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Allelopathic properties of compost: could we use a fertilizer as an herbicide for tree crops?

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Abstract Soil management in tree cropping systems employs techniques like grassing, mulching, and weed control to improve soil health and reduce chemical herbicide use. Weeds compete with crops, leading to yield losses and increased reliance on synthetic herbicides, which pose environmental risks and contribute to the development of herbicide-resistant weeds. Sustainable alternatives like organic mulches, particularly municipal solid waste compost, can enhance soil structure, fertility, and weed suppression, promoting sustainable agriculture. In this opinion paper, we focused on the antigerminative effects of compost, which can inhibit seed germination and growth due to the presence of allelochemicals such as phenolic compounds, terpenoids, fatty acids, and ammonia. These compounds affect water uptake, hormonal pathways, and cellular functions. These antigerminative properties, though traditionally seen as negative for annual crops, offer potential benefits in tree cropping systems for natural weed control. Challenges include determining optimal application rates and addressing problems related to variable efficacy due to environmental conditions. Additionally, manipulating the composting process to produce specific amendments for different cropping systems could reduce reliance on synthetic herbicides, improve soil health, and decrease the risk of herbicide-resistant weeds. Bacteria like *Pseudomonas* and *Bacillus* play a key role in composting by degrading nitrogenous compounds, thereby influencing nitrogen cycling and promoting the formation of nitrogenous compounds that may inhibit weed growth. Fungi such as *Alternaria alternata*, that may survive during the mesophilic composting phase as spores, produces phytotoxic tentoxin, which could be harnessed for bioherbicidal use. These processes are essential in compost maturity and plant growth impact. Further research is necessary to optimize compost applications for weed control and develop practical guidelines for its use.

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1 Introduction

1.1 Weed control in tree crops

1.1.1 Soil management and weed control

Soil management represents an important method for indirect control of plant physiology and productivity in tree cropping systems. Usually, different techniques are integrated, resulting in a different management of the space between rows and in-rows (40-60 cm in width) (Haynes 1980). Grassing is often encouraged intra-rows, due to its beneficial effects on soil erosion, organic matter content, biodiversity, mechanical bearing of the ground (Fig. 1).

In fact, it has been reported that grass cover in vineyards considerably reduced runoff and soil loss compared to tillage (Capello et al. 2019). However, in-row soil management usually requires weed control to reduce the competition with the tree crop; it is well known that weeds cause yield reduction. To decrease the use of synthetic herbicide applications, techniques have been studied to ensure fruit production using cost-effective strategies. Examples include tillage, grassing, and organic or synthetic mulches (Lipecki and Berbec 1997). In general, chemical herbicides and soil tillage are considered detrimental to soil quality, mainly due to the inhibition of soil N-cycling, disruptions to earthworm ecology and reduction of soil biodiversity (Karimi et al. 2020).

1.1.2 Compost mulching as a sustainable strategy

Mulching could be an interesting strategy used for over 10,000 years to control weed growth, improve crop development and achieve greater yields (Guerrini et al. 2019), however, plastic mulching (Fig. 1) could produce macroplastic and microplastic contamination in environments (Huang et al. 2020). It has been reported that organic mulches could be of significant importance, because they do not produce waste in the field and contribute to increasing the soil organic matter and soil function by 14.6% and 29.6% respectively in apple orchards (Tang et al. 2022). Furthermore, they also influence buffering soil temperature, thereby reducing excessive heating for the plant rootzone (Blanco et al. 2024). In particular, the use of organic waste compost, with a circular economy perspective, could be of major interest among the materials available for organic mulches. In fact, it is already known for its effectiveness as weed control when applied as mulch (Bajwa et al. 2015). Additionally, due to its chemical composition, compost has important fertilizing properties and results in higher or similar vegetable crop yields compared to mineral fertilization, with lower risk of groundwater pollution (Morra et al. 2021), which could be exploited also in conjunction with tillage thanks to bioremediation and restoration of microbial fertility (Ventorino et al. 2019). In general, compost applications are expected to enhance soil health by improving soil structure, increasing microbial activity, and providing essential nutrients, which can reduce the reliance on chemical herbicides. Healthier soils support crop competitiveness against weeds, indirectly reducing the impact of resistant weed populations. Additionally, compost can help foster a more diverse microbial environment that may play a role in degrading synthetic herbicide residues, thus lowering the selection pressure for resistant weeds (Singh and Singh 2014).

However, when considering organic mulches, the thickness of coverage needed to ensure weed inhibition could require huge amounts of materials (Blanco et al. 2024), which represents a limiting factor for its widespread application in cropping systems. In this opinion paper, we explored the possibility of using compost for weed control in tree cropping systems, focusing on its application intra row and exploiting its natural weed-suppressing properties, owing to its composition and to the presence of certain compounds, including ammonia and short-chain fatty acids (Fig. 2). This antigerminative effect may also be attributed to the physical properties of compost, such as pH and salinity. Advantages and drawbacks are highlighted and critically analyzed. The mechanisms at the basis of its antigerminative effect are presented and discussed.

