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# Anaerobic soil disinfestation: a biologically-based solution for sustainable crop production

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Anaerobic soil disinfestation (ASD) is a novel, eco-friendly method to improve soil health. This method creates oxygen-free conditions by adding organic amendments as a carbon source, saturating the soil to field capacity, and then covering it with plastic. These anaerobic conditions reduce soilborne pathogens, enhance microbial diversity, and increase crop productivity. This review provides an overview of the different organic amendments used in ASD, their impact on managing soilborne pathogens, the role of beneficial microbiomes, and the challenges associated with adopting ASD. It also emphasizes the potential benefits of ASD and the innovative approach to advancing it for sustainable agriculture.

## KEYWORDS

anaerobic soil disinfestation, organic amendments, soilborne pathogens, soil microbiome, sustainable agriculture

## 1 Introduction

### 1.1 Anaerobic soil disinfestation concept and significance

For many years, pre-plant soil fumigation using methyl bromide 1, 3-dichloropropene, chloropicrin, and methyl iodide has been the go-to method to manage several soilborne plant pathogens in various crops (Theis and Fery, 2002; Martin, 2003; Velders et al., 2007; Hanson et al., 2011; Panth et al., 2020). However, the phase-out of ozone-depleting fumigants, including methyl bromide, in 2005 due to environmental pollution (Hanson et al., 2011; Roskopf et al., 2015; Strauss and Kluepfel, 2015) has led to the exploration of alternative methods. Other soil fumigants such as trichloronitromethane, methyl isothiocyanate, allyl isothiocyanate (AITC), and dazomet were also used to manage soilborne pathogens (Martin, 2003). However, their use also has many drawbacks, such as reduced efficacy and regulatory concerns. The major soilborne pathogens are *Verticillium* spp., *Fusarium* spp., *Pythium* spp., *Rhizoctonia* spp., and *Sclerotinia* spp.

(Lamers et al., 2014), soil nematodes (Testen et al., 2021), and weeds (Strauss and Kluepfel, 2015; Panth et al., 2020). These pathogenic fungi can survive for long periods due to their ability to form resilient structures (Katan, 2017; Priyashantha and Attanayake, 2021). Non-chemical soil disinfestation, particularly anaerobic soil disinfestation (ASD), comes in as a potential integrated pest management (IPM) tool for managing soilborne pathogens (Rokunuzzaman et al., 2016). The potential of ASD to revolutionize pest management is a promising prospect for the future.

ASD, a unique approach that utilizes organic amendments as carbon sources, is gaining popularity in agricultural practices worldwide (Molendijk et al., 2009). This technique, known as biological soil disinfestation (BSD), was initially developed in Japan and the Netherlands (Blok et al., 2000; Momma et al., 2006). Unlike traditional organic amendments that increase organic matter, improve soil fertility, and enhance water-holding capacity, specific carbon sources can induce ASD (Poret-Peterson et al., 2019). This process stimulates the soil microbiome to efficiently break down and utilize the carbon source (e.g., sugar) as its sole energy source. By creating an oxygen-depleted environment within the soil, ASD significantly, enhanced anaerobic beneficial microbiomes compete with or suppress soilborne pathogens' populations (Molendijk et al., 2009; Lamers et al., 2014; Strauss and Kluepfel, 2015). For instance, a strict anaerobic bacterium, *Clostridia*, was sharply increased in soil-amended with wheat bran and cover crops such as *Brassica juncea* or *Avena sativa* as a carbon source (Mowlick et al., 2013a, b). This review aims to describe the current status of ASD and its potential

impacts on crop production systems, emphasizing future research directions regarding challenges and opportunities in using ASD (Figure 1).

## 1.2 The key steps and organic amendments used as a carbon source in ASD

ASD involves the addition of organic amendments to the topsoil to serve as a carbon source (Shennan et al., 2014, 2018). The first step is to till and moisten the soil to create optimal conditions. Then, a readily degradable organic material, such as fresh manure or compost, is incorporated into the soil to feed these beneficial microbes. Next, the soil surface is sealed with an impermeable tarp to create an oxygen-limited environment for 3 to 6 weeks, depending on soil temperature and target organisms. Finally, the tarp is removed, and the soil is tilled again to reintroduce oxygen and break down the organic matter (Blok et al., 2000; Momma et al., 2013; Shennan et al., 2014; Roszkopf et al., 2015; Strauss and Kluepfel, 2015; Shennan et al., 2018; Priyashantha and Attanayake, 2021; Lopes et al., 2022).

In recent years, three types of carbon sources have been utilized in ASD (Strauss and Kluepfel, 2015). The usual solid organic amendments used as carbon sources in ASD include rice bran, wheat bran, dry molasses, and mustard meal in the cultivation of fruits and vegetables (Shennan et al., 2014; Testen and Miller, 2018; Wang and Mazzola, 2019). For example, ASD with rice and wheat brans was used in strawberry fields in California

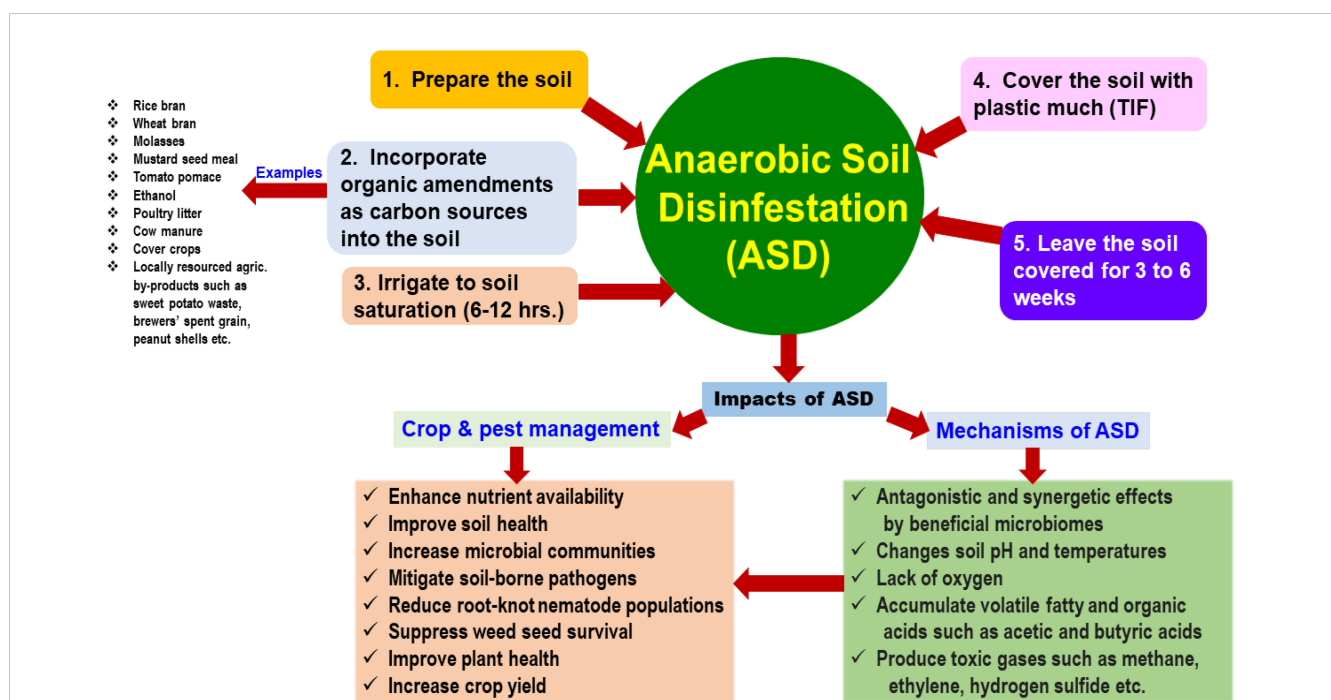


FIGURE 1

Overview of anaerobic soil disinfestation (ASD), which enhances soil structure, suppresses weeds, fosters microbial diversity, promotes plant health, and improves crop yield (Blok et al., 2000; Butler et al., 2012a, b; Momma et al., 2013; Hewavitharana et al., 2019; 2021; Hewavitharana and Mazzola, 2016; Lopes et al., 2022; Priyashantha and Attanayake, 2021; Shennan et al., 2014; 2018; Roszkopf et al., 2015; 2020; Strauss and Kluepfel, 2015).

