Forb	Annual	Temperate	Field – Pot	Nutrient imbalance or depletion	Katznelson, 1972
100	*Trifolium pratense*	Fabaceae	Forb	Perennial	Temperate	Growth chamber – *In vitro* and pot	Autotoxicity	Chang *et al.*, 1969
101	*Trifolium resupinatum*	Fabaceae	Forb	Annual	Temperate	Field – Pot	Nutrient imbalance or depletion	Katznelson, 1972
102	*Triteleia laxa*	Asparagaceae	Forb	Perennial	Temperate	Greenhouse – Hydroponic and pot	Autotoxicity	Asao *et al.*, 2007
103	*Triticum aestivum*	Poaceae	Grass	Annual	Temperate	Growth chamber – *In vitro*	Autotoxicity	Wu *et al.*, 2007
104	*Vanilla planifolia*	Orchidaceae	Perennial vine	Perennial	Subtropical	Greenhouse – Pot	Microbial shift and soilborne pathogens	Xiong *et al.*, 2014
105	*Vicia faba*	Fabaceae	Forb	Annual	Temperate	Growth chamber – *In vitro* / Greenhouse – Hydroponic	Autotoxicity	Asaduzzaman and Asao, 2012
106	*Vigna radiata*	Fabaceae	Annual vine	Annual			Autotoxicity	Tang and Zhang 1986 in Singh *et al.*, 1999
107	*Vigna unguiculata*	Fabaceae	Forb	Annual	Temperate	Growth chamber – *In vitro*	Autotoxicity	Huang *et al.*, 2010
108	*Vitis riparia*	Vitaceae	Perennial vine	Perennial			Autotoxicity	Brinker and Creasy 1988 in Singh *et al.*, 1999
109	*Vitis rupestris*	Vitaceae	Perennial vine	Perennial			Autotoxicity	Brinker and Creasy 1988 in Singh *et al.*, 1999
110	*Vitis vinifera*	Vitaceae	Perennial vine	Perennial	Temperate	Greenhouse – Pot	Soilborne pathogens and nematodes	Westphal *et al.*, 2002
111	*Zea mays*	Poaceae	Grass	Annual	Temperate	Growth chamber – *In vitro*	Autotoxicity	Martin *et al.*, 1990
					Temperate	Field – Plot	Nutrient imbalance or depletion	Gentry *et al.*, 2013
					Temperate	Field – Plot	Soilborne pathogens	Summer *et al.*, 1990

al., 2010; Packer and Clay, 2000). At a community scale, the Janzen-Connell recruitment distribution drives to the alternation in time and space of tree species in forest ecosystems (Fox, 1977; Whittaker and Levin, 1977), thus contributing to the maintenance of species diversity (Mangan *et al.*, 2010).

Perennial herbaceous plants capable of clonal propagation can actively move away from the hostile "home soil" by selective proliferation of new ramets in suitable soil patches (Blundell and Peart, 2004; Olff *et al.*, 2000). This type of clonal spreading is characterized by wave-like patterns, and by the production of regularly shaped rings. In a recent review, Bonanomi *et al.* (2014) reported that herbs, shrubs and trees capable of clonal propagation, during their ontogenetic cycles, produce clones with a "ring" shape that progressively degenerate in the older inner area, thus producing a "dieback" central zone (Fig. 4c). This vegetation pattern has been also called fairy rings, rings, hollow crowns, central dieback, and monk's tonsure-like gaps (Adachi *et al.*, 1996; Lewis *et al.*, 2001; Watt, 1947). Interestingly, in many cases the inner area is colonized by multiple species, different from the dominant plant that

generated the ring, thus resulting in an increased local biodiversity (Castellanos *et al.*, 1994; Bonanomi *et al.*, 2005b). Finally, short-lived plants (i.e. annual and biennial) can avoid the "home soil" by random searching for NPSF free sites through seed dispersal. In this regard, some studies reported that in natural grasslands short-lived plants show a rapid and continuous turnover at small spatial scales that, at the same time, results in a stable plant assemblage at community scale (Vincenot *et al.*, 2017). In other words, plants of different species alternatively occupy soil patches in time and space, resulting in a rapid rotation of species. This spatial-temporal pattern has been called "Carousel model" (Maarel and Sykes, 1993) because plants continuously move in time and space, changing their spatial position into the grassland. In this contest, a parallelism between natural ecosystems and agro-ecosystems can be highlighted: in the first, plants move away from sick "home soil" through seed dispersal, or clonal propagation resulting in a self-emerging species alternation or rotation. In agro-ecosystems, instead, farmers overcome SS through the ancient, yet very effective, agronomic practice of crop rotation.

MECHANISMS BEHIND SOIL SICKNESS AND NEGATIVE PLANT-SOIL FEEDBACK

Soil sickness is a complex, multi-factorial phenomenon influenced by plant species, crop rotation and soil management practices. In addition, environmental factors such as climate and soil type may increase the complexity of the phenomenon (Venugopalan and Pundarikakshudu, 1999). In order to explain the mechanisms causing SS and NPSF, three main hypotheses have been proposed: (i) soil nutrient depletion or imbalance (Howeler, 1991; Xiang *et al.*, 2009); (ii) build-up of soilborne pathogen and parasite populations (Manici *et al.*, 2013; Packer and Clay, 2000), coupled with a shift in soil microbial community composition (Kardol *et al.*, 2007; Klironomos, 2002); (iii) release of phytotoxic and autotoxic compounds during decomposition of crop residues (Singh *et al.*, 1999; van de Voorde *et al.*, 2012), or plant litter (Mazzoleni *et al.*, 2015a).

Soil nutrient depletion or imbalance. The first hypothesis proposed to explain SS and the consequent decline of crop production, suggests that depletion or immobilization of soil nutrients cause deficiency in plants (Börner, 1960; Ehrenfeld *et al.*, 2005). This hypothesis invokes the depletion of below-ground nutrients in the soil previously occupied by conspecifics. The majority of evidences from agro-ecosystem and natural plant communities does not support the nutrient depletion hypothesis.

At the beginning of the 1900s, pioneering studies compared ashes and nutrient content from different plants (reviewed by Börner, 1960). Nevertheless, differences in mineral composition resulted unrelated to SS and unable to explain the species-specificity of the phenomenon. A number of subsequent agronomical studies evaluated the capability of nutrient fertilization to overcome SS, but most of the experiments demonstrated that mineral fertilizers did not restore the normal growth in sick soils (reviewed by Zucconi, 2003). For example, in their study about the effects of cucumber monocropping on soil quality and plant growth performance, Zhou and Wu (2015) found that the content of macronutrients, such as nitrogen, phosphorus and potassium, in the soil increases with the number of cropping cycles. However, SS increased over time in monocropping, and the effects were particularly dramatic after five production cycles.