1.2 Herbicides – state of the art

1.2.1 Herbicides in modern agriculture: history and impact

According to the WSSA (Weed Science Society of America), weeds are plants that grow spontaneously

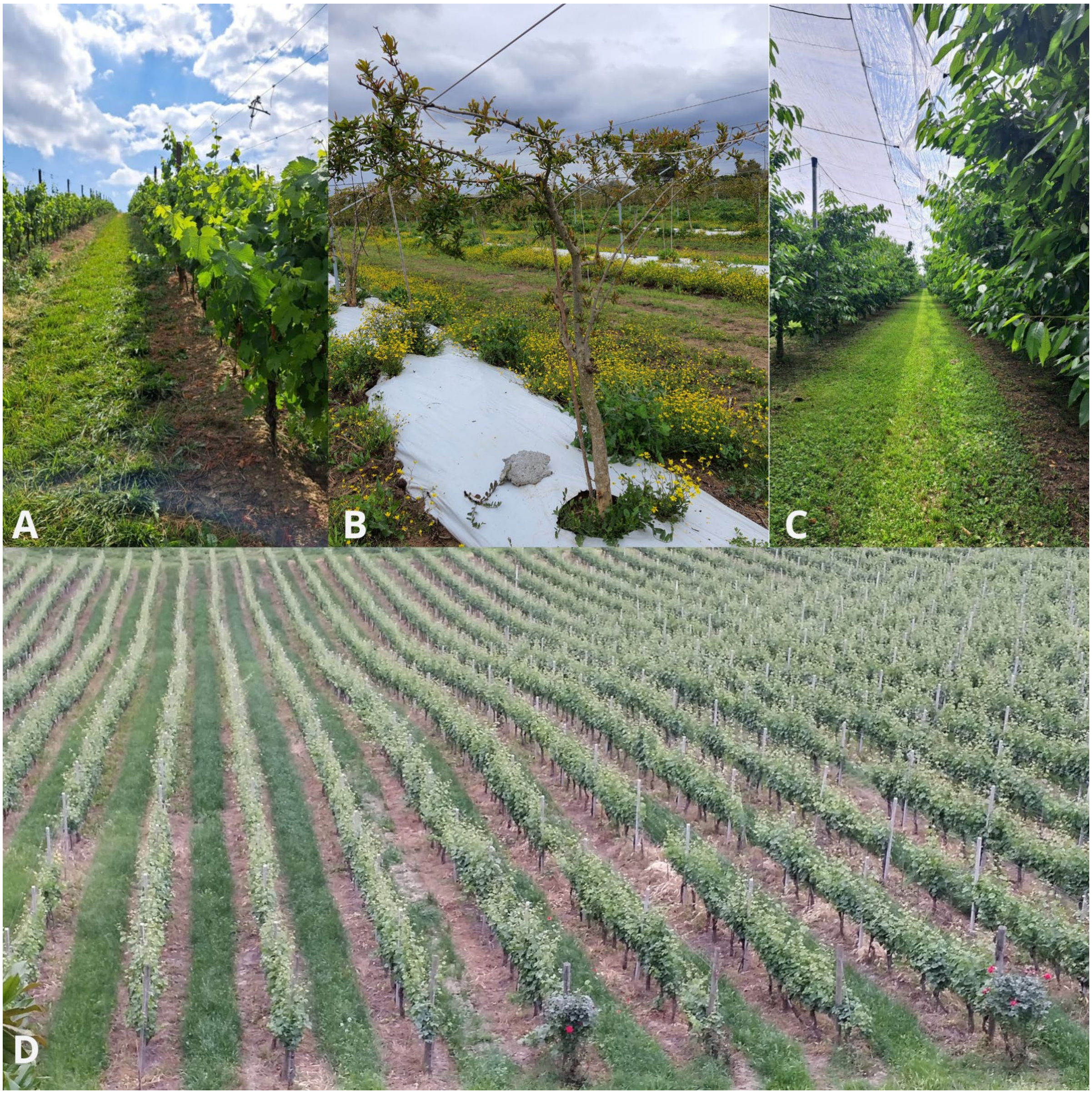

Fig. 1 Different integrated soil management techniques in tree cropping systems characterized by grassing intra rows and, under the canopy: top left **A** mulch with mowed grass; top center **B** plastic mulching; top right **C** tillage; bottom **D** chemical weed control

alongside cultivated plants without being intentionally planted; they can lead to economic loss, ecological damage, or health issues for humans and animals (Weed Science Society of America 2024). In agriculture, weeds compete with crops for resources like space, nutrients, light, and water, eventually affecting crop yield and quality (Riemens et al. 2022). Therefore, controlling weed growth is imperative in agriculture. For example, yield losses due to uncontrolled weeds for six agricultural commodities (wheat, cotton, maize, potato, rice, and soybean) have been estimated to be significantly higher (34%) compared to the 16% and 18% losses caused by crop pathogens and insect pests. (Oerke 2006). In 2007, in California (US), a dry year in comparison to the 2006, the herbicide treatments, the grape yield reductions of

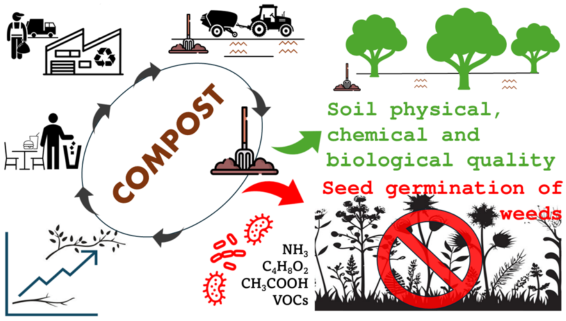

Fig. 2 Compost cycle and its possible exploitation in tree crop soil management

cultivation were around 22%, and those of the cover crop and untreated control were around 48% (Sanguankeo et al. 2009).