(Shennan et al., 2014) and for tomato and melon cultivation in Japan (Momma et al., 2013). Wheat and rice brans were both applied at a rate of 10 t/ha in the fields, effectively suppressing *Fusarium oxysporum* (Momma et al., 2010) and *Verticillium dahliae* (Shennan et al., 2018), respectively. Furthermore, when ASD with rice bran was applied at two rates (15.7 t/ha and 202.2 t/ha) to nut-tree nurseries in California, both of these rates significantly suppressed the populations of *Agrobacterium tumefaciens* and *Pythium* spp. in the soil (Strauss and Kluepfel, 2015). Liquid organic amendments, such as ethanol, liquid molasses, and sucrose, were commonly utilized as carbon sources in ASD (Strauss and Kluepfel, 2015; Lopes et al., 2022). For instance, a blend of dry molasses on a soy hull carrier and cornstarch applied at a 4 mg C/g soil rate with a carbon-to-nitrogen ratio of 30:1 has shown promise (Swilling et al., 2021). The combination of dry and liquid organic amendments used in ASD included composted poultry litter and liquid molasses or compost with solarization, significantly increasing soil inorganic N concentrations and suppressing soilborne fungi and *Meloidogyne* spp. root galling (Butler et al., 2012b, 2014; Strauss and Kluepfel, 2015).

In ASD application, the incubation period (anaerobic state) has been observed to last up to 3 weeks (Momma et al., 2010; Shennan et al., 2018). Several studies have investigated using various carbon sources in ASD for different durations in multiple crops. For example, fresh broccoli as a carbon source in ASD was studied for 15 weeks (Blok et al., 2000), while perennial ryegrass and potato haulms were used in potato cultivation for six weeks (Messiha et al., 2007). Wheat and rice brans were used in ASD in tomatoes and apples (Hewavitharana et al., 2014), and mustard was studied as a substrate for spinach over three weeks (Mowlick et al., 2013b). Grape pomace was used as a substrate in pepper cultivation for four weeks (Serrano-Pérez et al., 2017), and apple substrates were examined for two weeks (Mowlick et al., 2013a; Strauss and Kluepfel, 2015).

The critical steps of ASD involve the decomposition of carbon sources and changes in the soil microbiome and metabolome over three distinct phases (Hewavitharana et al., 2019). Briefly, in phase 1 (0 to 12 hrs), there is rapid consumption of oxygen, amino acids, and polysaccharides, with a dominance of aerobic and facultative bacterial taxa such as *Firmicutes* (*Bacillus* spp.), *Actinobacteria* (*Streptomyces* spp.), *Proteobacteria* (*Pseudomonas* spp.) and fungal phylum such as *Ascomycota* (*Trichoderma*). During phase 2 (peak at 48 hrs), bacterial taxa such as *Firmicutes*, *Actinobacteria*, *Proteobacteria*, and fungal phylum such as *Zygomycota* become dominant due to strict aerobes consuming oxygen. Lactic acid levels peak during this stage and strongly correlate with the rapid multiplication of *Bacillus* spp (Hewavitharana et al., 2019). Moreover, acetone, acetic acid, 1-butanol, and butanoic acid accumulate as *Clostridium* spp. multiply. In phase 3 (up to 3 weeks), antipathogen compounds produced by strict anaerobes, especially *Clostridium* spp., are frequently present in soil treated with ASD. These compounds, including acetate, butyrate, volatile acids, alcohols, volatile hydrocarbons, dimethyl di- and tri-sulfide, and dimethyl sulfoxide, are released during the final stage of ASD (Hewavitharana et al., 2019).

### 1.3 History of ASD and geographic application

In sub-tropical developing countries, reducing arable land due to industrialization and rapid population growth poses a significant threat to crop productivity (Priyashantha and Attanayake, 2021). Other issues include small-scale farming, multiple cropping, year-round crop cultivation, high crop and plant pathogen diversity, limited access to new technology and drip irrigation, and lack of knowledge among farmers (Phalan et al., 2013; Priyashantha and Attanayake, 2021). Crop productivity in developing subtropical countries is considerably lower than in temperate countries (Thottathil et al., 2016). Therefore, it is crucial to maximize soil health for sustainable agriculture (Priyashantha and Attanayake, 2021).

To effectively implement ASD for managing soilborne plant pathogens, it is crucial to understand its effectiveness in different settings, such as varying times of the year, cropping systems, and soil types (Poret-Peterson et al., 2019). Identifying the optimal carbon they play a vital role in reducing production costs (Strauss and Kluepfel, 2015; Shrestha et al., 2016). The effectiveness of ASD largely depends on selecting easily applicable, locally available, and easily degradable organic amendments or agricultural by-products (Strauss and Kluepfel, 2015; Lopes et al., 2022). Most ASD studies have been carried out in temperate and sub-tropical countries. Among temperate countries, 63.3% of ASD work was done in the United States (Priyashantha and Attanayake, 2021). However, limited ASD research has been conducted in tropical developing countries.

ASD has shown promise for high soil temperatures and sandy soil. Based on a meta-analysis conducted by Shrestha et al. (2016), in both laboratory and growth chamber conditions, a 61% pathogen suppression was observed, while the field and greenhouse conditions showed slightly higher suppression at 72%. The authors suggested that at higher soil temperatures, the pathogen reduction from ASD effect was about 10% higher than at moderate and lower temperatures (Shrestha et al., 2016). Furthermore, the ASD treatment in volcanic soil from Japan demonstrated a significantly higher suppression of plant pathogens compared to sandy soil (83% vs. 64%). At the same time, no significant difference was observed between soil type and clay, gray lowland, and loam soil (Shrestha et al., 2016). This is likely due to the suppression of pathogens and weeds by lethal temperatures and adding organic matter to the sandy soils (Strauss and Kluepfel, 2015; Shrestha et al., 2016). ASD studies conducted in temperate countries like Ohio, USA, showed that average soil temperatures ranged from 16.3 to 27.8°C for high tunnel tomato production in September and October (Testen et al., 2021) or 23.6 to 30.8°C for summer tomato production in muck soils (Testen and Miller, 2018). Despite these lower soil temperatures, the loss of iron oxide paint, which indicates soil-reducing conditions, was slightly lower in most trials than in ASD trials conducted with warmer soil temperatures (Testen and Miller, 2018; Testen et al., 2021). However, high soil temperatures (20 to 25°C) are required for effectively managing the tomato soilborne disease complex (Testen et al., 2021).

ASD was first launched in Japan and effectively managed soilborne fungal pathogens. The Netherlands followed and modified the model, and ASD was later adopted in other countries, including China (Ya'nan et al., 2019), Paraguay (Sanabria-Velazquez, 2018; Quintino et al., 2023), the USA (Butler et al., 2012a, b; Garcia Gonzalez, 2021; Shennan et al., 2018), Sri Lanka (Priyashantha and Attanayake, 2021), and Nepal (Bhandari et al., 2020; Khadka and Miller, 2021; Khadka et al., 2021) to combat soilborne pathogens (Figure 2).

## 2 Impacts of ASD

### 2.1 Impact of ASD on soil physiochemical properties and soil health

The success of ASD is influenced by both the physical and chemical changes and the biological shifts in soils (Strauss and Kluepfel, 2015; Shrestha et al., 2016), which may be related to the carbon sources used to induce ASD (Hewavitharana et al., 2014; Hewavitharana and Mazzola, 2016). ASD can influence individual microbial species' composition, functionality, and interactions, making them valuable soil health indicators (Preece et al., 2019). Additionally, it can significantly alter microbial composition and diversity and improve soil health (Messiha et al., 2007; Mowlick et al., 2013a; Poret-Peterson et al., 2019, 2020). Soil temperature, water-holding capacity, soil type, and carbon sources contribute to ASD (Strauss and Kluepfel, 2015; Shrestha et al., 2016; Shennan et al., 2018).

