Anaerobic Soil Disinfestation

Subjects: Microbiology

Contributor: Renuka Attanayake

Anaerobic soil disinfection (ASD) has been identified as an alternative soil-borne pathogen control strategy to chemical fumigation. ASD involves the application of an easily liable carbon source followed by irrigation to field capacity and maintenance of an anaerobic condition for a certain period.

soil-borne pathogens | chemical fumigation | anaerobic soil disinfestation | ASD | C source

1. Introduction

Crops are often attacked by various plant pathogens, plant-parasitic nematodes, insect pests, and weeds causing great economic losses around the world. Among diverse groups of plant pathogens, soil-borne phytopathogens pose a great threat to crop production [1][2][3]. Although soil is a home for billions of living organisms (both macro and microorganisms), they must face a multitude of challenges such as flood, drought, and agricultural practices. However, soil-borne pathogens can survive under these challenges and cause serious crop damage around the world. For example, waterlogged agricultural fields may be unfavourable for many organisms but favourable for root-infecting fungi and oomycetes such as *Pythium* and *Phytophthora* spp. [4][5][6]. Although drought conditions are unfavourable for most of the organisms, soil-borne pathogen species such as *Fusarium* spp. and *Verticillium* spp. [5] manage to cause severe infections. Hence, soil-borne phytopathogens show a great deal of evolutionary adaptations. They can survive in the soils for many years in the absence of host plants through the formation of resistant structures such as microsclerotia (*Verticillium* spp.), sclerotia (*Sclerotinia* spp.), chlamydospores (*Fusarium* spp.), or oospores (*Phytophthora* spp.) [7][8][9][10]. Microsclerotia and sclerotia have the same anatomical structure, consisting of outer melanized parenchyma cells and inner colorless medullary cells, and are asexual in nature. Chlamydospores are thick-walled asexual survival structures whereas oospores are thick-walled sexual structures with food reserves for better survival. These structures may be melanised or non-melanised. Melanisation of survival structures has several evolutionary advantages such as protection from UV radiation, successful penetration during infection, long-term survival, growth, and development [11][12]. Wilhelm [13] found the persistence of microsclerotia of *Verticillium alboatrum* for 14 years in soil, which were viable even after the exposure to desiccation at high temperatures. Ben-Yephet et al. [14] reported the survival of sclerotia of soil-borne *Sclerotinia sclerotiorum* declined after an outbreak of lettuce drop, nevertheless, about 5.5% were viable even after seven years. Babadoost and Pavon [15] assessed the survival of *Phytophthora capsici* oospores in the soil in Illinois (USA) and found three to four years of survivability. Apart from soil-borne fungal plant pathogens, plant-parasitic nematodes have been recognized as another group of challenging pathogens to manage [16].

Besides, each plant can be infected by several pathogen species and the complex nature of the soil environment, it is difficult to control diseases caused by soil-borne pathogens. Hence, successful control of soil-borne pathogens is a major challenge due to inherent difficulties of disease prediction, early detection, and accurate diagnosis [2]. Some modern crop production systems are based on raised-bed, plasticulture, and limited or short crop rotation-lengths, probably with the unavoidable application of broad-spectrum soil fumigants to manage pests and diseases [1]. Since the mid-20th century, synthetic chemicals have been used to control many plant diseases including a broad spectrum soil fumigant, methyl bromide (MeBr) [17][18][19]. Since then, MeBr has been heavily applied worldwide primarily to control soil-borne pathogens as well as the nematodes [20]. For example, five million kg of MeBr were used only in California in the year 2000 [21]. MeBr has been identified as a stratospheric ozone-depleting component by the U.S. Environmental Protection Agency (EPA) and the United Nations Environment Program (UNEP). Bolstered by the 1994 UNEP Montreal Protocol on Substances that Deplete the Ozone Layer, MeBr was identified as a major ozone-depleting compound [22]. Thereafter, MeBr was completely banned by the 1 January 2005 with few exceptions [19][21][23][24].