Weed management has been conducted manually for centuries, until the 1950s, when effective and economically affordable synthetic herbicides began to be developed (Kraehmer et al., 2014). The first widely used synthetic herbicides were phenoxyacetic acids like 2,4-D and similar (Timmons 1970). Since then, the application of these chemical products has become the most common method to control weeds because it is economical (at least, in the short term) and gives faster results due to their broad target effectiveness on most weeds (Harker O'Donovan 2013; Önemli̇ and Tetik 2023).

However, the excessive use of synthetic herbicides has significant environmental impacts, potentially causing long-term ecological issues (Aktar et al. 2009; Hongoeb et al. 2025; Mohd Ghazi et al. 2023; Raffa and Chiampo 2021). These chemicals could contribute to the pollution of air, soil, and water, and could enter the food chain. To mitigate these risks, the European Commission implemented Directive 2009/128/EC, which aims to promote the sustainable use of herbicides by reducing their risks and impacts on both human health and the environment. This directive advocates for integrated pest management and the use of non-chemical alternatives. Despite previous efforts, such as Directive 91/414/EEC (15 July 1991), which removed over 75% of certain active substances due to toxicity or ineffectiveness, many active molecules remain in use. Currently, the European Union authorizes over 150 different herbicides. These are applied to enhance agricultural productivity and crop quality, with around 350,000 tons per year sold across during the period between 2011 and 2020 (European Environment Agency 2023).

1.2.2 *Environmental concerns and herbicide resistance*

Moreover, while synthetic herbicides do not alter soil physical properties, they are known to affect the catalytic efficiency and behavior of soil enzymes, impacting the overall biological activity (Singh et al. 2018a, b). Misuse of pesticides can lead to the contamination of various ecosystems and pose threats to apiculture and surface waters (Souza et al. 2020). Furthermore, the persistent use of synthetic herbicides can select resistant weed biotypes, a problem exacerbated by the repetitive use of the same mechanism of action, leading to increased populations of herbicide-resistant weeds (Powles and Yu 2010; Shaner 2014). This practice imposes strong selective pressure on weed populations, favoring those individuals with mutations or traits that confer resistance. These resistant biotypes then reproduce, gradually dominating the weed population in treated fields (Powles and Yu 2010). Widespread herbicide resistance is highly significant for future agricultural practices as it implies several consequences: it threatens the efficacy of existing chemical controls, leading to increased synthetic herbicide use; increases production costs; and generates potential crop losses. This resistance also reduces the available options for effective weed management, imposing more integrated and sustainable approaches (Schütte et al. 2017). Thus, looking for alternative strategies for weed control in cropping systems is of utmost importance.

1.3 Categories of herbicides

There are various types of herbicides, each with specific mechanisms of action and ideal applications. The choice of herbicide depends on factors such as the type of weeds, the crop being cultivated, environmental constraints, regulations, and economic considerations. The Global Herbicide Resistance Action Committee (HRAC) updated the herbicide mode of action classification system in 2020. Herbicides act through various mechanisms, including the inhibition of photosynthesis (e.g., triazines and substituted ureas) (Chen 2014; Singh et al. 2018a, b), and the inhibition of amino acid synthesis (e.g., EPSP synthase inhibitors) (Steinrücken and Amrhein 1980). Other herbicides exert anti-microtubule activity (e.g., dinitroanilines, phosphoric amides and N-phenyl carbamates) (Morejohn and Fosket 1991; Morrissette et al. 2004). Some compounds disrupt cell membranes, such as diquat (Petry et al. 1992), or inhibit lipid synthesis (e.g., ACCase inhibitors) (Délye 2005). Additional mechanisms include the mimicking of plant hormones, for example by phenoxyacetates (Dehnert et al. 2019), and the inhibition of cellulose synthesis, as observed with isoxaben (Octobre et al. 2024).

1.3.1 Uses and applications

Selective herbicides: these herbicides target specific types of plants while leaving the desired crop unharmed. They are used in crops where weed species can be effectively controlled without severe damage to the yield (Katan and Eshel 1973). Examples include grass-selective and broadleaf-selective herbicides, such as 2,4-D (2,4-Dichlorophenoxyacetic acid) is a widely used selective herbicide, primarily employed to control broadleaf weeds without harming grass crops such as wheat, maize, and other cereals (Song 2014).

Non-selective herbicides: these herbicides kill or suppress a wide range of plant species, including both weeds and desired crops. They are often used for total vegetation control in non-crop areas such as fence rows, roadsides, or industrial sites (Boutin et al. 2014). An example of a non-selective herbicide is diquat, used to control terrestrial and aquatic vegetation (Magalhães et al. 2018) .

Systemic herbicides: these herbicides are absorbed by the plant and translocated throughout its system, effectively killing the entire plant, including its roots. They are often used for perennial weeds or weeds with extensive root systems (Pacanoski et al. 2020). One of the most common systemic herbicides is glyphosate, which inhibits the shikimic acid pathway and is crucial for the synthesis of essential amino acids in plants (Steinrücken and Amrhein 1980).