Different organic amendments used as carbon sources are rice straw, tobacco, rice bran, rapeseed meal, and sugarcane bagasse, significantly influencing soil fertility and health (Lopes et al., 2022). ASD can alter soil pH by producing organic acids and methane through anaerobic microbiomes (Priyashantha and Attanayake, 2021). Decomposing organic matter in ASD produces acetic and

n-butyric acids, lowering soil pH to around 5.5 and affecting soil-dwelling nematodes (Momma et al., 2006, 2013). This could be caused by anaerobic microbiomes consuming carbon sources, generating organic acids, and releasing iron ( $\text{Fe}^{2+}$ ) and manganese ( $\text{Mn}^{2+}$ ) ions, ultimately decreasing the soil pH (Momma et al., 2006, 2013). Adding rapeseed meal and tobacco stem in ASD significantly increased soil pH, lowered soil electrical conductivity (EC) and redox potential (Eh), and improved soil nutrient levels (Ya'nan et al., 2019). Additionally, using tobacco stems significantly increased the available potassium and organic matter levels in the soil. At the same time, rapeseed meals raised the levels of total nitrogen, organic matter, available nitrogen, and the activities of catalase and urease enzymes (Ya'nan et al., 2019). In China, soil treated with ASD using composted chicken manure showed a significant increase in ammonium nitrogen, nitrate-nitrogen, and organic matter (Song et al., 2020). Additionally, there was a substantial reduction in *Fusarium* spp. and *Phytophthora* spp. colonies in the strawberry field due to decreased oxidation-reduction potential (Song et al., 2020). The use of different carbon sources in ASD, such as alfalfa, maize, and rice straw, can result in an increase in  $\text{NH}_4\text{-N}$  content and a decrease in  $\text{NO}_3\text{-N}$  accumulation in the soil (Tan et al., 2019). This, in turn, can reduce soilborne pathogens like *Fusarium* and *Aspergillus* spp. Selecting carbon sources can also influence the C: N ratio and the soil's chemical and physical properties (Tan et al., 2019).

The C: N ratio is a crucial indicator of decomposition rate (Nicolardot et al., 2001). Shrestha et al. (2021) successfully used the ASD with organic amendments, using C: N ratios between 10:1 and 40:1, to suppress *Fusarium oxysporum* f. sp. *lycopersici* in soils above 25°C. Soil treated with ASD using wheat bran showed lower levels of water-soluble organic carbon and a higher C: N ratio compared to soil treated with other carbon sources, presumably due to the presence of recalcitrant carbon fractions such as cellulose, hemicellulose, and lignin in wheat bran (Lee et al., 2020). Dried

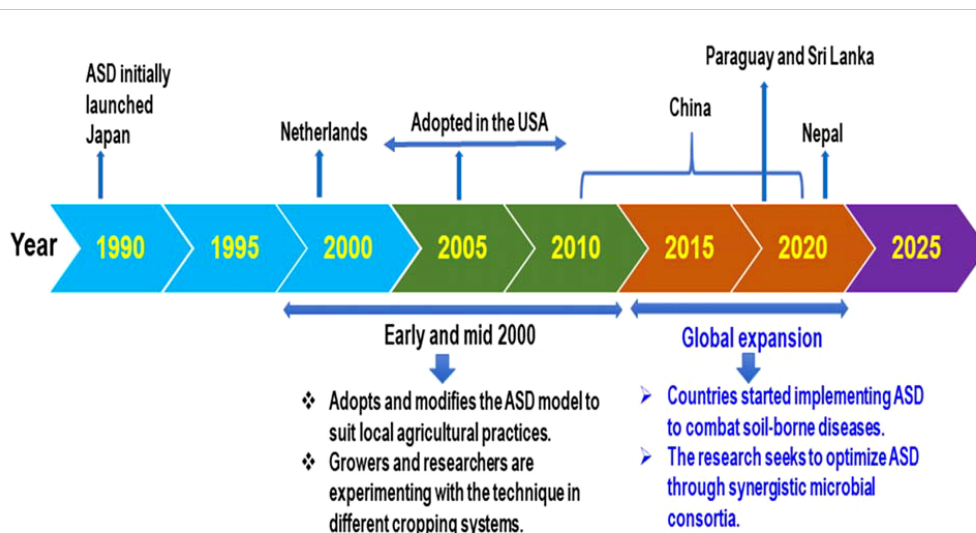


FIGURE 2

Mapping the global landscape: ASD innovation and adoption strategies (Momma et al., 2010; 2013; Khadka et al., 2021; Khadka and Miller, 2021; Priyashantha and Attanayake, 2021; Sanabria-Velazquez, 2018; Shennan et al., 2014; 2018; Quintino et al., 2023; Ya'nan et al., 2019).



molasses rapidly dissolved in the irrigation water during ASD due to its high water-soluble organic carbon fraction and C: N ratio (Lee et al., 2020). Previous studies have suggested that adding organic matter with a low C: N ratio to the soil could create the most anaerobic conditions and that the substrate C: N ratio is inversely related to the effectiveness of soil disinfestation (Blok et al., 2000; Shrestha et al., 2016; Testen and Miller, 2018). However, different substrates had various effects on the prokaryotic community, and the decomposition rate of the carbon sources, particularly the substrate's C: N ratio and water-soluble organic carbon content did not show a correlation with disinfestation efficiency (Lee et al., 2020).

Soils treated with ASD contained high levels of microbial communities capable of carrying out processes such as nitrogen fixation, denitrification, and sulfur, potassium, and phosphorus cycling, indicating that ASD may improve the availability of nitrogen, potassium, and phosphorus in the soil (Di Gioia et al., 2017; Poret-Peterson et al., 2019). Zhu et al. (2023a) found that the properties of the carbon source, crop cultivation, and soil chemical properties contributed to 66.2% and 39.0% of bacterial and fungal community variation, respectively. The results also indicated that factors such as the C: N ratio, crop cultivation, soil available phosphorus, and potassium significantly influenced bacterial community composition (Zhu et al., 2023b). Similarly, the C: N ratio, oxidized carbon contents, and crop cultivation were identified as crucial factors in shaping fungal community composition. The authors suggested that the C: N ratio and oxidized carbon contents of the carbon source were critical in soil microbiome reestablishment, *Fusarium* reproduction, and pepper crop performance in China (Zhu et al., 2023a).

## 2.2 Impact of ASD on microbial community composition and diversity

ASD with different carbon sources play a crucial role in improving soil microbial functioning and communities (Van Agtmaal et al., 2015; Shennan et al., 2018; Mao et al., 2022). When the soil is saturated with water, adding an easily available carbon source is thought to stimulate the rapid growth of aerobic microbiomes (Messiha et al., 2007). For example, bacterial phyla, such as *Firmicutes* and *Proteobacteria*, increased relative abundance in anaerobic conditions (Ya'nan et al., 2019). These microbiomes consume the remaining soil oxygen and create anaerobic soil conditions. This shift to anaerobic conditions can happen quickly and is influenced by factors such as soil water content, texture, structure, quality and quantity of the carbon source, and soil temperature (Butler et al., 2012a; Shennan et al., 2014). The bacterial community structure shifted 2 to 15 days after ASD initiation using ethanol (1% v/v) as the carbon source (Momma, 2015). However, Van Agtmaal et al. (2015) found a clear long-lasting impact of previous anaerobic stress on bacterial community composition three months after the ASD treatment. During the ASD process, Firmicutes phyla, such as *Bacillus*, *Clostridia*, and *Paenibacillus*, become the predominant bacterial population (Mowlick et al., 2013a; Mowlick et al., 2014; Strauss and Kluepfel, 2015).