Further evidences against the nutrient depletion hypothesis came from soilless cultivation experiments. Many experiments conducted in hydroponic systems, where the level of nutrients was continuously adjusted and balanced in function of the vegetative stage of the crop, showed that the reduction of plant performance observed with the "old" solutions cannot be related to a deficiency of any nutrients. In these cases, researchers ascribed SS to toxic substances released by the root system (Asaduzzaman and Asao, 2012; Asao *et al.*, 2007; Yu *et al.*, 1993), the spread of pathogenic microbes (Vallance *et al.*, 2009), and
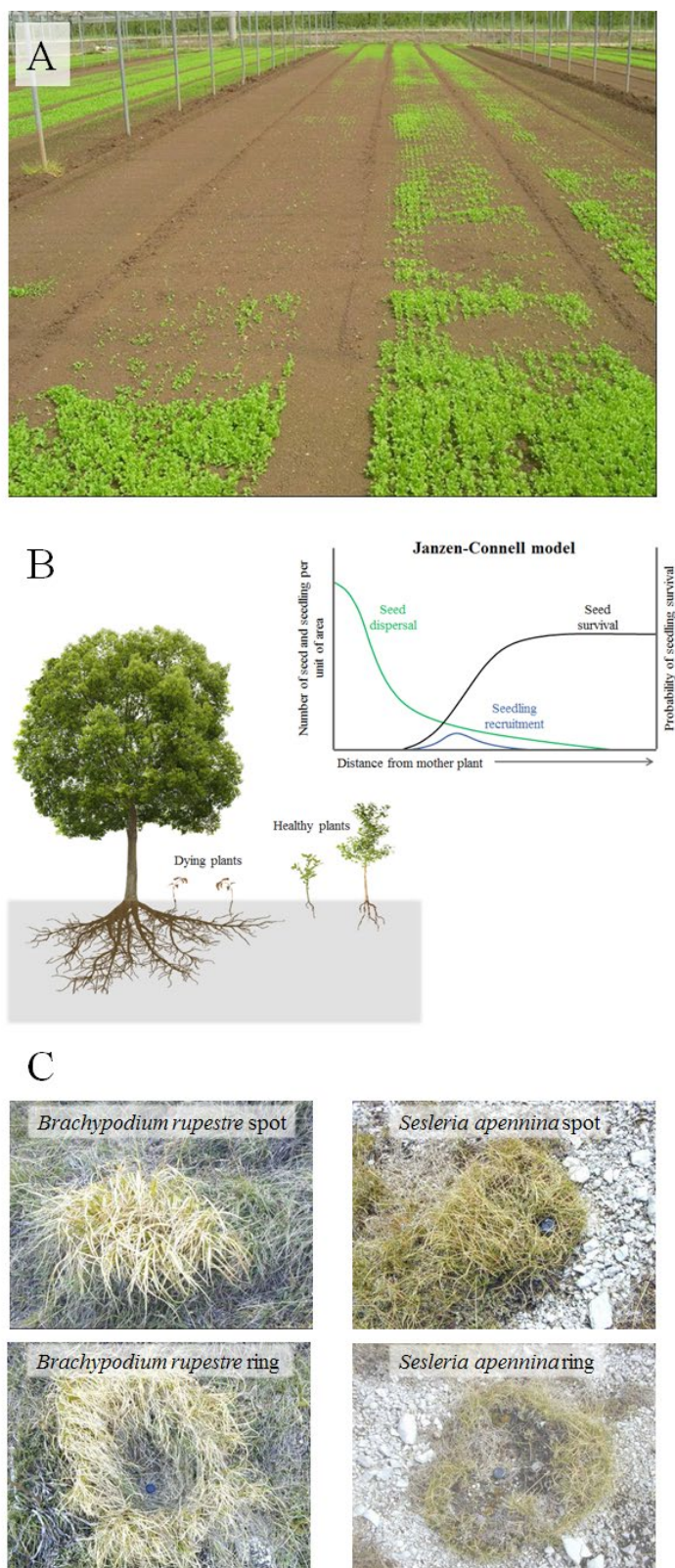

Fig. 4. Examples of soil sickness in agro-ecosystems and plant soil feedback in natural ecosystems. (A) Fourth range lettuce cultivation showing extensive damping-off symptoms; (B) Seedling failure under conspecific tree resulting in the Janzen-Connell recruitment distribution in natural forest; (C) Examples of spot and "ring" formed by perennial grasses capable of clonal propagation (pictures taken by Giuliano Bonanomi).

to the interaction between toxic substances and harmful microorganisms (Ye *et al.*, 2004; Zhang, 1993).

Another set of data against the nutrient depletion hypothesis comes from the observation that legumes, nitrogen-fixing species, develop severe NPSF (Tables 1 and Supplementary Table S1; Fig. 2 and Fig. 3). This is quite unexpected, considering that such type of plants enriches the soil with nitrogen and phosphorus. For instance, seedlings of *Medicago marina*, a plant that colonizes sandy shore in the Mediterranean basin, suffer a strong self-repulsion from mother plants (Bonanomi *et al.*, 2008). Greenhouse experiments with *M. marina* showed that seedlings are strongly inhibited in the "home" soil collected under the crown of the mother plant, in comparison to seedlings grown in the same type of soil not affected by conspecific, and taken from the adjacent sandy beach deprived of nutrients. Surprisingly, the seedlings were stunted in "home" soil despite having 5 and 6 times the amount of nitrogen and phosphorus and a lower salinity compared with the surrounding sandy soil (Bonanomi *et al.*, 2008). Similar findings were reported by Jennings and Nelson (2002) for the congeneric *Medicago sativa* in agricultural fields. More recently, Stinca *et al.* (2015) reported that the legume shrub *Genista aetnensis* that colonizes the bare lava flow of the Vesuvius Grand Cone ameliorates soil characteristics. In detail, *G. aetnensis* in a relatively short time span (i.e. *ca.* 40 years) is able to build-up an island of fertility under its canopy by accumulating stock of organic carbon, nitrogen, phosphorus, potassium, calcium and magnesium and by improving the hydrological properties of the soil. On the other hand, *G. aetnensis* seedlings were absent in the field under the canopy of conspecifics, and greenhouse bioassays showed that seedlings growth was inhibited in "home" soil compared to the barren, nutrient deprived substrate collected far from the canopy of conspecifics. Noteworthy, coexisting phylogenetically-unrelated plants thrive in the soil enriched with nutrients by *G. aetnensis* (Stinca *et al.*, 2015). Similar self-inhibitory effects have been demonstrated for other nitrogen-fixing species including *Alnus sinuata* during colonization of glacier moraine in Alaska (Chapin *et al.*, 1994), *Acacia papyrocarpa* in the Australian desert (Facelli and Brock, 2000), and for the nitrogen-fixing tree *Hippophae rhamnoides* in sandy shores of North Europe (Oremus and Otten, 1981). All these cases show the formation of "islands of fertility" with inhibitory effects on conspecific younger individuals.

A further evidence against the nutrient depletion hypothesis came from clonal perennial plants forming "ring" (Fig. 4c). For this type of plants, several studies reported a higher nutrient concentration in the inner "dieback" area compared with the soil outside the ring (Adachi *et al.*, 1996; Castellanos *et al.*, 1994; Incerti *et al.*, 2013; Lewis *et al.*, 2001; Otfinowski, 2008; Ravi *et al.*, 2008; Wikberg *et al.*, 2002). In an early study, Curtis and Cottam (1950) found that the prairie sunflower *Helianthus rigidus* in the field is able to form clones with central "dieback". In a subsequent experiment, the same authors reported that the growth of *H. rigidus* is not improved after the application of mineral fertilizer in the inner area. Similarly, Lanta *et al.* (2008) observed that the soil in the dieback area of the sedge *Eriophorum angustifolium*, showed a significantly higher nutrient content compared to the external soil, and the same pattern has been reported for the perennial grasses *Brachypodium rupestre* (Bonanomi and Allegrezza, 2004), and *Bromus inermis* (Otfinowski *et al.*, 2016). Moreover, some studies reported an increased water holding capacity in the "dieback" zone of the clones, a result associated with the higher soil organic matter (Lanta *et al.*, 2004; Pemadasa, 1981; Pignatti, 1997). These results indicate that self-inhibition paradoxically occur in "home" soil where a higher soil quality is usually recorded.