Contact herbicides: these herbicides kill only the parts of the plant they encounter. They are effective for controlling weeds with above-ground growth but may not effectively kill roots or rhizomes (Silva Santos et al. 2021). An example is glufosinate-ammonium, which inhibits the enzyme glutamine synthetase, leading to the accumulation of ammonia in plant tissues (Wild et al. 1987).

Residual herbicides: these herbicides remain active in the soil for an extended period, providing long-lasting weed control. They are commonly used in conjunction with pre- or post-emergence herbicides to manage weed growth throughout the growing season (Nurse et al. 2006). One of the most used is pendimethalin, which inhibits cell division and elongation in germinating seedlings (Strandberg and Scott-Fordsmand 2004).

Anti-sprouting herbicides: they are generally applied to inhibit the growth of sprouts from seeds or tubers that are already present in the soil. An example is carvone, a natural sprout inhibitor derived from caraway seed oil that interferes with sprout growth (Hartmans et al. 1995). The distinct mechanisms, such as inhibiting essential enzymes or mimicking plant hormones, make them effective against types of weeds while sparing others (Velini et al. 2010).

1.3.2 Timing of application

Pre-emergence herbicides: applied before weed seed germination, these herbicides create a barrier in the soil that prevents weed seedlings from emerging. They are particularly effective in preventing annual weeds from permanent establishment. Among the pre-emergence herbicides, the three most used and the most effective are oxadiazon, pendimethalin, and pretilachlor with safener. The efficiency of pre-emergence herbicides in controlling weeds is dependent on several factors such as soil moisture, soil tilth, weed flora, herbicides doses, and environmental conditions (Awan et al. 2016).

Post-emergence herbicides: applied after weed emergence, these herbicides target existing weed plants. They can be either selective or non-selective, depending on their mode of action and application (Kousta et al. 2024).

2 Antigerminative effects of compost

In the study of compost's influence on seed germination, specific molecules exhibiting antigerminative properties play a pivotal role. One primary mode of action is the inhibition of water absorption, a critical process for initiating germination (Babiano et al.

1984; Marambe et al. 1993). Certain molecules create conditions that prevent seeds from effectively absorbing water, thus interrupting their development at the initial stage. Additionally, these compounds may interfere with biochemical pathways essential for germination, such as those involving gibberellins, the plant hormones crucial for breaking seed dormancy (Reynolds 1978; Weir et al. 2004). Among these molecules, phenolic acids, fatty acids, hormones and hormone-like substances, and terpenoids, are spontaneously produced during the organic matter decomposition in compost (García et al. 1992; He et al. 1992). These categories of compounds are known to directly impact seed germination by various mechanisms and belong to the group of so called allelochemicals. Allelopathy, derived from the Latin words "*allelon*" (meaning 'of each other') and "*pathos*" (meaning 'to suffer'), refers to the chemical inhibition of one species by another. While the term is most associated with the chemical interactions between two plants, it has also been used to describe microbe–microbe, plant–microbe and plant–insect or plant–herbivore chemical communication. In plants, allelochemicals can be found in leaves, bark, roots, root exudates, flowers, and fruits. These chemicals are typically introduced into the rhizosphere through processes such as leaching from leaves and other aerial parts, volatile emissions, root exudation, and decomposition of bark and leaf litter (Weir et al. 2004).

2.1 Main molecules with allelopathic properties

2.1.1 Phenolic compounds

Phenolic acids, derived from the decomposition of plant material such as leaves, stems, and roots, play a significant role in inhibiting seed germination and root development. These compounds are not easily degraded and are known for their antioxidant, antimicrobial, and anti-inflammatory properties. Highly phenolic compounds take a longer time to compost due to their complex chemical structure (Ayilara et al. 2020, Aylai and Adani 2023, Luo et al. 2018). Most phenolic compounds remain in the residue, leading to an underestimation of the phenolic potential of the food products. Furthermore, they could be extracted from food wastes by certain microorganisms such as *Aspergillus*, *Clostridium*, *Lactobacillus*, *Pediococcus*, *Saccharomyces* and others during the decomposition process. Therefore, fermentation has been used to release bound phenolics, offering a cost-effective and environmentally friendly method (Gulsunoglu-Konuskan and Kilic-Akyilma 2022). By contributing to both the suppression of pathogenic microbes and the stabilization of the composted material, phenolic compounds triggers oxidative responses, interfere with hormonal pathways, and inhibit crucial enzymatic activities necessary for seed development. Their presence in compost can disrupt the production of lignin and other complex organics, which further inhibits weed seed germination (Muscolo et al. 2001; Shindo et al.1978). For instance, vanillic acid, which can be obtained from ferulic acid by means of *Aspergillus niger*, affects the viability of soybeans (Sathiyamoorthy 1990). Catechin and catechol, extracted by *Aspergillus niger* from quercetin, have an inhibitory effect on seeds of *Brassica nigra*, *Chenopodium murale*, *Melilotus indicus* and *Sonchus oleraceus* (Veluri et al. 2004).