The type of organic carbon source used can significantly influence the dominant bacterial species. For example, ASD using rice bran as a carbon source can increase the abundance of *Acidobacteria* and *Burkholderia* (Strauss and Kluepfel, 2015). In contrast, ASD with alfalfa as the carbon source can lead to

TABLE 1 Summary of the impact of anaerobic soil disinfestation (ASD) using common organic amendments as a carbon source on the composition of the microbial community.

Key carbon source used in ASD	Impact	Microbial diversity and composition	References
Wheat bran, blackstrap molasses, and ethanol	It shifts composition, reduces diversity, and favors anaerobes	<i>Firmicutes</i>	(Testen and Miller, 2018)
Sugarcane molasses and poultry litter	Doubling molasses boosted acid production but lowered microbiome diversity compared to a single application.	<i>Firmicutes</i> and <i>Proteobacteria</i>	(Hong et al., 2018)
<i>Brassica</i> seed meal, rice bran, composted steer manure, ethanol, and orchard grass	In general, ASD treatments recruit microbial elements that persist during the anaerobic phase of soil incubation, which may contribute functionally to suppressing <i>Rhizoctonia solani</i> AG-5 and <i>Pratylenchus penetrans</i>	Specific fungal taxa, such as <i>Ascomycota</i> , and bacterial taxa, such as <i>Acidobacteria</i> , <i>Actinobacteria</i> , <i>Chloroflexi</i> , and <i>Planctomycetes</i> , were more abundant	(Hewavitharana and Mazzola, 2016; Wang and Mazzola, 2019)
Dune sand, glacial, organic substrate addition, and anaerobic incubation	The proportion of <i>Firmicutes</i> bacteria increased in the total population and eradicated potato cyst nematode in all ASD treatments	<i>Firmicutes</i> (spore-forming, involved in fermentation)	(Runia et al., 2014)
Compared 100, 200, and 300 kg/ha activated carbon + solar radiation membrane with dazomet and chloropicrin	Treatment caused less soil bacterial damage than chemicals, showing promise as an alternative	Dominate phyla <i>Proteobacteria</i> , <i>Acidobacteria</i> , <i>Chloroflexi</i> , and <i>Firmicutes</i> (30.25 %)	(Yun et al., 2020)
Biochar + electron promoted anaerobic soil interaction.	Dechlorination and methanogenesis reactions took place	<i>Chloroflexi</i> increased by 11.3 %	(Zhu et al., 2023b)

*Flavisolibacter*, *Rhodanobacter*, and *Ruminococcaceae* becoming dominant bacterial genera (Huang et al., 2016). After applying ASD in vegetable production systems, the polyethylene tarp or mulch can be either removed or punctured with holes for planting (Shennan et al., 2014). This reintroduces oxygen into the soil, which helps in restructuring the diversity of the microbial community back to an aerobic state (Husson, 2013). The 16S amplicon sequencing of post-ASD samples (three weeks before transplanting) showed significant soil microbiome changes and increased *Firmicutes* and *Proteobacteria* abundance compared to non-treated controls (Hong et al., 2018). Various experiments with different carbon sources have shown that ASD enhances specific soil microbiomes (Table 1).

Temporal changes in the microbiome composition and metabolome were observed in soil treated with ASD (Guo et al., 2018; Hewavitharana et al., 2019, 2021). Hewavitharana et al. (2019) found that *Firmicutes* were the most abundant bacterial communities in the soil during the anaerobic period following ASD treatment. Initially, *Bacillus* spp. dominated the *Firmicutes* community, but as the ASD treatment progressed, anaerobic *Clostridia*, specifically *Clostridium intestinale* and *Clostridium roseum*, displaced *Bacillus* spp. Poret-Peterson et al. (2019) also observed similar trends in the changes to *Firmicute* populations during the incubation period. Lactic acid production was noted during the aeration period between 21 and 32 days, attributed to lactic acid bacteria such as *Enterobacter hormaechei* and *Enterobacter ludwigi* (Hewavitharana et al., 2021). Carbon sources such as rice bran, orchard grass, and wheatgrass are rich in polysaccharides, monosaccharides, and amino acids, and serve as ideal substrates for soil microbiomes (Miller and Chibnall, 1932; Singh and Sogi, 2016). Several soil fungi (Christakopoulos et al., 1989; Panagiotou et al., 2005) also utilize d-glucose and sucrose as readily available and rapidly consumable substrates in ASD treatments (Hewavitharana et al., 2021). After treating the soil with ASD using a small amount of rice bran, the authors discovered a rapid sugar decrease on the first day (Hewavitharana et al., 2021). However, sugars in orchard grass and wheatgrass used for ASD were broken down during the aeration phase. Rice bran is readily digested by the soil microbiome (Hewavitharana et al., 2019), while the slower consumption of grass substrates other than rice bran may result from differences in cellulose composition (Hewavitharana et al., 2021). Consequently, increased beneficial microbial populations after applying ASD leads to pathogen suppression, competition for substrate, and an increase in the soil's total microbial community, improving soil health (Roskopf et al., 2020).

ASD with rapeseed meal and tobacco stem significantly altered the composition of bacterial communities and increased the number of anaerobic bacteria (Ya'nan et al., 2019). When wheat bran, sugar-contained diatoms, and dried molasses were used as substrates in ASD in a greenhouse, the microbial communities were significantly affected by variations in the substrate and disinfection period (Lee et al., 2020). Likewise, using non-rice bran carbon substrates revealed that specific types of bacteria positively respond to ASD (Poret-Peterson et al., 2019). These bacteria can perform

crucial functions such as denitrification, nitrogen fixation, and fermentation (Poret-Peterson et al., 2019).

ASD influences bacterial alpha diversity in clay-textured soils (Stefan et al., 2021). Furthermore, they found that this characteristic promotes microbial proliferation through enhanced aggregate formation, increased water retention, and improved nutrient preservation. Variations in soil microbial Shannon index responses, phylogenetic diversity, and specialized microbial Shannon index to organic amendments notably depended on the initial soil pH (Shu et al., 2022). These indicators were more evident in acidic soil, possibly due to the alkalizing effects of organic amendments (Chen et al., 2019).

Applying ASD with different carbon sources reduced microbial diversity (Hewavitharana and Mazzola, 2016; Testen and Miller, 2018; Poret-Peterson et al., 2019, 2020). The shift from aerobic to anaerobic conditions in soil reduces the available niche space for the resident microbiome (Spietz et al., 2015; Strauss et al., 2017). In addition to the fungal structure, Poret-Peterson et al. (2020) show significant changes in fungal diversity when using different organic substrates for soil disinfestation. This shift in fungal diversity was mainly driven by how soil fungi compete for resources (Hanson et al., 2008). Additionally, Poret-Peterson et al. (2020) discovered that the overall fungal Chao1 richness, Shannon diversity, and Pielou's evenness were similar to those of the no carbon control (NCC) communities. The Shannon diversity varied significantly between the NCC and ASD treatments using rice bran, red grape, or tomato pomace, and it changed over time (Poret-Peterson et al., 2020).

The Shannon's diversity index decreased on day 4 and remained relatively constant. However, the density of *Fusarium oxysporum* in tomato fields decreased after day 4 (Liu et al., 2016). Messiha et al. (2007) found that microbial diversity did not differ between carbon source-amended and non-amended soils after ASD treatment, but their community structure differed. On the other hand, ASD conducted using molasses did not alter the community structure (Shennan et al., 2014). These studies collectively suggest that microbial diversity, community structure, and soil redox potential (Eh) are not correlated with disease incidence (Lee et al., 2020).