Alternative synthetic fumigants such as 1,3-dichloropropene, 1,3-D, chloropicrin, trichloronitromethane, methyl isothiocyanate, allyl isothiocyanate (AITC), and dazomet were tested and applied by the farming communities around the world yet were poorly accepted due to geographic limitations, reduced efficacy, and regulatory constraints [25][26][27]. Moreover, many criticisms have been generated from the public and from the scientific communities against the use of such chemical soil disinfestation methods due to their toxicity on humans and undesirable effects on non-target organisms such as beneficial microflora, groundwater pollution, and development of resistance [19][28][29][30][31][32].

Therefore, farmers were compelled to use non-chemical approaches. Traditionally a number of environmental friendly approaches such as mixed cropping, crop rotation, resistant cultivars/selective breeding, application of biocontrol agents, flooding, solarisation, steaming, pasteurisation, hot water treatment, and bio-fumigation have been applied by farmers around the world to mitigate soil-borne diseases [19][33][34][35]. Nevertheless, these applications were not as popular as chemical fumigants due to several limitations [19]. Application of mixed cropping systems may be helpful in increasing the crop yield while addressing some of the soil-borne pathogen problems [36], yet it is not always economically feasible when the rotation is done with low economical value crops [35]. Although selective breeding shows some level of effectiveness against soil-borne pathogens, host resistance breakdown has been reported, and no completely resistant cultivars are available for all the crops [35] Another option would be the use of biocontrol agents, however, these are highly specific for particular pathogen species if not for strains, and effectiveness is greatly dependent on the environmental factors [37]. Similarly, other non-chemical approaches have their own disadvantages, hence there have been limited applications [33][36][38][39][40][41].

1.1. Anaerobic Soil Disinfestation (ASD)

To minimize the above drawbacks of chemical and non-chemical methods of soil-borne pathogen control, researchers found alternative methods, and one such promising approach is anaerobic soil disinfestation (ASD), also called biological soil disinfection (BSD) or reductive soil disinfection (RDS). This method was first described

independently by researchers in Japan [42][43] and in the Netherlands [44] and was later adapted to the USA [45] to control soil-borne pathogens in strawberry and vegetable fields. Thereafter, researchers around the world started applying this method, showing a great potential to control various soil-borne phytopathogens [44][45][46][47][48][49][50][51][52][53][54][55].

The method is characterized by non-chemical pre-plant control of soil-borne phytopathogens using few simple steps [29][56]. The first step of ASD is the incorporation of organic amendments (usually an easily labile carbon source) to the topsoil. The soil is later wetted to field capacity and covered with a clear (preferably black) and gas-impermeable polyethylene sheet for a defined period of time to maintain an anaerobic condition [57]. The effectiveness of ASD has been evaluated against soil-borne diseases such as potato brown rot [46], spinach and tomato wilt diseases [48], *Prunus* [58] and apple replant disease [50], Fusarium wilt of banana [59], root and crown rot diseases of pepper [60], etc., with promising results. ASD has now become popular in organic agriculture worldwide and is practiced under greenhouse and field conditions as well [47][51][61]. There is some evidence that ASD also can contribute to the development of disease-suppressive soils [57].

2. Trends and Gaps in Application of ASD

2.1. Geographical Projection

When ASD was first introduced in Japan, it was initially suggested to be used with organic materials such as wheat bran, molasses, rice straw, and rice bran specifically at 1 to 2 tons per 0.1 ha, followed by flooding and plastic film covering of the soil surface [42]. In Netherlands, Blok et al. [44] carried out a two-year ASD field experiment in 1994 and 1995 using fresh broccoli or grass (3.4 to 4.0 kg fresh weight m^{-2}) as C sources. They came up with the landmark finding that there was a significant control of soil-born fungal pathogens: *Fusarium oxysporum*, *Rhizoctonia solani,* and *Verticillium dahliae.* The study was published in 2000 and concluded that this novel method could control a wide range of phytopathogens [44]. Based on the published data, it is clear that the initial development of ASD was restricted to the Netherlands and Japan and was later expanded to the USA. However, beyond this point, ASD research showed slow progress until 2014, in which the number of publications were more than doubled (Figure 1). During the past few years, several other countries have also attempted to mitigate soil-borne diseases through ASD.