2.1.2 Terpenoids

A broad class of organic compounds predominantly produced by plants, terpenoids (Pichersky and Raguso 2018) found in compost originate from the decomposition of plant material containing them (Sánchez-Monedero et al. 2018). Terpenes are volatile organic compounds that make up the aromas and odors of various crops and flowers; besides, they are molecules present everywhere in higher plants, for example, compartmentalized in structures such as trichomes of the plant surface. They are involved in various plant functions such as protection from microbial diseases or attraction of pollinators; furthermore, they can contribute to the antimicrobial properties of compost (Pichersky and Raguso 2018; Sundberg et al. 2011; Komilis et al. 2004). Terpenoids modify soil microbes, affecting nutrients and pathogens, which indirectly influence seed germination. Their ability to mimic or inhibit growth hormones and disrupt cellular membranes makes them effective natural herbicides (Langenheim 1994; Pichersky and Raguso 2018; Weston and Duke 2003; Verdeguer et al. 2020). In addition, they can disrupt the cellular membranes of seeds, affecting both their permeability and integrity (Grana et al. 2012; Weston and Duke 2003). Their allelopathic properties further contribute to a biochemically hostile environment that suppresses the growth and germination of neighboring plant seeds, serving as a natural form of weed control (Verdeguer et al. 2020). Among the terpenoids responsible for a strong herbicide activity, there are: borneol; pinocarvone; camphene; *exo*-fenchol; *trans*-*p*-mentha-1(7); 2,2,5,5-tetramethyl-4-(2-hydroxy-2-methylbutyliene); cyclopenta-1,3-dione; 8 dien-2-ol, α-terpineol; (Z)-ocimenone; epiglobulol; myrtenol; *trans*-pinocarveol; (E)-caryophyllene; α-campholenal; *trans*-carveol; 6-camphenone and leptospermone (Verdeguer et al. 2020).

2.1.3 *Hormones and hormones-like substances*

Compost can serve as a source of plant growth regulators such as auxins (indole-3-acetic acid, IAA) and cytokinins (Miezah et al. 2008; Sienkiewicz et al. 2024; Szymańska-Pulikowska et al. 2016), which can either stimulate or inhibit plant growth depending on their concentration and the sensitivity of the target plants. One study detected notable concentrations of auxin, gibberellic acid, and kinetin in compost and vermicompost, attributing their presence to the combined activity of earthworms and microorganisms (Ravindran et al. 2016). Additionally, a recent review reports that microbial communities in compost can synthesize plant growth hormones (Aguilar-Paredes et al. 2023). Among microorganisms found in compost, bacteria and fungi that synthesize auxin and abscisic acid (ABA) are most directly associated with the inhibition of seed germination (Liu et al. 2013; Miransari and Smith 2014). These organisms collaboratively synthesize hormones during composting by metabolizing organic substrates and these hormones persist in mature compost (Rath et al. 2022). For example, ABA can inhibit water uptake in seed embryos by preventing cell wall loosening, affecting cell wall extensibility and growth potential (Schopfer and Plachy 1985). These phytohormones play a crucial role in modulating plant physiological responses and can contribute to the suppression of weed germination and establishment (Ravindran et al. 2016; Ye and Zhao 2016; Scaglia et al. 2015).

2.1.4 *Fatty acids*

Compost contains various fatty acids, including short-chain fatty acids like acetic acid (Wang et al. 2022a, b) and long-chain fatty acids such as myristic and palmitic acids, which are potent inhibitors of seed germination (Marambe et al. 1993). These fatty acids alter water uptake dynamics, forming physical barriers that restrict seed hydration and affecting the permeability of the seed coat to water and ATP concentration of germinating seeds (Bewley et al. 2013). Their higher prevalence in composts that include animal fats or plant oils highlights their significant role in suppressing unwanted plant growth (Babiano et al. 1984; Shiralipour et al. 1997; Stewart and Berrie 1979). It should be noted that especially short chain fatty acids, being highly volatile, could be lost largely in the early stages of composting (Kong et al. 2023).

2.1.5 *Ammonia*

The decomposition process in compost also produces volatile compounds like ammonia and certain alcohols, which exhibit phytotoxic effects that inhibit weed germination. These compounds are typically short-lived in the composting environment, dissipating rapidly. However, their initial presence can significantly impact seed germination (Kong et al. 2023). Ammonia, in particular, can cause toxicity in plants, affecting root growth and leading to leaf chlorosis by altering intracellular pH, osmotic balance, and nutrient absorption (Kong et al. 2023; Shilpha et al. 2023). A high ratio of NH_4^+ especially shortens primary roots, preventing cell expansion and division in the meristems. Additionally, it influences the biochemical and biological composition of the plant by modifying the internal pH, osmotic balance, phytohormone and polyamine metabolism, and nutrient absorption (Luo et al. 2018). Ammonium toxicity is also associated with lower concentration of chlorophyll a and b, and carotenoid, resulting in a decline of photosynthesis rates. Furthermore, it leads to an increase in ethylene production, exacerbating responses to adverse conditions in plants (Shilpha et al. 2023).

2.2 Main physical characteristics affecting seed germination

Compost's physical characteristics, particularly pH and salinity, significantly influence seed germination and crop performance by altering soil conditions and plant physiological processes. Acidic compost (pH <5) may inhibit root elongation and reduce biomass accumulation during later growth stages (Mandic et al. 2023). Similarly, higly alkaline compost (pH >8) can impair seed germination by disrupting proteolytic enzyme activity and interfering with the metabolism of seed storage compounds (Wang et al. 2022a, b).