In conclusion, evidence from both agricultural and natural ecosystems indicates that the nutrient depletion hypothesis cannot be a satisfactory explanation for the development of SS and NPSF. However, the phenomenon of soil nutrient depletion does exist and has been frequently observed in poor and undeveloped countries where the use of fertilizers, both organic and synthetic, often represents a limit due to their poor availability or high cost. For example, in a study on yield decline in banana (*Musa* sp.), Bekunda (1999) shows that the intensification of intercropping practice, the removal of crop residues and the poor application of fertilizers have led to a loss of soil fertility and, consequently, to a reduction in banana production. Similar results were reported for the cultivation of cassava (*Manihot esculenta*) by Howeler (1991). In this case, the continuous cultivation under low input of fertilizers has determined a soil nutrient depletion, especially in potassium, with negative effects on crop production.

Soilborne pathogens and microbial shift. Soil microorganisms are key components of natural and agricultural ecosystems, given their contribution to chemical and biological processes including break-down of organic matter, carbon and nitrogen cycles, stabilization of soil aggregates, nutrient acquisition, and degradation of environmental pollutants (Bever, 1994; Bronick and Lal, 2005; Ehrenfeld *et al.*, 2005; Kardol *et al.*, 2006; Reinhart and Callaway, 2006). The composition and abundance of soil microbes are controlled by soil properties (e.g., temperature, moisture, aeration, pH), but also by higher plants through rhizodeposition (Paterson *et al.*, 2007), and accumulation of leaf and root debris (Wardle *et al.*, 2004; Zak *et al.*, 2003). In this way, plants promote the development of beneficial microbes such as nitrogen fixing bacteria and mycorrhizal fungi (Artursson *et al.*, 2006; Hayat *et al.*, 2010), but may also favour the spread of soilborne pathogens, plant parasitic nematodes and deleterious rhizobacteria (Bennett *et al.*, 2012; Huang *et al.*, 2013; Shipton, 1977).

The hypothesis that SS is due to the accumulation of pathogens in the soil was proposed after the observation that soil sterilization restores crop productivity in

soils subjected to monoculture (Savory, 1966). For example, Hoestra (1965) reported that the poor growth of young cherry trees (*Prunus avium*) planted on soil previously occupied by the same species ("home" soil) was associated with a strong infestation by the endoparasitic nematode *Pratylenchus penetrans*, and by the soilborne fungus *Thielaviopsis basicola*. When the soil was fumigated, instead, an improved growth was observed supporting the hypothesis that harmful microorganisms are the main cause of the replanting problem. Since then, the efficacy of soil sterilization in restoring sick soil has been proved in several agro-ecosystems (Table 1). Pankhurst *et al.* (2005) suggest that the poor growth and yield decline of sugarcane (*Saccharum* spp.) grown in continuous monoculture is due to the presence of deleterious soil organisms. In particular, they reported that both soil fumigation and the application of fungicide combined with nematicide increased the growth and yield of sugarcane in comparison with the untreated soil. Concerning orchards, replant disease of apple has been reported in all major apple growing regions and extensively studied (Mazzola and Manici, 2012). Mazzola (1998) assessed the relative role of different soil microbial groups in the development of apple replant disease by the application of selective pesticides. The results demonstrate that the application of fungicides was as effective as soil pasteurization in improving the growth of plants, whereas the application of antibiotic and nematicide did not improve plant performances. *Cylindrocarpon destructans*, *Pythium* spp., *Phytophthora cactorum* and *Rhizoctonia solani* were repeatedly isolated from symptomatic plants in field conditions, confirming the key role of fungi and oomycetes in apple replant disease. However, the relative occurrence of *Pythium* and *R. solani* isolates within the root rot microbial complex largely varied from site to site. In Italy, Manici *et al.* (2003) confirmed that apple replant problem is associated with a complex pathogenic microbiota that includes *R. solani*, *P. intermedium*, *Cylindrocarpon spp.* and *Fusarium solani*. Several pathogens were involved also in the black root rot of strawberry, where *R. solani*, *C. destructans*, *F. oxysporum* and *F. solani* play the major role (Manici *et al.*, 2005). In natural ecosystems, Packer and Clay (2000) provide clear evidence of NPSF driving to the Janzen-Connell recruitment pattern for black cherry (*Prunus serotina*) in temperate forest of USA. In detail, the authors observed extensive seedling failure under conspecific adults, by identifying *Pythium* sp. as the primary causal agent. It is notable, from the aforementioned studies, that most of the pathogens associated with SS as well as NPSF are polyphagous fungi and oomycetes. The evidence that soilborne pathogens are consistently isolated from symptomatic plants, supports the pathogenic hypothesis, but the polyphagous nature of these pathogens does not fit the paradigm because SS is highly species-specific. In fact, SS has been associated with species-specific pathogens only in very few cases (Table 1). An exception is the asparagus

(*Asparagus officinalis*) replant early decline caused by *F. oxysporum* f. sp. *asparagi* (Blok and Bollen, 1996).

Although extensive research on soilborne pathogens and parasites has been carried out in agricultural systems, similar studies in natural eco-systems are relatively rare. On the other hand, the studies about NPSF in natural plant communities are numerous (Fig. 1; Supplementary Table S1), but most of these used a multi-spet, "black-box" approach (Bever, 1994; Kardol *et al.*, 2007; Klironomos, 2002). In the first step, defined as the conditioning phase, soil is cultivated with selected plant species for which the feedback mechanism is investigated. During this phase, plant interacts with biotic and abiotic soil components by altering them. In the second step, the effects of the conditioning phase are assessed by comparing the growth of a new plant in self-cultivated or "home" soil, and non-self-cultivated soil also indicated as "away" soil. If the plant grows more in the self than in the other cultivated soils, the feedback is considered positive, otherwise is negative. A large and still growing body of data demonstrates that the negative feedback is more common than the positive one (Supplementary Table S1; Kulmatiski *et al.*, 2008). Moreover, several studies found significant changes in microbiota composition using culture-based as well as culture-independent methods (Van Der Heijden *et al.*, 2008; Bever *et al.*, 2013). In some experiments, NPSF was transferred from different soils by using small aliquots of "sick" soil as a microbial inoculum (Kardol *et al.*, 2007). Many researchers interpreted the observed NPSF as a result of some, often undescribed, microbial shift that occurs during the conditional phase of the experiment. In accordance with this, we pointed out that in literature the microbial shift was found as the main putative cause of NPSF in 65.8% of the studies (Supplementary Table S1; Fig. 4). However, for a better understanding of the role of soil biota in NPSF, the evaluation of composition and changes in the entire microbial community is a necessary step. Recent studies have demonstrated that the net effect of plant-soil feedback is the balance between beneficial and detrimental microbes. Bennett *et al.* (2017), using 55 populations of North American trees, reported that soil collected beneath conspecifics showed NPSF for most of the studied species. Most notably, the type of mycorrhizal association with plant species explained a large fraction of the variation in NPSF, with arbuscular mycorrhizal trees suffering a more intense NPSF than ectomycorrhizal ones. The authors suggested that ectomycorrhizal trees may protect plant roots from soilborne pathogens that accumulate under conspecifics. Similar findings were reported by Teste *et al.* (2017) from hyper-diverse Australian shrublands. In this work NPSF has been considered as the result of an imbalance of soil microbiota, with plants harboring ectomycorrhizal fungi that are more protected from detrimental microbes compared to plants that establish the symbiosis with arbuscular mycorrhizal fungi. It is interesting to note that many cultivated plants, which suffer strong SS, are associated with arbuscular mycorrhizal fungi.