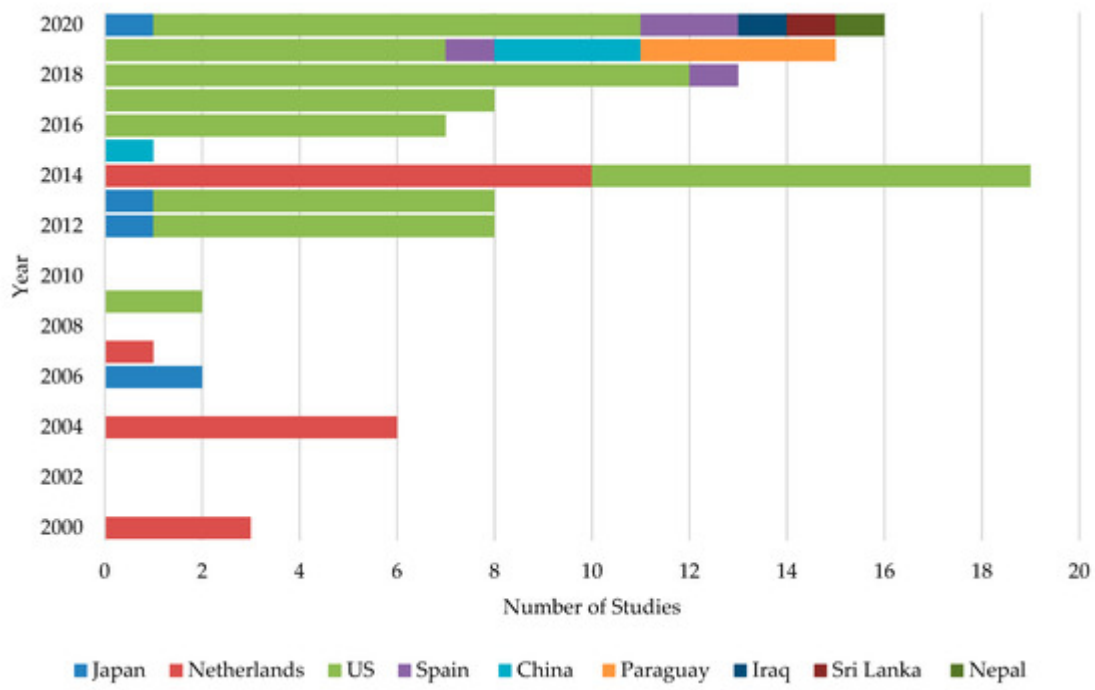

Figure 1. International distribution of ASD studies conducted in each year.

It is interesting to note that almost all the studies have been restricted to nine countries—primarily the USA (63.3%) followed by the Netherlands (18.3%) and Japan (4.6%). Spain, China, and Paraguay shared about 11.1% of ASD studies equally. The rest of the studies were conducted in Iraq, Sri Lanka, and Nepal, where only one study has been conducted in each country.

2.2. Application of ASD to Control Pathogens, Weeds, and Effect on Crop Yield

Initially, ASD studies were applied to control soil-borne phytopathogenic fungi [44]. Later on, it expanded towards control of nematodes, oomycetes, weeds, and protozoans. However, studies on ASD targeting soil borne-fungi have been extensively carried out mainly due to their broad host range, enormous losses in crop yield and quality, worldwide distribution, management difficulties, and extensive use of synthetic fungicides [62]. For example, 46.8% of the studies were concentrated on the control of fungal pathogens followed by 26.6%, 5.5%, and 4.6% of studies dedicating to testing the effects on nematodes, yield increase, and weed control, respectively. Moreover, about 12.8% of studies have been carried out with different aspects such as evaluating the effect of ASD on soil microflora and cost benefits of the application of ASD. Figure 2 shows the number of studies conducted in each year targeting soil-borne pathogens and other aspects. A majority (63%) of ASD studies were carried out under field conditions. About 35.1% of studies were performed as greenhouse or growth chamber experiments, while about 1.9% of the studies were conducted as lab experiments.