High salinity in compost exacerbates soil salt accumulation, leading to osmotic imbalance and ion toxicity (Ullah et al. 2021); moreover, elevated salt concentration, high salinity and high pH may have synergistic effects that reduce germination (Liu et al. 2014).

2.3 Factors affecting the persistence of antigerminative effects

The persistence of antigerminative effects in compost varies depending on several factors. Environmental conditions, such as temperature, humidity, and pH, can significantly influence the stability and activity of antigerminative compounds. Higher temperatures can increase the rate of decomposition of antigerminative compounds, thereby reducing their effective lifespan. On the contrary, cooler temperatures may slow down this decomposition, prolonging the effects (Azim et al. 2018). Moist conditions typically enhance microbial activity, which can lead to quicker breakdown of antigerminative compounds. On the other hand, dry conditions may preserve these compounds longer (Liang et al. 2003). The acidity or alkalinity of the soil can affect both stability and solubility of antigerminative molecules: in certain pH conditions, some of them are more stable and remain active for a longer time than others. For instance, phenolic compounds are unstable at high pH (Friedman and Jürgens 2000), and simultaneously, ammonia is lost more rapidly at elevated pH. Therefore, maintaining a lower pH would enhance the persistence of these substances (Azim et al. 2018). The composition of the compost itself also plays a critical role. The presence of specific organic materials can alter both breakdown rate and longevity of these molecules. For example, municipal solid waste compost is a nitrogen-rich material, and it stimulates microbial growth and activity (Crecchio et al. 2001) that can lead to a faster decomposition of phenolic compounds and fatty acids. In addition, for example, tannins are known for their ability to form complexes with various organic molecules, including proteins, polysaccharides, and phenolic compounds. This interaction can affect the bioavailability and stability of these compounds in the compost or soil, potentially reducing their degradation rate (Kanerva et al. 2006). Moreover, mature compost generally has more stabilized forms of nutrients and fewer volatile antigerminative compounds (Abdelhamid et al. 2004). In contrast, fresh compost might have higher concentration of these active compounds but for a shorter duration (Ozores-Hampton et al. 2002). Furthermore, the method of compost application, particularly the depth of burial, affects its exposure to oxygen and light, which in turn impacts the degradation of antigerminative agents. The microbial community within compost plays a crucial role in breaking down organic matter. High microbial activity can lead to faster degradation of antigerminative compounds, whereas lower activity can sustain their presence longer (Kong et al. 2023).

2.4 Sensitivity of different plant species

2.4.1 Sensitivity of seeds to antigerminative molecules in compost

Different plant species exhibit varying degrees of sensitivity to the antigerminative molecules occurring in compost. Generally, plants with smaller seeds and limited energy reserves are more susceptible (Ligneau and Watt 1995). The permeability of a seed coat can determine how much of a given antigerminative compound the seed can absorb. Thicker and less permeable seed coats might protect the seed by limiting the absorption of harmful substances. Some seeds have natural protective compounds in their seed coats that can neutralize or mitigate the effects of antigerminative chemicals (Galussi and Moya 2017; Powell 2009). Species that naturally delay germination until optimal conditions occur, may avoid periods of antigerminative compounds peak concentration (Evenari 1949). Narrow leaves plants like grasses are not affected as severely as the broad leaves plants or dicot species (Iqbal et al. 2020). Species such as lettuce and certain grasses, like *Lepidium sativum* (Zucconi et al. 1981), are particularly sensitive and thus are used as indicators of the antigerminative potential of compost in agricultural settings (Ozores-Hampton et al. 2002). This variability in plant response necessitates careful consideration when applying compost in diverse herbaceous cropping systems, as well as in its exploitation as herbicide in tree cropping systems. While the antigerminative effect of compost has traditionally been viewed as a disadvantage for herbaceous crops, it could be an advantage when using compost in tree cultivation. Therefore, it is useful to understand the optimal chemical composition of the compost and the best application rate to avoid negatively affecting the existing tree systems in the cultivated field.

2.4.2 *Tolerance of mature plants to antigerminative molecules in compost*

Fortunately, mature plants, such as productive trees, are less sensitive to these allelochemicals. This phenomenon can be attributed to several factors. Mature plants have developed more robust defense mechanisms and chemical tolerance systems compared to seeds. Adult plants have thicker cuticles on their leaves (Fernández et al. 2017) and bark on their stems (Pearce 1996), providing physical barriers that reduce the absorption of harmful substances. Additionally, their established root systems can either avoid or detoxify harmful substances present in the soil (Alagić et al. 2015; McCully 1999), providing them with a protective advantage over germinating seeds. Root exudates modulate soil properties to adapt and ensure plant survival under adverse conditions by changing soil pH, chelating toxic compounds, and attracting beneficial microbiota (Vives-Peris et al. 2020). Roots provide physical anchorage to the soil, enable water and nutrient uptake, and play a central role in plant adaptation to unfavourable environments (Vives-Peris et al. 2020). Mature plants often benefit from associations with soil microorganisms, such as mycorrhizal fungi and beneficial bacteria, which can help mitigate the antigerminative effects (Mercado-Blanco et al. 2018). These attributes of adult plants highlight their robustness and adaptability to various environmental challenges, including exposure to antigerminative compounds.