Testen and Miller (2018) examined the effects of ASD using different carbon sources on soil bacterial composition and diversity in two farms in Ohio, USA. They found that the alpha diversity of bacterial communities in soil samples following ASD with wheat bran was significantly lower than non-amended soils (Testen and Miller, 2018). Similarly, the alpha diversity was significantly reduced in soils following ASD with ethanol in both Highland soils. However, no significant difference in alpha diversity was observed when molasses was used in ASD compared to the control soils on either farm (Testen and Miller, 2018). In another study, a reduction in total organic carbon in the soil harmed fungal community composition. This was evident in the significant decrease in fungal Shannon and Chao1 diversity indexes, further exacerbating *Fusarium* spp. reproduction (Saleem et al., 2019). In China, Zhan et al. (2021) investigated the effects of ASD or reductive soil disinfestation (RSD) using animal feces on soil physicochemical properties, bacterial composition, and both alpha

diversity and beta diversity. The results showed that the RSD-treated soil had unique core microbiomes and diverse disease-suppressive microbiomes. Additionally, changes in bacterial structure were observed, with lower bacterial richness, diversity, and evenness compared to untreated control soil (Zhan et al., 2021).

## 2.3 Impact of ASD on soilborne plant pathogen suppression

ASD is an environmentally friendly and sustainable approach to managing soilborne bacterial, fungal, and nematode plant pathogens (Mao et al., 2022). Differential production of ASD antipathogen factors may explain the differing soilborne pest management. For example, wheat bran and ethanol created the most effective soil-reducing conditions (Testen and Miller, 2018). Consequently, a moderate correlation between iron oxide paint loss and disease severity data suggests that wheat bran could influence soilborne pathogen management compared to molasses (Testen and Miller, 2018).

Compared to non-treated soil, changes in the prokaryotic community in ASD-treated soil effectively reduced the *Fusarium oxysporum* in tomatoes within three days (Lee et al., 2020). The population of *Fusarium oxysporum* in tomatoes decreased during the early stages of ASD due to a significant increase in the levels of Clostridia and Bacilli (Lee et al., 2020). Additionally, Bacilli, such as *Bacillus* and *Paenibacillus*, are well-known biocontrol agents for *Fusarium oxysporum* in tomatoes (Ueki et al., 2018). Some Clostridia can kill *Fusarium oxysporum* f. sp. *lycopersici* directly by producing chitinase (Momma, 2008; Ueki et al., 2017). Some Bacilli may contribute to the rapid decrease in soil Eh during the initial stage of ASD treatment through oxygen consumption (Mowlick et al., 2013b). Furthermore, the increase in clostridial populations in ASD-treated soils may be associated with a higher production of VFAs and could potentially be toxic to soilborne plant pathogens (Momma et al., 2006; Mowlick et al., 2013a).

Using different carbon sources, such as peanut, rice, and wheat brans, significantly reduced tomato bacterial wilt caused by *Ralstonia solanacearum* (Mao et al., 2022). The disease incidence was reduced by 83 to 100%, promoting tomato growth (Messiha et al., 2007; Mao et al., 2022). This is likely due to improved soil conditions, such as lower Eh,  $\text{NO}_3^-$ ,  $\text{SO}_4^{2-}$ , and increased pH, as well as increased biological activity, such as higher dehydrogenase and urease activities (Momma et al., 2006; Mowlick et al., 2013b). Additionally, anaerobic treatments with carbon sources led to elevated production of antagonistic compounds, including  $\text{Fe}^{2+}$ ,  $\text{Mn}^{2+}$ , citric acid, succinic acid, and ammonia (Lamers et al., 2014; Ueki et al., 2018). Applying ASD with orchard grass, wheat, and rice brans in strawberries has been found to alter the soil microbiome. This results in changes in the presence of *Clostridium* spp. and *Bacillus* spp. in the soil, reducing infections caused by *Macrophomina phaseolina* and *Fusarium oxysporum* f. sp. *fragariae* (Hewavitharana et al., 2021). Additionally, the mechanisms of ASD-mediated disease suppression were presumably due to the production of antifungal compounds such as volatile organic acids, hydrocarbons, and sulfur (Hewavitharana

et al., 2021). These compounds and acids can suppress *Verticillium dahliae* in tomatoes and strawberries (Testen and Miller, 2018; Washburn, 2018; Testen et al., 2021). Similarly, *Sclerotinia minor*, *Sclerotinia sclerotiorum*, and root-knot nematodes suppressed entirely in muck soils treated with ASD (Sanabria-Velazquez, 2018). Recent studies have shown that certain microbes, like *Clostridia* and *Zopfiella*, found in soil treated with ASD, could reduce disease occurrence (Momma, 2008; Ueki et al., 2017; Liu et al., 2019). This suggests a specific microbiome may be essential for suppressing disease through ASD.

## 2.4 Impact of ASD on nematode suppression

There has been limited research on how ASD affects nematode suppression in soil. *Meloidogyne incognita* extracted from tomato root tissue and root gall ratings were generally low in all ASD using cover crop, carbon source, molasses C source, or composted poultry litter (Butler et al., 2012b). However, ASD combined with soil solarization reduced tomato root-knot nematode populations (Butler et al., 2012a). Another study examined the use of ASD with composted poultry litter and two rates of molasses in Immokalee and Citra, Florida (Di Gioia et al., 2016). ASD effectively suppressed root-knot nematode (*Meloidogyne* spp.) in both locations. The depth of the soil significantly influenced the effectiveness of ASD. In deep and shallow soil profiles, nematode populations decreased by 82% and 70%, respectively (Shrestha et al., 2016). However, at a moderate depth, there was a near-significant increase in nematode populations following ASD treatment. They found that an incubation period of less than two weeks significantly increased nematode survival, whereas an incubation period of 4 to 6 weeks significantly suppressed the nematode population (Shrestha et al., 2016). Although both liquid and solid carbon sources equally suppressed nematode populations, not mixing carbon sources was more effective than combining those (Shrestha et al., 2016). In Nepal, ASD with rice bran reduced root-knot severity in okra and eggplant less effectively than mustard cake and molasses (Khadka et al., 2019).

The efficacy of ASD with cover crops for their susceptibility to three common root-knot nematodes, *Meloidogyne arenaria*, *M. incognita*, and *M. javanica*, was tested on tomato cv. 'Rutgers,' a susceptible host (Kokalis-Burelle et al., 2013). They found that most cover crops tested were less susceptible to *M. arenaria* than tomatoes. Additionally, these cover crops did not support high populations of *M. incognita* in roots. Among the cover crops, arugula, cowpea, and sorghum-sudangrass were found to have low levels of all three *Meloidogyne* spp (Butler et al., 2012a, b). However, the susceptibility of other crops varied, depending on the specific species of *Meloidogyne* spp. tested (Kokalis-Burelle et al., 2013). In general, the microbial community shifts toward facultative and obligate anaerobes, the anaerobic decomposition of labile carbon sources produces short-chain organic acids (such as acetic, n-butyric, and propionic) and volatile compounds. These compounds are likely toxic to plant-parasitic nematodes (Momma et al., 2006; Momma, 2008).

The *Pratylenchus penetrans* density in apple roots was reduced based on the carbon source used for ASD (Hewavitharana et al., 2014). The nematicidal activity of acetic and n-butyric acids, both generated by ASD using wheat bran, was nearly equal, or additive (Katase et al., 2009). Notably, volatile fatty acids (VFAs) increased nematicidal activity as the pH decreased, suggesting their effectiveness is closely tied to their ionization (Katase et al., 2009). These findings underscore the crucial role of VFAs produced by the soil microbiome in low-oxygen soil in suppressing *Meloidogyne incognita* (Momma et al., 2006; Katase et al., 2009). ASD with ethanol can lead to the accumulation of acetic acids (Momma et al., 2010).

Plant-parasitic potato cyst nematodes (PCN) can be managed through ASD, with over 99.5% inactivation achieved in various soils (Runia et al., 2014). This high efficacy was attributed to the absence of organic matter. The use of 'arugula' could serve as a trap crop for *Meloidogyne* spp. (Melakeberhan et al., 2006) and may be more economically feasible than cover crops in rotations immediately preceding ASD treatments (Kokalis-Burelle et al., 2013).