The hypothesis that SS is associated to soilborne pathogens presents some strengths and several weaknesses. The effectiveness of soil sterilization to overcome SS is often interpreted as a clear-cut proof that harmful microorganisms are the main driving factors of SS. However, an improved plant growth in sterilized compared to non-sterilized soils can be related also to other side effects of this treatment. Soil sterilization alters biotic and abiotic soil properties, providing a nutrient flush resulting from a rapid mineralization of the dead microbes (Troelstra *et al.*, 2001). In addition, organic phytotoxic compounds may be subjected to thermal degradation. Therefore, the greatest availability of nutrients or the degradation of toxic compounds induced by soil sterilization may accidentally reduce the negative effects and promote positive vegetative responses in plants driving to ambiguous interpretation of the results (Troelstra *et al.*, 2001). On the other hand, the frequent isolation of pathogenic oomycetes, fungi and parasitic nematodes from symptomatic plants strongly supports the pathogenic hypothesis. However, the observation that most of the isolated microbes are polyphagous is not coherent with the species-specificity of SS.

In the last few years, the assumption that sick soil is associated to one or few specific microbes progressively evolved towards a more complex idea that involves an unbalance in the microbiota that generates inhospitable soil conditions. Recent studies based on high-throughput sequencing of bacterial and eukaryotic rRNA gene markers revealed that soil is inhabited by thousands of different species that form complex food-web (Mendes *et al.*, 2013; Bonanomi *et al.*, 2016). The extensive application of new analytical tools will be very useful to establish if a sick soil is related to an overall shift in soil microbiota structure, rather than to changes in single or few microbial species.

Phytotoxicity and autotoxicity. The idea that harmful chemical compounds, either released through root exudation or by decaying of plant debris, are involved in SS dates back at the beginning of the 1900s (Russell and Petherbridge, 1912; Schreiner and Shorey, 1909). Only few studies, however, clearly demonstrated that plants exudate through the roots chemical compounds that specifically harm conspecifics (Perry *et al.*, 2005; Webb *et al.*, 1967). The authors explain this event as a density-dependent regulation of population to avoid overcrowding and reduce intraspecific competition. The idea that SS could be caused by actively released toxins has been heavily criticized because such compounds are rapidly degraded by the soil microbes into non-toxic molecules, thus having a limited impact in field conditions (Fitter, 2003; Harper, 1977).

On the other hand, many studies reported that plant residues, either leaf or root debris, can have an inhibitory effect on plant growth (Table 1; Fig. 5). In controlled conditions, soil amendment with crop residues derived from conspecific impaired root and shoot growth of peach

(Collina and Zucconi, 1967; Proebsting and Gilmore, 1941; Tagliavini and Marangoni, 1992), apple (Borner, 1959), olive (Endeshaw *et al.*, 2015), tea, coffee (Putnam, 1994), alfalfa (Miller, 1996), and many herbaceous plant species (review by Patrick, 1971; Putnam, 1994; Table 1). Data from natural ecosystems further demonstrated that leaf litter can have a detrimental impact on plant growth. Three recent studies, based on 21 (Lopez-Iglesias *et al.*, 2014), 64 (Bonanomi *et al.*, 2011c) and 65 (Meiners, 2014) different plant residues, demonstrated that litter inhibitory effects are common, but may largely vary in relation to the composition of plant residues, which in turn depends on plant biochemical activity and on litter decomposition stage. Bonanomi *et al.* (2006) reported that phytotoxicity of leaf and root debris depends on plant functional type with the following rank: annuals >> perennials ≥ woody. Noteworthy, undecomposed leaves of nitrogen-fixing species were invariably the most toxic plant tissue.

Microbial decomposition plays a key role in affecting phytotoxicity of plant debris. A better understanding of this process is crucial to appreciate the real role of crop residues and plant litter on SS and NPSF. During decomposition, the abundance and activity of nitrogen and phytotoxic compounds continuously change over time, because of sorption and polymerization on soil organic matter and clay minerals, as well as the chemical transformation driven by soil microbes (Blum *et al.*, 1999). Considering these processes, two mutually non-exclusive hypotheses have been proposed to explain the inhibitory effect of plant debris on root growth: nitrogen (N) immobilization by microbial competition (Hodge, 2004), and phytotoxicity by labile, low molecular weight organic compounds (Rice, 1984). According to the first hypothesis, in presence of decaying plant residues with a high C/N ratio, saprophytic microbes would compete with plants for N, causing a temporary immobilization of this nutrient (Hodge *et al.*, 2000; Fig. 5). The second hypothesis sustains a direct negative effect on root growth exerted by a wide array of inhibitory compounds, early released by decomposing litter, including short-chain organic acids (Armstrong and Armstrong, 2001; Huang *et al.*, 2010), tannins (Mizutani *et al.*, 1979) and phenols (Chen *et al.*, 2005; Chon *et al.*, 2002). Examples of toxic compounds involved in SS and isolated from soil and plant debris include phlorizin for apple (Borner, 1959), amygdalin for peach (Patrick and Koch, 1958), medicarpin for alfalfa (Miller, 1996), caffeine for coffee (Chou and Waller, 1980), and coumaric, syringic and vanillic acids for rice (Chou and Lin, 1976). In this context, microbial decomposition is of utmost importance because it affects the impact of plant residues on plant growth, by modulating the relative abundance and activity of phytotoxic compounds. Studies that specifically investigate the role of microbial decomposition reported a rapid degradation of most allelochemicals into non-toxic molecules in the early phases of this process (An *et al.*, 2001; Bonanomi *et al.*, 2011c). These studies demonstrated
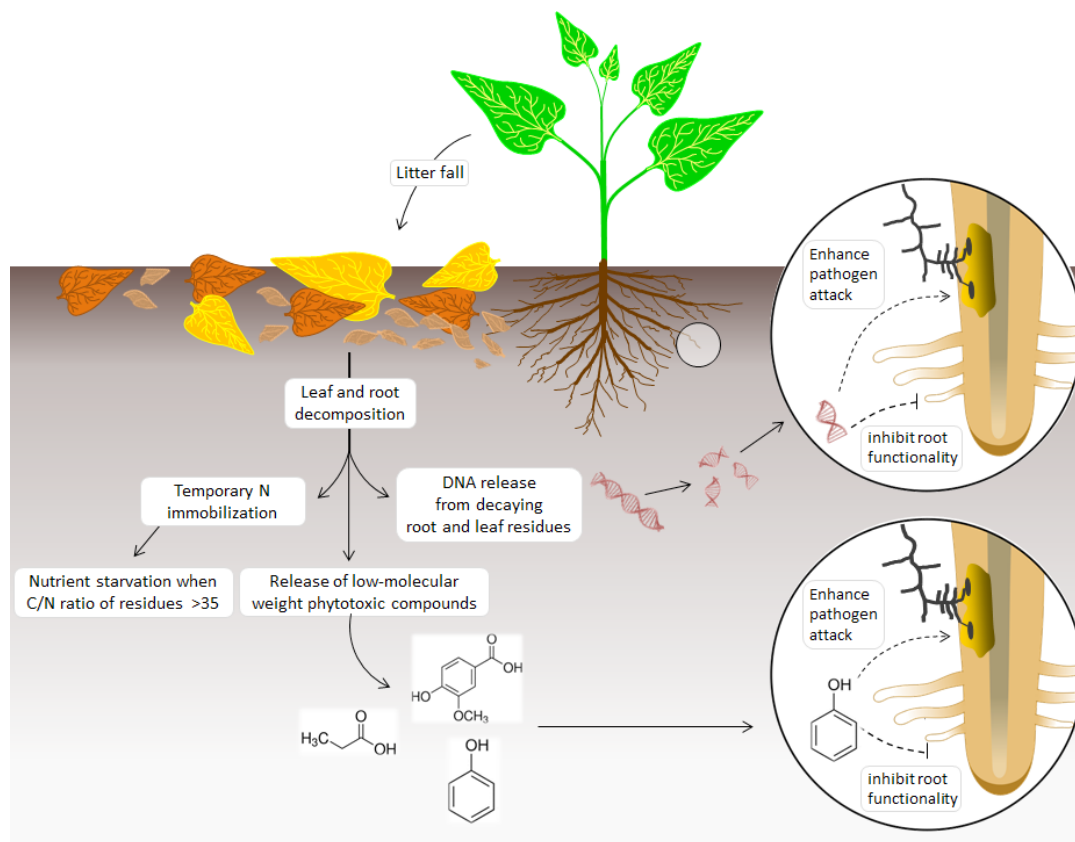
Fig. 5. Schematic representation of autotoxicity effects associated with the decomposition of crop residues, including nutrient immobilization due to microbial competition, release of low-molecular weight phytotoxic compounds and extracellular DNA from conspecific plants tissues.