2.4.3 *Implications for the use of compost in tree cropping systems*

Understanding the contrasting sensitivity between seeds and mature plants to antigerminative molecules in compost offers new perspectives for agricultural management. While the antigerminative effect of compost has traditionally been viewed as a disadvantage, particularly for herbaceous crops, it could represent a valuable advantage when used strategically in tree cropping systems. In such systems, the natural tolerance of mature plants to allelochemicals allows the application of compost without negatively affecting the main crop, while potentially suppressing weed emergence.

Beyond its antigerminative properties, compost is recognized as a higly beneficial and sustainable input in tree cropping systems. It not only enhances plant growth and improves the nutritional status of trees, but also boosts productivity and fruit quality (Okba et al. 2025). Compost contributes significantly to soil health, enriching organic matter, improving soil structure and water retention, and supporting the soil microbiome. In vineyards, for example, compost has demonstrated promise as an eco-friendly weed control strategy, acting through both physical suppression and allelopathic mechanisms, thus reducing the reliance on synthetic herbicedes and fertilizers (Romano et al. 2025).

Moreover, the synergistic use of compost with microbial inoculants, such as mycorrizhal fungi or plant growth-promoting rhizobacteria, can further amplify these benefits by enhancing nutrient uptake and improving plant resilience under adverse conditions (Okba et al. 2025). This integrated approach not only supports the long-term sustainability of tree cropping systems, but also opens new pathways for environmentally sound weed management based on ecological principles.

By incorporating this knowledge into compost application strategies, farmers and horticulturist can optimize the benefits of compost while taking advantage of its inhibitory effects on seed germination.

3 Microbial metabolism during composting process for allelochemicals production

3.1 The composting process and the role of microbes involved

Composting is the process in which a mixed array of organic material from different sources is converted into a product, which is rich in humus and can be used as amending for agriculture. The composting process consists of three phases: mesophilic, thermophilic and maturation, each characterized by both a different microbial community and distinctive physico-chemical conditions.

In the first stage, the mesophilic phase, characterized by temperatures of 20-40°C, bacteria like *Pseudomonas*, *Bacillus*, *Flavobacterium*, as well as *Actinobacteria*, and fungi, decompose the easily-degradable compounds, like non-polymeric sugars and amino-acids. Their metabolism produces an increase of temperature, thus leading to the second stage, the thermophilic phase, characterized by temperatures of 45–70 °C. This is a critical stage for the sanitization of the compost, since high temperatures allow the elimination of both human- and plant-pathogenic microbes, as well as kill weed seeds. Thermophilic microorganisms are especially bacteria, such as *Thermus* spp., *Bacillus stearothermophilus*, and some thermophilic *Actinobacteria* like *Thermoactinomyces*: these are responsible for the decomposition of more recalcitrant chemical compounds, such as cellulose, hemicellulose, and lignin (Bertoldi et al. 1983; Insam and Bertoldi 2007). Temperature monitoring is critical to ensure proper sanitization: maintaining 55–65 °C for at least three days is generally considered as sufficient to effectively reduce the presence of pathogens (Haug 2018).

The final stage is maturation: during this phase, the temperature gradually decreases, and mesophilic microorganisms become eventually active again. *Actinobacteria* and ligninolytic fungi (e.g., *Trichoderma*, *Penicillium*, etc.) play a key role in the transformation of residual, recalcitrant organic matter, contributing to humus formation. This phase can last from weeks to months, depending on both the environmental conditions and the nature of the composted materials (Zucconi and Bertoldi 1987).

It is important to highlight that pathogenic microorganisms can be present at the beginning of the process, as they may derive from household waste or sewage sludge. Poor temperature control or inadequate aeration may allow for their persistence, thus compromising the hygienic quality of the final compost product (Sidhu 2001).

3.2 Nitrogen dynamics during composting

Previous research has reported that the application of compost, particularly immature compost, could inhibit both germination and negatively affect the growth in early stages of either herbaceous and tree crops (Selim et al. 2012; Zucconi et al 1981). This is primarily due to several factors such as high microbial activity, which reduces the amount of available oxygen, decreased available nitrogen (N) in the soil, and the presence of phytotoxic compounds including heavy metals, ethylene, phenolic compounds and ammonia. The concentration of heavy metals must be lower than the legal limits considered acceptable in order not to have a significant environmental impact or generate health issues. Furthermore, phytotoxic substance concentration must conform to specific standards to ensure the compost usability. To this end, tests such as germination assays are conducted, providing clear and reliable evaluations of compost phytotoxicity (Selim et al. 2012).

Carbon and nitrogen, abundant in compost, are key factors contributing to microbial development. Nitrogen in compost is primarily found in organic forms, such as within proteins and nucleic acids (e.g., DNA). During composting, N is involved in several processes including ammonification, NH_3 volatilization, and nitrification. Protein degradation and ammonification are the processes that characterize the starting steps of the degradation of organic substances, leading to an increase in the quantity of ammonium ions (NH_4^+) (Cáceres et al. 2018).

During composting process, the nitrogen present in the organic substance is mineralized by a plethora of heterotrophic microorganisms, such as bacteria and fungi, degrade nitrogen-containing compounds, such as urea or amino acids, into more easily absorbable molecules in addition to an amount of NH_3. Many microorganisms can perform ammonification; among bacteria, notable groups include members of the Proteobacteria and the Firmicutes phyla, such as *Pseudomonas* and *Bacillus* genera, ubiquitously distributed, which play an important role in the global N cycle. Regarding fungi, *Acremonium*, *Alternaria* and *Penicillium* genera are recognized for their high ammonification activity in composting. These microorganisms also produce a series of enzymes which catalyze the hydrolysis of proteins and urea into ammonia, influencing the conversion of ammonium into ammonia (Xu et al. 2023).