## 2.5 Impact of ASD on weeds

Integrating ASD with cover crops can be an effective weed management strategy (Khadka et al., 2021). The effectiveness of ASD also depends on its ability to suppress weeds by accelerating the decomposition of organic matter, producing toxic acids, inhibiting seed respiration, and altering soil conditions to kill weed propagules (Fujita et al., 2020). When combined with carbon sources under anaerobic conditions, ASD has been shown to reduce weed populations by up to 95% (Singh et al., 2022). ASD treatment can eliminate weeds such as creeping yellow-field cress and common chickweed, although the overall weed population may remain unaffected (Molendijk et al., 2009; Shennan et al., 2018; Vincent et al., 2024). In organic farms, ASD was effective against snow thistle (Molendijk et al., 2009). Although ASD is generally effective in weed control, the control of annual weeds such as *Amaranthus retroflexus* with ASD can vary. For instance, low success rates or outright failure have been reported, especially when using rice bran or molasses for ASD (Karimmojeni et al., 2014).

## 2.6 Impact of ASD on plant health and crop yield

The formation of soil aggregation and pore spaces contribute to improved root development, nutrient absorption, and plant health (Priyashantha and Attanayake, 2021; Lopes et al., 2022; Hu et al., 2023). In Ohio, ASD with wheat bran significantly increased tomato plants' dry shoot and root biomasses compared to ASD with molasses and ethanol (Testen and Miller, 2018). In China, ASD with composted chicken manure significantly increased strawberry plants' height, stem thickness, and yield (Song et al., 2020). ASD did not reduce the total fruit yield of crops compared to a fumigant control. However, the yield was significantly higher than a non-

mended control (Shrestha et al., 2016). Furthermore, the application of manures and increased amendment rate led to an increased yield of over 50% compared to fumigated and non-amended controls (Shrestha et al., 2016).

ASD triggers several positive effects to suppress plant pathogens through specific beneficial bacterial and fungal communities, particularly those that produce antimicrobial substances and siderophores and may produce plant growth-promoting phytohormones and improve soil fertility (Lopes et al., 2022). These microbiomes compete for resources, produce antibiotics, and exhibit parasitic behavior, strengthening the soil's defense against soilborne pathogens (Zhang et al., 2022). ASD can reduce soilborne pathogen, *Thielaviopsis basicola*, which can lead to increased biomass yield in tobacco varieties (Haji and Brandle, 2001). Soilborne diseases such as Verticillium wilt and charcoal rot can significantly reduce strawberry yields (Carpenter et al., 2000; Hewavitharana et al., 2021). However, ASD-amended soils showed significantly greater fresh strawberry biomass than non-treated controls in a study involving wilt and charcoal rot. Specifically, in the Fusarium wilt trial, ASD-amended plants exhibited twice the fresh biomass compared to the control (Roskopf et al., 2015; Shennan et al., 2018; Hewavitharana et al., 2021).

When ASD with molasses was combined with solarization, the ASD plots produced equal or higher marketable bell pepper and eggplant yields than methyl bromide fumigation plots (Butler et al., 2014). The effect of ASD using a combination of composted poultry litter (22 t/ha) and two different levels of molasses (13.9 t/ha and 27.7 t/ha) on fresh-market tomato yields was assessed in two locations: Immokalee and Citra, Florida (Di Gioia et al., 2016). They found that in Immokalee, the ASD plots produced more marketable tomatoes compared to the soil fumigation plots. In contrast, the soil treatments did not affect the yield in Citra (Di Gioia et al., 2016). Additionally, soil treatments did not significantly influence the quality of the tomato fruits, although fruit mineral content was similar or higher in ASD plots than in soil fumigation plots (Di Gioia et al., 2016). The ASD treatments reduced redox potential (Eh) and lowered pH (Momma, 2008). This may significantly influence the soilborne plant pathogens and the entire soil-microbiome-plant system (Strauss and Kluepfel, 2015; Van Agtmaal et al., 2015).

Soil fumigation effectively suppressed nematodes in resistant tomato cultivars, increased tomato fruit yield (Regmi and Desaeger, 2020), and improved marketability (Theis and Fery, 2002). In contrast, ASD has less impact on managing soil nematode than resistant cultivars grown in non-fumigated soil (Gullino et al., 2022). An alternative method to chemical control involves using chitin, ASD, and marigolds. These strategies were effective in managing plant-parasitic nematodes and *Verticillium dahliae*, and increased yield (65%) over six years (Korthals et al., 2014).

## 3 Mechanisms of ASD

Although the mechanisms of soilborne plant pathogen suppression by ASD are not fully understood, available evidence suggests that ASD alters soil microbial communities through three



TABLE 2 Impact and mechanisms of anaerobic soil disinfestation (ASD) using various organic amendments as a carbon source on suppression of specific soilborne pathogens and pests.

Pathogen	ASD treatment	Control mechanism	Remarks	References
<b>Bacteria</b>				
<i>Ralstonia solanacearum</i>	Methanol	VOCs like dimethyl sulfide suppress pathogen growth and mobility. Anaerobic conditions starve oxygen-dependent pathogens	ASD with methanol in tomato fields reduces <i>R. solanacearum</i> populations, improving crop health and yield	(Shrestha et al., 2016; Mao et al., 2022; Shikoli, 2022)
<i>Agrobacterium tumefaciens</i>	Vermicompost	Changes in community composition, total microbial abundance, and the production of antibiotics	<i>A. tumefaciens</i> suppressed by vermicompost decreased reliance on MeBr or other soil fumigants	(Strauss et al., 2015)
<b>Fungi</b>				
<i>Rhizoctonia solani</i>	Composted rice bran	VOCs like ethanol disrupt fungal membranes. - Increased microbial activity suppresses pathogen growth during potato stem canker infection	ASD with composted rice bran in potato fields reduces disease incidence by up to 50%, leading to increased tuber yield.	(Hewavitharana and Mazzola, 2016)
<i>Sclerotinia sclerotium</i> and <i>S. minor</i>	Crop lettuce treated with ASD combined with biocontrol agent: <i>Streptomyces</i> spp., <i>Bacillus</i> spp., and <i>Pseudomonas</i> spp.	<i>Pseudomonas</i> and <i>Bacillus</i> reduced fungal sclerotia viability by >70% <i>in vitro</i> , while ASD achieved >80% reduction.	ASD-generated organic acids harmed sclerotia viability.	(Sanabria-Velazquez, 2018)
<i>Sclerotium rolfsii</i>	Organic soil amendments	Volatile fatty acids (VFAs), such as acetic and n-butyric acid reduce pathogen viability.	Endemic soil populations of <i>Trichoderma</i> spp. were intact.	(Swilling et al., 2021)
<i>Fusarium oxysporum</i>	Wood chips	Lowered soil pH due to organic matter decomposition inhibits fungal growth. - Beneficial bacteria compete with pathogens for resources	ASD with wood chips in strawberry fields suppresses <i>F. oxysporum</i> , promoting plant growth and fruit production	(Akhter et al., 2015; Shrestha et al., 2021)
<i>Macrophomina phaseolina</i> and <i>Fusarium oxysporum</i> f. sp. <i>fragariae</i>	Orchard grass, wheat, and rice bran low rate' amendment (approx. 24 °C)	Initial proliferation was followed by a decline in soil density of the <i>Fusarium</i> wilt pathogen, coinciding with the generation of antifungal compounds	<i>Clostridium</i> spp. population increases were linked to metabolite generation. Disease suppression was significantly affected by carbon input and incubation temperature but not duration.	(Hewavitharana et al., 2021)
<i>Stromatinia cepivora</i>	Ethanol and sucrose at 5%	ASD with ethanol or sucrose reduced the viability of <i>S. cepivora</i> sclerotia	ASD is anticipated to be more effective in pathogen control than soil saturation alone	(Quintino et al., 2023)
<b>Nematodes</b>				
<i>Meloidogyne incognita</i>	Chopped grass	Ammonia produced during organic matter decomposition disrupts nematode hatching and mobility. Beneficial fungi and bacteria parasitize nematodes.	ASD with chopped grass in tomato fields reduces <i>M. incognita</i> populations, improving root development and plant growth.	(Butler et al., 2012a; Testen, 2017)
<i>Meloidogyne hapla</i>	Organic amendments molasses, wheat bran, or mustard greens at 20.2 t/ha, or 2% ethanol	ASD performed in growth chamber trials and ASD-treated soil suppressed root-knot nematode, regardless of carbon sources	Organic acid concentrations in ASD varied based on the carbon source used, with the highest recorded for molasses.	(Sanabria-Velazquez, 2018)
<i>Meloidogyne javanica</i>	Ethanol and sucrose at 5%	Ethanol-based ASD decreased J2 nematode numbers in soil and galls in tomato roots by over 93%	ASD exhibited more potent nematocidal effects compared to soil saturation with water	(Quintino et al., 2023)
<b>Weeds</b>				
<i>Cirsium arvense</i> , <i>Rorippa sylvestris</i> , <i>Sonchus arvensis</i> , <i>Calystegia sepium</i> , <i>Equestium arvense</i> , <i>Tussilago farfara</i> , <i>Elymus</i>	ASD treatments involved incorporating weed biomass with 40 tons/ha of fresh grass into the plow layer (c. 25 cm) or using weed biomass alone.	ASD alone reduced soil coverage by at least 96%, but adding fresh grass increased it to at least 98.5%, surpassing the effect of plastic sheets alone on all weed species	The grass was added to enhance soil oxygen utilization, extending the duration of anaerobic conditions	(Huiting et al., 2011)