the occurrence of a temporal phytotoxic 'window' during decomposition of crop residues, which ranged from 5 to 30 days. In all cases, however, phytotoxicity dropped in time and, after 60-90 days of decomposition, "aged" organic matter showed neutral or even stimulatory effects on root proliferation.

All the aforementioned data, related to natural as well as to agro-ecosystems, demonstrated that root growth inhibition by undecomposed plant residues is a general phenomenon not restricted to few "allelopathic" plants. However, it is also well-established that phytotoxicity of plant debris is a transient phenomenon that usually lasts from few days to some weeks. Thus, some researchers raised serious concerns about the possible role of plant residue phytotoxicity on SS and NPSF (Fitter, 2003; Van Der Putten, 1997). Two main criticisms were addressed: (i) toxins from plant debris are rapidly degraded by soil microbial activity, being ineffective after a few weeks, while SS in the field can last for months or even years; (ii) many, if not all, of the organic compounds extracted from sick soil and plant residues (e.g. Huang *et al.*, 2013; Rice, 1984; Singh *et al.*, 1999; Chen *et al.*, 2015), showed a general phytotoxicity, which is in contrast with the species-specificity of SS. For example, Armstrong and Armstrong (2001) associated *Phragmites australis* "die-back" to the accumulation in the sediment of propionic, butyric and caproic acids and

sulphides produced during anaerobic decomposition of root and rhizomes. However, these low-weight carboxylic acids showed phytotoxic effects on a wide range of higher plants (Himanen *et al.*, 2012). Singh *et al.* (1999) reported 76 cases of plant autotoxicity caused by their own residues or root exudates. In Table 1 we found out up to 60.2% of the experimental studies reporting soil sickness in agro-ecosystems ascribed to autotoxicity. However, as observed also by Singh *et al.* (1999), autotoxicity was demonstrated exclusively using conspecific as test plants, while other phylogenetically unrelated species were not considered. This is a common bias in the current literature that leaves serious doubts about the real species-specificity of plant residues autotoxicity.

It appears clear that most of the low molecular weight phytotoxic compounds can hardly explain SS and NPSF because of their short persistence into the soil and lack of species-specific effects. A recent finding, reporting the species-specific inhibitory effects of extracellular DNA (exDNA) (Mazzoleni *et al.*, 2015a), may reconcile the toxicity hypothesis with the occurrence of SS. Mazzoleni *et al.* (2015a, 2015b) reported that fragmented extracellular self-DNA (i.e. DNA originating from conspecifics) produces species-specific inhibitory effects on several wild plants. First, the analysis of plant debris showed a significant accumulation of exDNA during the decomposition process,

although in fragmented forms. Thereafter, *in vitro* experiments demonstrated that the inhibitory effect of self-DNA was highly species-specific. Noteworthy, the authors found that only highly fragmented self-DNA was effective (i.e. fragment size range between 50 and 2000 bp). In addition, the application of activated carbon, known to selectively adsorb allelopathic organic compounds, was not able to remove autotoxicity, neither to restore plant growth. Conversely, heterologous exDNA from phylogenetically unrelated plant species had no inhibitory effects. This is consistent with a previous work (Paungfoo-Lonhienne *et al.*, 2010), where heterologous DNA was taken-up by root and used as a source of phosphorus. Moreover, the strong persistence of exDNA in the environment (Levy-Booth *et al.*, 2007) is in agreement with the persistence of SS observed in both natural vegetation and agro-ecosystems. Finally, since exDNA is destroyed during soil sterilization by autoclaving or gamma irradiation, the well-known effectiveness of this treatment to overcome SS cannot be used to discriminate between exDNA toxicity and the pathogenic hypotheses. Thus far, the authors concluded that self- exDNA is a good putative candidate to explain SS and NPSF (Mazzoleni *et al.*, 2015a). The hypothesis that exDNA can be involved in SS is intriguing, but further works are needed to validate this idea. In detail, quantitative data are required about the accumulation of self- exDNA in field conditions, as well specific experiments to confirm the inhibitory effect of purified conspecific DNA on seed germination and root growth of cultivated plants (Barbero *et al.*, 2016).