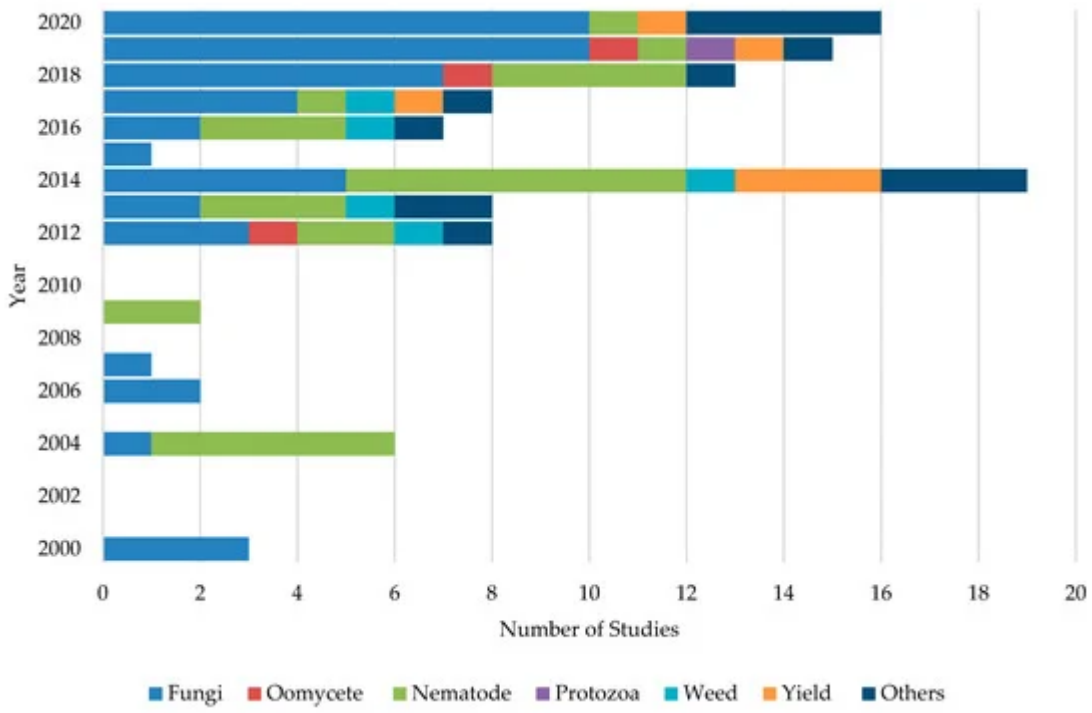

Figure 2. Different ASD studies conducted during the past two decades targeting each group of soil-borne pathogens and other aspects of crop production systems.

About 28.7% of the ASD studies were targeted to control tomato pathogens while 13%, 9.3%, and 7.4% of the studies were targeted to control strawberry, potato, and bell pepper pathogens, respectively. About 12.9% of the studies did not report the target crop or the intended pathogen to control. The remaining studies were carried out to control soil-borne pathogens associated with lettuce, mustard green, spinach, carrot, cabbage, cauliflower, eggplant, lily bulb, and common bean production fields. Studied organisms included pathogenic fungi: *Fusarium oxysporum, Verticillium dahlia, Colletotrichum coccodes, Sclerotinia sclerotiorum,* and *S. rolfsii,* nematodes: *Meloidogyne hapla, M. incognita* and *Pyrenochaeta lycopersici*, oomycetes: *Phytophthora capsici* and protist: *Plasmodiophora brassicae* etc.

2.3. C Source Dependency of ASD

The effectiveness of ASD predominantly depends on the selection of C source, C:N ratio, rate of its application, and anaerobic period. However, soil temperature, water holding capacity of soil, and climatic conditions should also be considered before implementing ASD [63][64][65]. C sources should be easily applicable, readily available/locally available, easily degradable, affordable, and able to control a broad spectrum of phytopathogens [65]. Careful selection of C source seems to play the key role in ASD since several studies have shown the emission of volatile compounds with strong pathogen inhibitory activities. Use of *Brassica juncea* cv. Pacific Gold seed meal (seed meal is a waste product of the oil extraction process) as the C source caused the release of isothiocyanates, alcohols, organic acids, organic sulphides, and esters, while application of orchard grass residues released organic sulfides, ketones, organic acids, and hydrocarbons. Similarly, the application of rice bran-treated soils emitted a spectrum of volatile compounds containing organic acids, alcohols, and esters [50][66]. Mahalingam et al. [55]

conducting a gas chromatography-mass spectrometry (GC-MS) analysis of cabbage and leek cull piles reported the presence of antifungal volatiles.