(Continued)

TABLE 2 Continued

Pathogen	ASD treatment	Control mechanism	Remarks	References
<b>Weeds</b>				
<i>repens, Rumex obtusifolius, and Polygonum amphibium</i>				
Nutsedge ( <i>Cyperus</i> spp.)	Mustard seed meals (MSM) + ASD	Decrease weed density in comparison to the control group	A combination of composted broiler litter and solarization proved more effective than anaerobic conditions alone	(Shennan et al., 2018)
Yellow nutsedge	Molasses at 8.2 t/ha for 3 weeks	ASD performed: Molasses has been administered both through irrigation lines and as a diluted spray on the soil surface	Reduced weeds along with RKN in eggplant field	(Butler et al., 2012a)
Yellow nutsedge	Four cover crop residue treatments (sorghum-sudangrass, sunn hemp, both, or none) in aerated or non-aerated soil, with the cover crops grown for 75 days	A decrease in yellow nutsedge populations is linked to phytochemicals produced by anaerobic microbes during ASD, with possible soil solarization effects facilitated by clear plastic mulch	Highlights the effectiveness of ASD with cover crops for yellow nutsedge control in plasticulture tomato production, revealing synergistic effects	(Singh et al., 2022)
<i>Chenopodium album</i>	10-week period and various types of carbon amendments were utilized, along with soil saturation or flooding and soil covering, typically with polyethylene mulch	Outperformed ASD treatments in weed control compared to uncovered controls	Impact of sampling depth, with shallow depths exhibiting significantly higher weed suppression, while moderate depths favored weed populations	(Shrestha et al., 2016)
<i>Amaranthus viridis</i>	6-7 weeks at > 40.9 - 47.1°C at a 15 cm soil)	Olive processing waste (OPW) with solarization exhibited the best result.	Demonstrating the efficacy of different treatments for controlling specific weed species in tomatoes grown in a greenhouse	(Boz, 2009)

primary mechanisms: (i) the decomposition of carbon sources that enhance beneficial microbiomes, (ii) the production of antimicrobial compounds or antagonism by anaerobic microbiomes, and (iii) the absence of oxygen (Mowlick et al., 2013a; Mowlick et al., 2014; Strauss and Kluepfel, 2015; Van Agtmaal et al., 2015; Priyashantha and Attanayake, 2021). Consequently, ASD effectively reduces the persistence of pathogen inoculums in the soil and reduces infections by soilborne pathogens and pests (Table 2).

The impact of ASD using various carbon sources in anaerobic processes to manage soilborne pests (Ludeking et al., 2010; Arriaga et al., 2011; Lamers et al., 2014; Runia et al., 2014). These specific factors are low oxygen levels, accumulation of toxic products from anaerobic decomposition such as organic acids, methyl sulfides, CO<sub>2</sub>, NH<sub>3</sub>, H<sub>2</sub>S, CH<sub>4</sub>, and N<sub>2</sub>O, and antagonism by anaerobic microbiomes (Momma et al., 2006; Runia et al., 2014; Shennan et al., 2014; Momma, 2015; Guo et al., 2017; Hewavitharana et al., 2019). The oxygen concentration in the soil decreases to below 1% within the first few hours after covering it with impermeable plastic, and this low oxygen level persists throughout the treatment period (Hewavitharana et al., 2019). Consequently, a decrease in soil redox potential (Eh) reduces the levels of oxygen, nitrate (NO<sub>3</sub><sup>-</sup>), manganese ion (Mn<sup>4+</sup>), ferric ion (Fe<sup>3+</sup>), and sulfate (SO<sub>4</sub>) and even allows for methane production. Additionally, atmospheric conditions of O<sub>2</sub> concentration < 4% and CO<sub>2</sub> > 19.2% favor the production of organic acids acetate and butyrate (Runia et al., 2014).

Prokaryotes, specifically *Clostridium* spp., degrade the fungal cell wall, resulting in biological control of the spinach wilt pathogen (Ueki et al., 2017). Researchers examined the use of cover crops in ASD (Butler et al., 2012b; Hewavitharana et al., 2014); however, their effectiveness in muck soil systems is still unknown. In this context, cover crops could potentially be used as trap crops to stimulate the germination of *Plasmodiophora brassicae* (club root disease) resting spores before ASD (Friberg et al., 2006). ASD using mustard seed meal releases antifungal volatile compounds upon the hydrolysis of glucosinolates (Dassanayaka et al., 2023). Gases produced during the anaerobic phase from soils treated with ASD with ethanol, grass residues, or *Brassica juncea* seed meal effectively inhibited the growth of *Rhizoctonia solani* AG-5, *Pythium ultimum*, and *Fusarium oxysporum* (Dassanayaka et al., 2023; Hewavitharana et al., 2014). Furthermore, several volatile compounds, including dimethyl sulfide, carbon disulfide, di- and dimethyl tri-sulfide, are produced by the soil microbiome during the anaerobic phase of ASD (Hewavitharana et al., 2014).

Some of the sulfide compounds, such as dimethyl trisulfide, have been reported to have antifungal properties (Blok et al., 2000; Fernando et al., 2005) and nematicidal activities (Cabrera et al., 2009). Specific organic acetic acid and butyric acid were produced, reducing the survival of *Fusarium oxysporum* f. sp. *lycopersici* and *Ralstonia solanacearum* populations in soil (Momma et al., 2006). Changes in soil pH and nutrient availability also create an unfavorable environment for specific pathogens (Ebihara and Uematsu, 2014). In summary, the potential mechanisms for

suppressing specific soilborne pests include producing organic acids through anaerobic decomposition of added carbon sources, releasing volatile fatty acids (VFAs), and biocontrol by the microbiome that thrives during the process (Momma et al., 2006; Shrestha et al., 2016).

## 4 Combination of ASD with biological control agents, fungicides, and grafting

When integrating ASD with other disease management tools, it is crucial to determine whether the effects are synergistic or antagonistic. *Trichoderma* spp. are beneficial fungi (Singh et al., 2014) and provide numerous benefits in crop production, such as promoting growth, suppressing diseases, improving soil quality, and enhancing nutrient availability in the soil (Harman et al., 2021; Singh et al., 2014). Soil-treated with ASD reduced the viability of *Athelia rolfsii* sclerotia in acidic soil conditions, with minimal impact on native *Trichoderma* spp (Swilling et al., 2021). Additionally, a significant increase of over 300% in *Trichoderma* spp. populations were reported in ASD-amended soil compared to non-amended soil. Available evidence suggests that *Mucor* spp. colonize sclerotia post-ASD treatment, presumably due to the potential mycoparasitic role of *Mucor* spp. against *Sclerotinia sclerotiorum* (Harvey et al., 1995).