Beside the underlying causal mechanisms, the autotoxicity hypothesis poses an evolutionary paradox: why a plant species should harm its own off-springs? Some authors suggested that autotoxicity acts as a density-dependent regulation mechanism to avoid population overcrowding (McNaughton, 1968; Perry *et al.*, 2005; Singh *et al.*, 1999). Our idea, instead, is that all living organisms, such as bacteria, fungi, algae and animals, produce by their metabolic pathways different catabolites (by-products and wastes). Why higher plants should be an exception? Interestingly, catabolic wastes that are toxic for the producing species may be at the same time a resource for other species. In this regard, it is notable that floating plants (e.g. *Eichhornia crassipes*, *Lemna* spp., *Pistia* spp.), mangrove forests (*Avicennia* spp., *Nypa fruticans* Wurmb., *Rhizophora* spp.), seagrass (*Posidonia* spp., *Thalassia* spp., *Zostera* spp.), seaweed and kelp forests (*Fucus* spp., *Laminaria* spp., *Macrocystis pyrifera*), as well as sessile animals (e.g. mussel, barnacle, polychaete and porifera) that live in aquatic environments, do not suffer autotoxicity at all because their wastes are continuously removed by flushing water (Bonanomi *et al.*, 2010). In fact, stable and self-perpetuating monospecific stand in nature occurs only in aquatic environment where the plant mineral nutrition is almost completely decoupled from decaying of conspecific debris, thus nullifying their autotoxic impact. In contrast, in terrestrial ecosystems,

autotoxicity accumulates in the close proximity of the producing individual, resulting in a patchy, localized negative feedback neighborhood. Finally, we believe that SS results from the unavoidable constraint of localized waste accumulation combined with the sessile nature of terrestrial plants.

Synergic interaction between pathogens and toxins. SS is a complex, multifaceted phenomenon determined by an overall deterioration of soil quality. Unfortunately, most of available studies focused on a single causal factor to explain SS, with plant pathologists addressing the role of soilborne pathogens and parasitic nematodes, organic chemists searching for toxic molecules, and agronomists looking for depletion and imbalance of nutritional factors (Table 1). Only few researchers explored the possibility that multiple stress factors, both biotic and abiotic, may contribute to the development of SS.

More than 50 years ago, Patrick *et al.* (1963) proposed that toxic compounds, either released by roots during exudation or during decomposition of plant residues, promote the activity of soilborne pathogens by weakening the plant, thus reducing their fitness and resistance to pathogens. Since then, several studies confirmed the Patrick's hypothesis (Table 2). Xia *et al.* (2015) found that regeneration failure of Chinese fir (*Cunninghamia lanceolata*) in monospecific forest plantations was due to the strong concentration of cyclic dipeptides produced and released by the plant itself. These compounds not only were autotoxic for seedling roots, but also altered the microbial community composition, favouring the build-up of soilborne pathogens. A study carried out in hydroponic conditions, reported that the cinnamic acid contained in the root exudates of cucumber (*Cucumis sativus*) predisposed the roots to infection by the pathogen *Fusarium oxysporum* f. sp. *cucumerinum* through a direct biochemical and physiological effect (Ye *et al.*, 2004). Studying the *Asparagus officinalis* replant disease problem, Hartung and Stephens (1983) reported that soil amendment with dried crown and root tissues promoted seedling attack by *F. oxysporum* f. sp. *asparagi* and *F. moniliforme*. Similarly, Bonanomi *et al.* (2007) found that tomato (*Solanum lycopersicon*) wilting caused by *F. oxysporum* f. sp. *lycopersici* increased when the soil was amended with tomato leaves that showed an autotoxic effect *in vitro*. Few years later, these finding were extended to polyphagous soilborne pathogens. Specifically, Bonanomi *et al.* (2011a) reported that alfalfa (*Medicago sativa*) seedling damping-off caused by *Pythium ultimum* and *Rhizoctonia solani* dramatically increased when soil was amended with alfalfa residues, an organic material having a strong autotoxic effect. The authors suggest that *P. ultimum* and *R. solani*, having the ability to growth saprophytically on crop residues, increased their potential inoculum, and this impacted the disease incidence and severity. Benizri *et al.* (2005) studied the bacterial community structure in both healthy and

Table 2. List of experimental studies reporting a promotion of soilborne pathogens activity by autotoxic factors released by roots during exudation, or during decomposing of plant residues.

Species	Autotoxic compounds	Microorganisms	References
Angelica sinensis	Root exudates	Microbial shift	Zhang *et al.*, 2015
Arachis hypogaea	P-hydroxybenzoic acid, vanillic acid and coumalic acid	*Fusarium solani*	Li *et al.*, 2010a
Asparagus officinalis	Root and rhizome tissues	*Fusarium oxysporum* f. sp. *asparagi* and *Fusarium moniliforme*	Hartung and Stephens, 1983
Citrus aurantium	Root residues	*Phytophthora citrophthora, Pythium aphanidermatum* and *Fusarium solani*	Hassan *et al.*, 1989
Cucumis melo	Gallic acid, phthalic acid, syringic acid, salicylic acid, ferulic acid, benzoic acid and cinnamic acid	*Fusarium oxysporum* f. sp. *melonis*	Yang *et al.*, 2014
Cucumis sativus	Cinnamic acid	*Fusarium oxysporum* f. sp. *cucumerinum*	Ye *et al.*, 2004
Medicago sativa	Leaves residues	*Pythium ultimum* and *Rhizoctonia solani*	Bonanomi *et al.*, 2011
Pseudostellaria heterophylla	Root exudates	*Talaromyces helicus, Kosakonia sacchari*	Wu *et al.*, 2016
Scutellaria baicalensis	flavone baicalin (7-glucuronic acid, 5,6-dihydroxy-flavone)	*Pythium ultimum* and *Rhizoctonia solani*	Zhang *et al.*, 2010b
Solanum lycopersicum	Leaves and roots residues	*Fusarium oxysporum* f. sp. *lycopersici*	Bonanomi *et al.*, 2007

sick soils aiming to understand the role of microbes and toxins in the peach replant disease. The authors observed a higher abundance of *Bacillus* strains in sick rather than in healthy soil, whereas an opposite trend was found for *Pseudomonas* strains. In addition, more than 60% of the strains isolated from the sick soil were able to produce cyanides as secondary metabolite. These results suggested that peach replant disease can be caused directly by the presence of pathogenic microorganisms, and indirectly by the release of toxic compounds during the decomposition of peach root residues (Benizri *et al.*, 2005; Yang *et al.*, 2012).

Recently, Mazzoleni *et al.* (2015a) hypothesized that weakening of plants as a result of exposure to extracellular self-DNA with autotoxic effects, could increase its susceptibility to subsequent pathogen attack. However, the role of self-DNA in affecting plant-pathogen interactions is far to be fully understood, also in the light of the findings of Wen *et al.* (2009). Using the *Pisum sativum-Nectria haematococca* pathosystem, these authors demonstrated that exDNA is a component of root cap slime and is necessary for the protection of root tip from pathogen attack. The selective elimination of exDNA from the rhizosphere by the application of DNase I, resulted in the loss of root tip resistance, driving to fungal infection. These apparently contradictory findings underline the importance of further studies to clarify the role of exDNA on plant-pathogen interactions.

Finally, it should be pointed out that none of the studies listed in Table 2 demonstrated an effective reduced plant resistance after the application of purified chemical compounds or plant residues with autotoxic effect. Future studies based on physiological, proteomic and transcriptomics approaches are needed to test this hypothesis.

OVERCOMING SOIL SICKNESS AND NEGATIVE PLANT-SOIL FEEDBACK

Farmers face SS since the time of ancient Greek and Roman Empire, being so forced to develop agronomic practices to overcome this problem. On the other hand, terrestrial plants that live in natural ecosystems evolved under the selective pressure of NPSF, driving single individuals to move in time and space to avoid their own "home" soil. The comparison between management strategies aimed at overcoming SS in agro-ecosystems and plant behavior to avoid NPSF in natural plant communities provide interesting parallelisms (Table 3).