Moreover, fresh and dried plant materials and composted broiler litter have been tested in multiple studies as the C source in ASD-based studies [54][65][67]. Ethanol has been incorporated as a C source in controlling phytopathogens due to the inefficiency of some of the commonly used C sources. As an example, Momma et al. [68] found that the use of wheat bran alone is not effective in controlling *Fusarium oxysporum* infection of tomato. However, once the soil is saturated with 1% ethanol solution (ethanol medicated ASD treatment), high levels of suppression of *F. oxysporum* were observed. Hewavitharana et al. [53] also reported that ethanol (10%) mediated ASD effectively controlled apple root infection caused by *Rhizoctonia solani* AG-5 and *Pratylenchus penetrans.* In addition, it has been reported that ethanol temporarily increased the anaerobic bacterial population [68]. A summary of C source, application rate, target pathogen group, and optimum temperature along with the reference are shown in the Table 1 below.

Table 1. Details of successful ASD experiments conducted during the past few years.

C Source	Application Rate of C Sources (t ha^{-1})	Pathogens Suppressed	Mean Soil Temperature/Range (°C)	Treatment Period	Crop	Field/Greenhouse	Country	Reference
Fresh broccoli (*Brassica oleracea*)	34,38	*Fusarium oxysporum*, *Rhizoctonia solani, Verticillium dahliae*	25–32, 29–39	15 weeks	N/A	Field, plot	Netherlands	[44]
Perennial ryegrass (*Lolium perenne*)	40	*Fusarium oxysporum*, *Rhizoctonia solani, Verticillium dahliae*	25–32, 29–39	15 weeks	N/A	Field, plot	Netherlands	[44]
Grass or potato	30	*Ralstonia solanacearum*	N/A	6 weeks	Potato	Laboratory, field	Netherlands	[46]

C Source	Application Rate of C Sources (t ha^{-1})	Pathogens Suppressed	Mean Soil Temperature/Range (°C)	Treatment Period	Crop	Field/Greenhouse	Country	Reference
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Wheat bran	2	*Meloidogyne incognita*	35.0	24 days	Tomato	Greenhouse, plot	Japan	[47]
Cereal rye (*Secale cereale*)	0.134	*Rhizoctonia solani*	20.8	4 weeks	Tomato, bell pepper	Field, plot	USA	[49]
Mustard (*Brassica juncea*) seed meal	4.9	*Rhizoctonia solani, Pythium ultimum, Fusarium oxysporum*	18–24	2 weeks	Apple	Growth chamber, pot	USA	[50]
Grass residues	40.0	*Rhizoctonia solani, Pythium ultimum, Fusarium oxysporum*	18–24	2 weeks	Apple	Growth chamber, pot	USA	[50]
Rice bran	20	*Verticillium dahliae*	21–23	4 weeks	Strawberries	Field	USA	[50]
Radish roots	100	*Fusarium oxysporum*	33.1	3 weeks	Spinach	Greenhouse, field	Japan	[48]

C Source	Application Rate of C Sources (t ha^{-1})	Pathogens Suppressed	Mean Soil Temperature/Range (°C)	Treatment Period	Crop	Field/Greenhouse	Country	Reference
Mixture of fresh rye-grass species	50	*Verticillium dahliae, Pasteuria penetrans*	N/A	12 weeks	N/A	Field	Netherlands	[48]
Mustard (*Brassica juncea*)	50	*Fusarium oxysporum*	33.1	3 weeks	Spinach	Greenhouse, pots, field	Japan	[48]
Wheat bran	20	*Fusarium oxysporum*	33.1	3 weeks	Spinach	Green house, pots, field	Japan	[48]
Rice bran	4.4	*Rhizoctonia solani*, *Pratylenchus penetrans*	18–24	2 weeks	Apple	Growth chamber, pot	USA	[53]
Fresh orchard grass residues	20	*Rhizoctonia solani*, *Pratylenchus penetrans*	18–24	2 weeks	Apple	Growth chamber, pot	USA	[53]
Mustard (*Brassica juncea*) seed meal	4.4 [74]	*Rhizoctonia solani*, *Pratylenchus penetrans* [52]	18–24	2 weeks	Apple	Growth chamber, pot [73]	USA	[53] [70]

riculture, available ASD has SA [71][72] ontrol of whereas , tomato plant residues with fresh sheep manure were effective in controlling *M. incognita* [75]. Korthals et al. [52] reported that ASD was more effective and longer-lasting against *P. penetrans* and *V. dahliae* than chemical control, and Di Gioia et al. [76] also reported ASD was effective as chemical soil fumigation against *Meloidogyne* sp. However, it should be noted that the selection of C source should be done carefully, and targeted organism should be taken into account. As an example, Korthals et al. [52] demonstrated that *B. junceae* leaf incorporation (no anaerobic condition was imposed) increased *P. penetrans* density in soil.