Certain *Trichoderma* strains exhibit average growth at high temperatures (37 to 40°C), producing stress-protectant sugars such as trehalose, mannose, and raffinose, which help them thrive in extreme conditions (Poosapati et al., 2014). In Nepal, Khadka and Miller (2021) found that combined ASD with wheat bran, molasses, chicken manure, and mustard greens, along with *Trichoderma harzianum* T22 and *Trichoderma asperellum* NT25 achieved the lowest severity and incidence of Rhizoctonia root rot in radish plants. They observed that combining *Trichoderma harzianum* T22 with ASD using molasses and *Trichoderma asperellum* NT25 with ASD-wheat bran showed a synergistic effect in reducing disease severity (Khadka and Miller, 2021). Conversely, *Trichoderma harzianum* T22 with ASD-chicken manure showed an antagonistic interaction (Khadka and Miller, 2021).

ASD treatments were compared with fungicides and found to have significant impacts on managing Stevia stem rot and Septoria leaf spot (Sanabria-Velazquez et al., 2023). ASD effectively reduced the viability of *Sclerotium rolfsii* sclerotia in laboratory tests and micro-plot in North Carolina. In contrast, in Mexico and Paraguay, the viability of the sclerotia decreased significantly in soils treated with ASD using cornmeal plus molasses or wheat bran plus molasses in field trials (Sanabria-Velazquez et al., 2023). Combining ASD with grafting could be a practical disease management tool for specific soilborne disease complexes of tomatoes. For instance, in Ohio, ASD using wheat bran and molasses was used along with grafting tomato plants onto 'Maxifort'-resistant rootstock to manage soilborne diseases such as corky root (caused by *Pyrenochaeta lycopersici*), black dot root rot (*Colletotrichum coccodes*), Verticillium wilt (*Verticillium*

*dahliae*), and root-knot nematodes (*Meloidogyne hapla* and *M. incognita*) (Testen et al., 2021). The ASD treatment generally reduced the severity of root and taproot rot and root-knot galling. Non-grafted tomato plants grown in untreated soils showed the highest corky root rot severity, while the lowest levels were observed in plants grafted with 'Maxifort' rootstock (Testen, 2017; Testen et al., 2021).

## 5 Challenges and opportunities

ASD is a biological method that reduces the need for chemical fumigation and promotes sustainability (Van Agtmaal et al., 2015). However, the effectiveness of ASD can vary depending on several factors, such as soil types, temperatures, target soilborne pests, and carbon sources (Butler et al., 2012a; Zavatta et al., 2014; Roskopf et al., 2015; Hewavitharana and Mazzola, 2016; Hewavitharana et al., 2021). Despite its benefits, ASD also presents challenges, especially in managing weeds and plant-parasitic nematodes at greater soil depths. Dry organic amendments used in ASD are tilled to a depth of 15 to 20 cm, which may not effectively manage soil nematodes. For instance, in Central California tree-crop nurseries, nematodes have been found to migrate from depths of over 1.5 m, exceeding the nematode management depth achieved by ASD in fields (McKenry, 2002; Zavatta et al., 2014).

When implementing ASD, selecting a suitable carbon source is crucial. Familiar carbon sources for ASD include cereal barns such as rice and wheat bran, mustard meal, animal manures, and other carbon-rich amendments (Priyashantha and Attanayake, 2021; Lopes et al., 2022). However, one significant limitation of using ASD is the high associated production costs. Thus, the cost-benefit ratio of the ASD application for soilborne pest management in fields is a critical consideration. For instance, the cost of ASD technology can be high due to the use of large quantities of carbon sources and costs of transportation, increased labor wages, application of expensive virtually impermeable plastic films (VIF), and irrigation facilities, thus making it less accessible for growers to adopt ASD (Muramoto et al., 2020; Daugovish et al., 2021, 2023). Alternatively, using locally available and renewable organic amendments or agricultural bio-products could be cheaper and reduce production costs. Recent studies have shown that carbon sources such as tomato pomace and Gramineae used for ASD were effective and altered the soil microbiome and metabolome (Poret-Peterson et al., 2019; Hewavitharana et al., 2021; Daugovish et al., 2023). Additionally, locally sourced agricultural by-products such as almond hulls, sweet potato waste, brewer's spent grains, grape pomace, and orchard grass may offer promising carbon source alternatives for ASD (Butler et al., 2012a; Zavatta et al., 2014; Hewavitharana et al., 2021; Adhikari et al., 2023).

Agriculture in tropical developing countries includes small-scale farming systems, multiple cropping patterns, high pathogen diversity, the impact of climate changes (e.g., drought, increased temperature), and lack of agricultural technologies. As a result, crop productivity in these countries is lower than in temperate countries (Priyashantha and Attanayake, 2021). Therefore, translational

research should focus on finding biodegradable farm by-products as carbon sources and utilizing durable and low-cost plastic mulch for ASD in developing countries. Importantly, ASD will be more beneficial for high-value crops such as strawberries and tomatoes than low-value crops such as eggplant, okra, and spinach. Adopting ASD technology provides a significant income from pesticide-free products for resource-poor farmers and improves soil health. Recently, the ASD strategy has been contemplated as an IPM tool to manage soilborne pathogens of *Stevia* in Mexico and Paraguay (Sanabria-Velazquez et al., 2023) and mitigate weed, root-knot nematode and soilborne pathogens of vegetables in Nepal (Khadka et al., 2019; Khadka, 2021; Khadka and Miller, 2021; Khadka et al., 2021).

Adding carbon sources to the soil is a common practice in all ASD treatments and provides a substrate for microbial activities (Butler et al., 2012a, b; Daugovish et al., 2015; Roszkopf et al., 2015; Hewavitharana and Mazzola, 2016; Roszkopf et al., 2020; Hewavitharana et al., 2021). Different carbon sources in ASD can affect microbial community composition and diversity (Hewavitharana and Mazzola, 2016; Testen and Miller, 2018). For instance, *Clostridium* spp. play a significant role in ASD by producing by-products during anaerobic respiration (Mowlick et al., 2013a; Strauss and Kluepfel, 2015; Ueki et al., 2017). ASD treatments also increased the predominant bacterial phyla *Proteobacteria*, *Actinobacteria*, *Firmicutes*, and *Bacteroidetes*, while *Bacillus*, *Burkholderia*, *Enterobacter*, and *Pseudomonas* were the most common bacterial genera (Huang et al., 2015; Roszkopf et al., 2015; Hewavitharana and Mazzola, 2016; Huang et al., 2016; Poret-Peterson et al., 2019; Roszkopf et al., 2020; Hewavitharana et al., 2021). Some bacterial endophytes are plant growth-promoting rhizobacteria (PGPR) and may enhance plant growth by producing phytohormones, antibiotics, and siderophores (Lodewyckx et al., 2002).

Specific microbiome genes contributing to plant-beneficial microbe interactions are crucial to identify them (Finkel et al., 2017). Culturable beneficial bacterial and fungal strains can be used to determine their biological functions (Armanhi et al., 2016, 2018). This approach will involve isolating single colonies of strains or multiple strains to establish community-based strains (Oberhardt et al., 2015). In addition, utilizing 'meta-omics' approaches such as metagenomics, metabolomics, metatranscriptomics, and metaproteomics can aid in analyzing microbial diversity, composition, and regulatory co-occurrence networks (Aguilar-Pulido et al., 2016). This will also facilitate our understanding of the interplay between plant-microbiome interactions. Additionally,

engineering synthetic communities (SynComs) can improve plant health and activate the plant's immune system to combat plant pathogens. This translation research aims to shift from using chemicals to advancing a novel, eco-friendly, biologically-based pest management (BBPM).

In conclusion, ASD offers promising opportunities for sustainable agriculture, but it also presents challenges and limitations that must be addressed for widespread adoption. Continued research and innovation are crucial for maximizing ASD's potential in diverse agricultural production systems in developed and developing countries.

## Author contributions

SM: Methodology, Writing – original draft, Writing – review & editing. ANP: Writing – review & editing. TBA: Conceptualization, Software, Writing – original draft, Writing – review & editing.

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