Crop rotation. Crop rotation is probably the most ancient agronomic method to overcome SS, being already cited by Columella (4-70 AD) more than 2,000 years ago. Crop rotation alleviates SS as it decreases the pathogen inoculum, and it reduces the effect of autotoxic compounds in the soil (Curl, 1963; Huang *et al.*, 2013; Zucconi, 2003). These effects are achieved by mixing the residues of different crops that succeed in time. Plant debris of some *Brassica* species are also highly effective in controlling some soilborne pathogens and parasitic nematodes thanks to their high content in glucosinolates (Lawrence and Matthiessen, 2004; Lazzeri *et al.*, 2004). Rotation between cereal crops, such as wheat and maize, with nitrogen-fixing legumes (e.g. clover, alfalfa, soybean, etc.) is probably one of the most common practices worldwide to alleviate SS. Alternation of grasses and nitrogen-fixing legumes in natural grassland has been also reported (Turkington *et al.*, 1977). Although the effectiveness of this rotation is commonly linked to an increased content of nitrogen in the soil, changes in soil microbiota and the alleviation of autotoxicity could be important as well.

Table 3. Comparison between management strategies aimed at overcoming soil sickness in agro-ecosystems, and plant behavior evolved in natural ecosystems to avoid NPSF.

Agro-ecosystem	Natural ecosystem
Crop rotation (Gresta *et al.*, 2016; Huang *et al.*, 2013)	Alternation of trees species in temperate (Fox 1977; Whittaker and Levin, 1977) and tropical forests (Augspurger, 1984; Mangan *et al.*, 2010)
	Cyclic succession in heathland and shrubland (Watt 1947; Bonanomi *et al.*, 2005a)
	"Carousel" dynamics in grassland dominated by short-lived plants (Maarel and Sykes, 1993; Vincenot *et al.*, 2017)
Polyculture (Matson *et al.*, 1997) and soil amendment with organic amendment (Bulluck *et al.*, 2002; Stark *et al.*, 2007)	Litter "mixing" effect and "herd" immunity hypothesis (Hättenschwiler *et al.*, 2005; Wills *et al.*, 1997)
Replacing sick soil (Zucconi, 2003)	Soil accretion in sand dune (Van der Putten *et al.*, 1993) and river banks (Bonanomi *et al.*, 2014)
Use of activated carbon in field conditions and in soilless systems (Elmer and Pignatello, 2011; Yu *et al.*, 1993)	"*Terra preta*" soil rich of charred organic materials in semi-natural ecosystems (De Luca *et al.*, 2006; Glaser and Birk, 2012; Kammann *et al.*, 2016)
Soil flooding (Newhall, 1955; Nie *et al.*, 2009)	Lack of NPSF in aquatic environments (Bonanomi *et al.*, 2011)

In natural plant communities, alternation of species in space and time is the most common strategy to escape NPSF (Table 3). In fact, alternation of different species has been observed in forest (Fox, 1977), shrubland (Watt, 1947) and grassland (Maarel and Sykes, 1993). In general, plants move away from sick "home soil" previously occupied by conspecific by mean of seed dispersal or clonal propagation. The resulting spatial and temporal patterns depend on the growth form, resulting in the Janzen-Connell distribution for trees and shrubs, "ring" and "wave" growth in perennial clonal plants, and a rapid turnover in annual species (Vincenot *et al.*, 2017). In all cases, however, the plant community behaves in response to NPSF producing a sort of natural, self-emerging alternation or rotation of different species in time and space. We are still far from a comprehensive understanding of dynamics and mechanisms behind natural alternations, but a better comprehension of these processes would be invaluable for modern and sustainable agriculture.

Polyculture and organic amendment. Polyculture, the contemporaneous cultivation of different plant species in the same field, is the most effective system to avoid SS. In fact, polyculture does not allow the development of SS because this requires a certain time of monoculture to build-up in soil. Polyculture substantially mimics a natural ecosystems where different plant species coexist in mixed communities. Theoretical as well as empirical studies demonstrated that polyculture reduces the incidence of diseases and pests by means of "herd" protection (Matson *et al.*, 1997; Wills *et al.*, 1997; Boudreau, 2013). In this model, heterospecific crowding protects different species because each individual is hidden by the surrounding vegetation, resulting in fewer host-pathogen compatible interactions. Polyculture can avoid the build-up of SS also trough a "dilution effect" of autotoxic compounds. In monospecific stand, single species plant debris accumulate punctually, and autotoxicity progressively increases. Conversely, in a multiple species stand different plant residues are mixed, resulting in the dilution of autotoxic compounds. Thus, despite some unavoidable effects at the individual level,

there is a positive outcome at the community level. Interestingly, under these assumptions, competitive effects occur on a short-term scale, but positive reciprocal species interactions emerge only if all species suffer from negative feedback (Bonanomi *et al.*, 2005c). The role of mixing plant debris has been extensively studied in relation to decaying rate and nutrient dynamics (review in Gartner and Cardon, 2004; Hättenschwiler *et al.*, 2005), while no data are available about its feedback effect on plant growth.

Unfortunately, polyculture cannot be applied in most of intensive agricultural systems because of their complex management and the large amount of manpower required. A practical method to alleviate SS is the application of exogenous organic amendments. By this technique, a certain amount of organic matter is applied to soil to improve physical, chemical and biological properties (Bulluck *et al.*, 2002; Diacono and Montemurro, 2010; Reeves, 1997; Stark *et al.*, 2007). Organic amendment operates by "diluting" the autotoxic effect of crop residues that are mixed with organic matter of different nature. However, the effectiveness of organic amendment to overcome SS depends on the amount of organic carbon applied and on the chemical quality of the amendment itself (Zucconi, 2003).

Replacing sick soil. Removal of sick soil and its replacement with "fresh" one is a simple and effective method to overcome SS (Zucconi, 2003). For obvious economic reasons this method cannot be applied in field conditions, being limited to some cultivations in nurseries and in public as well as private gardens. Interestingly, the replacement of sick soil has been observed under specific ecological condition in natural ecosystems. Studying sand dune communities in North Europe, Van der Putten *et al.* (1993) reported that the accumulation of soilborne pathogens and plant-parasitic nematodes are responsible for NPSF in Marram grass. However, detrimental soil conditions to this plant do not develop until sand accretion from the near seashore occurs. In fact, every year the shoot of this plant is buried by 20-100 cm of sand blow material. Marram grass is adapted to burial, a stress that will kill most of other plants, thanks to creeping rhizomes. Moreover,

the rhizome benefits of the "fresh" sand, free from any pathogen, thus remaining vigorous. A similar behaviour has been described for several grasses that live in sandy deserts (Danin *et al.*, 2012).

Soil accretion commonly occurs during flooding along river banks. Bonanomi *et al.* (2014), studying the perennial sedge *Scirpus holoshoenus* that live in Italian river banks, found that this plant generates two types of tussocks according to different environmental conditions: (i) loose tussocks with low tiller density and central "dieback"; (ii) compact tussocks with high tiller density and concave surface, without central "dieback". After extensive plant excavation and analysis of rhizome architecture, the authors showed that in the first case plants form "rings" because the rhizomes grow radially and did not resprout in the inner, "dieback" area of the clone. Such rhizome architecture was found only in not inundated grasslands. In the case of compact and concave tussocks, the rhizome is able to grow vertically, following substrate accretion that occurred during previous flooding events. Orthotropic rhizome grown following tussock burial demonstrates that the new accreted soil, free from pathogens and toxins, is suitable for root development, differently from the soil present in the inner area of the clone.