2.5. Effect of ASD on Weed Control and Yield

C Source	Application Rate of C Sources (t ha^{-1}) [77]	Pathogens Suppressed	Mean Soil Temperature/Range (°C)	Treatment Period	Crop	Field/Greenhouse	Country	Reference
Rice bran	20	*Phytophthora nicotianae* [66]	15–35	4 weeks [64]	Pepper	Field [49]	Spain	[54]
Rapeseed cake	20	*Phytophthora nicotianae*	15–35	4 weeks	Pepper [78]	Field, plot	Spain [79]	[54]
Grape pomace	40	*Phytophthora nicotianae* [19][80]	15–35	4 weeks	Pepper	Field, plot	Spain	[54]
Rice bran	20	*Fusarium oxysporum*	18–24	15 days	Strawberry	Growth chamber, pot	USA	[69]

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t al. [52] bulb and

reported that ASD produced higher yields in all the crops compared to the untreated control. However, Di Gioia et al. [81] reported that ASD had no significant effect on tomato yield when composted poultry litter (22 Mg ha^{-1}) and molasses (13.9 and 27.7 m^3 ha^{-1}) were used as the C sources. Nevertheless, plant nutrients such as potassium, calcium, magnesium, and iron accumulation had improved in ASD treated plants. Yield improvement might have resulted due to the combined effects of disease control, weed control, and improved soil nutrients.

2.6. Mechanism of ASD

Only 34% of studies have reported the mechanism of ASD. Nevertheless, the exact mechanism of ASD is still not clear, and further studies are necessary. In ASD, the use of different carbon sources helps boosting soil microbial biomass and enzyme activities [54]. Covering with a plastic trap as well as the utilization of available oxygen by the aerobic microorganisms ultimately create an anaerobic soil condition. Figure 3 shows possible soil pathogen control mechanism(s) by ASD.