Removal of soil toxins. Selective removal of phytotoxic compounds has been proposed as another strategy to alleviate SS and NPSF. In this regard, activated carbon (AC) has been used because of its strong capacity to absorb organic chemicals, including pollutants and allelopathic compounds (Downie *et al.*, 2009; Hille and den Ouden, 2005). AC sorption capability has been exploited in soilless system as well as in field conditions. For example, application of AC to circulating solution in hydroponic systems increases the productivity in tomato, and in asparagus in a range of 15-30% (Asao *et al.*, 2003; Yu *et al.*, 1993; Yu and Matsui, 1994). Noteworthy, nutrient solutions collected after one cultivation cycle, resulted toxic for the seedling of conspecific plants, but no toxic effect was observed when the solution was treated with AC. Similar findings were reported for several cucurbit crops in soilless systems (Yu, 2001). The use of AC in sick soil was less effective, with a significant alleviation of the replant problem in *Asparagus* (Motoki *et al.*, 2006), but having negligible effects on other species (Petermann *et al.*, 2008). The complex interaction between toxins, native organic matter, soil microbiota and AC may explain the variable results achieved in field conditions compared to soilless systems. In natural soils, biochar can accumulate as a result of natural or anthropogenic burning of vegetation (De Luca *et al.*, 2006; Glaser and Birk, 2012). Burning of crop residues or natural vegetation produces highly heterogeneous materials, ranging from little affected plant tissues, to a variety of charred substrates, up to mineral ash (González-Pérez *et al.*, 2004). The amount and chemical properties of burnt organic residues depend on both the biochemical composition of the

plant tissues (Knicker, 2007), and the fire intensity that is controlled by pre-fire biomass moisture, fuel spatial arrangement and local microclimatic conditions (Certini, 2005). For instance, in the Amazonian basin pre-Columbian populations developed the so-called "*terra preta*" or "*dark earth*" by repeating cycles of fire and cultivation, i.e. the slash-and-char cultivation system (Glaser and Birk, 2012). The described "*terra preta*" contains very large amounts of biochar, reaching also 10-40% of the whole soil (Kammann *et al.*, 2016). The accumulation of biochar and other pyrogenic organic materials transformed a poorly nutritious and highly weathered acidic soil into a fertile one, capable of sustaining mono-cropping of maize and other crops for centuries (Kammann *et al.*, 2016).

Soil flooding has been applied by farmers to overcome SS in Japan and China. Periodical soil flooding for several weeks or some months can potentially leachate water soluble autotoxic substances and control some soilborne pathogens (Newhall, 1955; Nie *et al.*, 2009). For instance, rice (*Oryza sativa*) was subjected to a more intense yield decline in monoculture under aerobic cultivation, compared to flooded conditions (Nie *et al.*, 2007; Peng *et al.*, 2006). Moreover, periodical flooding of aerobic rice cultivation alleviated the symptoms of SS (Nie *et al.*, 2009). Flooding has been proved to be effective against SS in field conditions also for sugarcane (Chou, 1995), but no studies investigated the real movement, and the eventual leaching, of the putative autotoxic compounds in the field. The effectiveness of flooding in overcoming, or in alleviating SS, is consistent with the lack of NPSF in plants that live in aquatic ecosystems (Bonanomi *et al.*, 2010). As already stated, stable and self-perpetuating monospecific stand in nature can be observed only in aquatic environments, with examples that include floating (e.g. *Eichhornia crassipes*, *Lemna* spp., *Pistia* spp.), as well herbaceous perennial (*Phragmites autsralis*, *Posidonia* spp.) and woody (*Avicennia* spp., *Rhizophora* spp.) plants rooted in the sediments. In aquatic ecosystems, plants do not suffer autotoxicity and, therefore, NPSF because their wastes (i.e. leaf and root residues) are continuously removed by flushing water. Moreover, in such aquatic ecosystems, plant mineral nutrition is almost completely decoupled from decaying of conspecific debris because roots absorb nutrients from the water, thus the potential autotoxic impact of organic residues are nullified. Noteworthy, periodical "die-back" due to litter autotoxicity has been observed also in aquatic systems, but only after reductions of water regimes that, presumably, do not allow an efficient removal of decaying debris and their autotoxic by-products. Examples include the "die-back" of *Phragmites australis* (Armstrong and Armstrong, 2001; Van Der Putten, 1997), *Typha latifolia* (McNaughton, 1968), as well as several seagrasses and seaweed (e.g. Borum *et al.*, 2005; Frederiksen *et al.*, 2007). In other words, we speculate that human-managed monocultures can only be sustained in the long-term by decoupling the resource acquirement from autotoxic plant debris. This

can be achieved by either removal of crop residues (e.g. by using burning, selective removal, etc.), or mixing the residues through crop rotation or consociation, or leaching autotoxic factors trough flooding or biochar sequestration.

CONCLUSIONS AND FUTURE PERSPECTIVES

Soil sickness affects most of the major field crops, ornamental and horticultural species, as well as orchards. Intensive cultivations systems, based on monoculture, undeniably lead to the development of detrimental soil conditions that limit the cultivation of the same crop. There is an urgent need to find sustainable strategies to avoid or at the least alleviate SS, also considering the progressive ban of fumigants, that actually are the most effective method to temporary overcome the problem, and allow the cultivations. In this regard, a better understanding of the causes of SS is a necessary step to develop eco-friendly solutions. Evidence from both agro-ecosystems and natural plant communities undoubtedly ruled out the nutrient deficiency as a primary causal factor of SS. The massive use of mineral fertilizers, especially in intensive cultivation systems, appears an incorrect strategy because it does not aim to solve the cause of SS, but it actually exacerbates the decline in soil quality often by inducing acidification and salinization (Bonanomi *et al.*, 2011b; Ju *et al.*, 2007).

Soilborne pathogens have been often isolated from symptomatic plants and many autotoxic compounds have been identified and quantified from sick soil. However, both the pathogenic and autotoxicity hypotheses are still unable to fully explain the species-specificity and the long durability of soil sickness in field conditions. In other words, the relative role of detrimental microbial consortia and autotoxic factors in SS is far to be completely understood. Determining which microbes determine the observed plant decline require testing Koch's postulates, which are based on the selective exclusion of all possible microbes one by one and adding them back again one by one. The enormous diversity of soil microbiota makes this approach practically infeasible, especially if all possible interactions are considered. Innovative approaches are required to circumvent this methodological limitation. Recently, Van der Putten (2017) described soil microbiome as an orchestra where different microbial groups contribute to the whole symphony. Then, which microbial group creates the dissonance in sick soil? Studies from natural ecosystems suggest that an unbalance between mycorrhizal fungi and soilborne pathogens is a pivotal factor. More holistic approaches, for instance based on metagenomics, would be very useful in agro-ecosystems where the reductionist approach does not seem to give clear cut answers. The recent discovery that exDNA has self-inhibitory effects renewed the interest on the autotoxicity hypothesis, nevertheless this is a totally new topic, and more solid and systematic field investigations are needed.

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