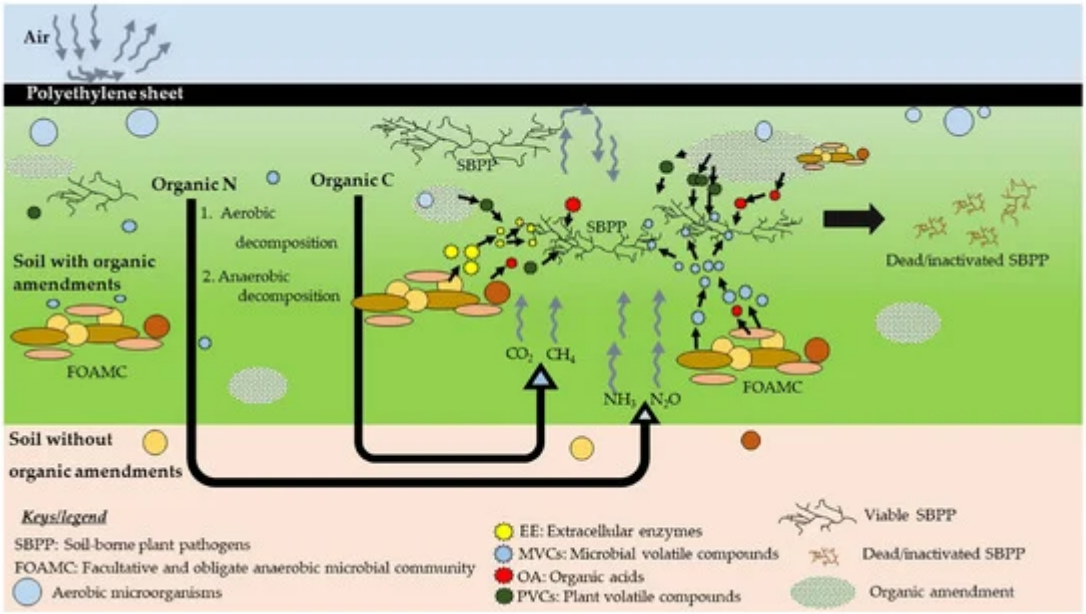

Figure 3. Proposed pathogen control mechanism(s) (simplified) during ASD. The decomposition of organic amendments is initiated by the activities of aerobic microorganisms (e.g., *Bacillus* spp.). Later, the growth of anaerobic bacteria (e.g., *Clostridium* spp.) is stimulated with the depletion of oxygen, and anaerobic decomposition of organic matter is initiated. This pathway is more complex and less energy demanding than that of the aerobic decomposition. Facultative and obligate anaerobic microbial communities (FOAMC) decompose the added organic C and produce several gases such as CO_2, CH_4, and volatile compounds. Decomposition of organic N leads to produce soil ammonium (NH_4^+) via mineralization. Finally, due to series of activities, CO_2, CH_4, N_2O, and NH_3 are released, and these gases have toxic effect on living matter. Combined effects of above released gases along with organic acids (OA), microbes released extracellular enzymes (EE), microbial volatile compounds (MVCs), and plant volatile/non-volatile compounds (PVCs) along with the change of soil physical properties may cause the inhibition of soil-borne phytopathogens (SBPP).

Polyethylene sheets prevent further penetration of oxygen to the treatment creating a conducive environment for anaerobic microorganisms (e.g., Clostridial species). These anaerobic decomposers use C source to respire while releasing toxic anaerobic by-products such as CO_2, NH_3, H_2S, CH_4, and N_2O [19]. However, these by-products are released to the atmosphere quickly, as soon as the tarp is removed or the holes are punched [79]. Researchers predicted that the limitation of oxygen along with the trapping of toxic compounds and lowered pH could control soil-borne phytopathogens [44]. Under the flooded conditions, microbes decompose liable C sources and release gases (or by-products) suppressing some of the phytopathogens [19]. ASD has shown significant changes in the whole soil microbial communities [46][65]. Mowlick et al. [82] reported the changes in microbial community structures (through clone library analysis) after ASD treatment. They observed ASD caused a reduction in diversity of bacterial communities of various phylogenetic groups and a domination of anaerobic clostridial class bacteria.

In ASD, accumulation of various volatile compounds with the potential to control phytopathogens greatly depends on the C source used [50][55][66][83][84]. In addition to pathogen control, plant growth promotion abilities of microbial volatile compounds (MVCs) have also been extensively reported [84][85][86]. These volatile compounds spread

through soil by diffusion, and efficacy of volatile compounds is greater than non-volatile compounds [87][88][89]. Compared to the other MVCs such as enzymes, antibiotics, and toxins, microbial organic volatiles are typically small in size (up to 20 carbon atoms) with molecular mass ranging from 100 to 500 Daltons [85]. MVCs have a good diffusing ability under normal temperatures and pressures [90]. Volatile compounds produced by the bacteria are dominated by alkenes, alcohols, ketones, terpenes, benzenoids, pyrazines, acids, and esters, while fungal volatiles are dominated by alcohols, benzenoids, aldehydes, alkenes, acids, esters, and ketones [85]. Antifungal compounds such as dimethyl disulfide, dimethyl trisulfide, and acetoin are well reported [90]. Studies found that the fungal species such as *Aspergillus giganteus*, *Fusarium oxysporum*, *Penicillium viridicatum*, *Trichoderma viride*, and *Zygorhynchus vuilleminii* have abnormal morphologies in their conidiophores and hyphae when exposed to VOCs from bacteria and actinomycetes [91]. Rather than the production of volatile compounds [48], soil anaerobic bacterial communities could kill the phytopathogenic fungi through extracellular enzymes such as 1,3-glucanase and chitosanase, whereas obligate anaerobic *Clostridium beijerinckii* could suppress the spinach wilt fungi, *F. oxysporum* and *F. spinaciae* [61]. However, the prevailing groups of the microorganisms may be different based on the type of C source used and the treatment period of ASD, since some microorganisms are responsive to fluctuating redox potentials [45][92].

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