Depending on both pH and temperature conditions, ammonium can follow two pathways: it may be transformed into NH_3 and volatilized, or oxidized into more soluble compounds like nitrates through nitrification (Cáceres et al. 2018). Higher pH and temperatures favor the formation of molecular ammonia and also leads to a higher ionised ammonia (Purwono et al. 2023). Nitrification occurs during the curing phase and consist of two stages: first, NH_4^+ is oxidized to NO_2^-, and then to NO_3^- . This process is driven by microorganisms as ammonia-oxidizing bacteria or archaea (AOB/AOA) and the nitrite-oxidizing bacteria (NOB) (Cáceres et al. 2018). All these microorganisms, through chemical reactions of their respective energy metabolisms, convert ammonium into nitrite and finally to nitrate, which is more easily assimilated by plants (Naghdi et al. 2018).

Among the fundamental parameters that have more influence on the formation of ammonia, pH and temperature promote the shift of the NH_4^+/NH_3 equilibrium towards ammonia. It is reported that another effect of high temperature is the inhibition of nitrification, which therefore contributes to the increase in ammonia volatilization (Pagans et al. 2006).

3.3 Fungal secondary metabolites and VOCs as potential herbicides in compost

Several studies have documented the presence of *Alternaria alternata* during the mesophilic phase of composting (Ryckeboer et al. 2003). This fungus produces several secondary metabolites, including tentoxin—a nitrogen-containing cyclic peptide with phytotoxic effects on some plants. Tentoxin can induce chlorosis in germinating seedlings of certain angiosperms by targeting chloroplast ATPases, thereby disrupting photosynthesis (Bendejacq-Seychelles et al. 2024; Fracchiolla and Montemurro 2007).

The optimal temperature for spore germination in most *Alternaria* is approximately 25°C, with a maximum threshold around 35°C (Malathrakis 1983). For *A. alternata*, optimal germination temperatures vary by host: in tomatoes is approximately 29°C, with a maximum temperature of 40°C, while in apples, the optimal temperature is 28°C (Malathrakis 1983). These findings indicate that this fungus can germinate over a broad temperature range. In some cases, the optimal temperature for infection aligns with that for germination, likely reflecting a general physiological requirement of the fungus. However, in other cases, these temperatures differ, potentially indicating a host-specific response where infection occurs under conditions not necessarily ideal for spore germination or penetration (Troncoso-Rojas and Tiznado-Hernández 2014). Moisture, from rain, dew, or high humidity, is critical for infection, with most species requiring a minimum of 9-18 hours of moisture exposure (Mamgain et al. 2013).

Substrate composition also affects toxin production in *A. alternata*. Cereal-based substrates, especially rice, have been asscociated with increased mycotoxins synthesis (Logrieco 1990; Visconti et al. 1986). Optimal pH for tentoxin production is around 7, with greater release at extreme high pH. The specifics of tentoxin biosynthesis remain poorly understood, but it is catalyzed by a multienzyme complex likely with a molecular mass between 200 and 250 kDa (Ramm et al. 1994).

Given the phytotoxic properties of *A. alternata*, the composting process could be strategically modified to favor its growth and the production of tentoxin, inducing chlorosis in germinating seedlings (Bendejacq-Seychelles et al. 2024; Fracchiolla and Montemurro 2007). Specifically, *A. alternata* is present in the mesophilic phase of composting, during which a maximum temperature of approximately 40°C is reached, coinciding with the optimal germination conditions for the fungus (De Gannes et al. 2013). This may represent a potential alternative to chemical herbicides. To achieve this result, the composting process can be halted during its initial phase, known as the mesophilic phase, to maintain optimal conditions for fungal growth. This intervention can be implemented by lowering the pH, Indeed, the low pH can delay the thermophilic stage (Yu et al. 2019). Further studies are needed to deepen and validate this theory, exploring its implications and confirming its potential interest for future scientific advancements.

A decline in microbial activity has been noted in the transition from mesophilic to thermophilic conditions when composting food waste or other acid wastes. In particular, the inhibition of the metabolic activity of thermophilic microorganisms was observed at a pH of approximately 6 even in the presence of good ventilation during the process (Sundberg 2004). Additionally, the transition from mesophilic to thermophilic conditions during the initial phase of composting is accompanied by a change in pH from acidic ($pH = 4.5–5.5$) to alkaline ($pH = 8-9$). Such a low pH is mainly attributable to the presence of short-chain organic acids, primarily lactic acid and acetic acid. These acids, produced by lactic acid bacteria such as *Pediococcus* spp. and *Weissella* spp., are present during the initial stages of food waste composting (Tran et al. 2019) and significantly influence the composting process as their metabolic products lower the pH, inhibiting the activity of other bacteria such as thermophilic ones (Sundberg et al. 2011). The presence of these short-chain organic acids in acidic conditions and their absence in alkaline conditions suggest that these compounds are key factors in pH regulation in composting processes.

In addition, volatile organic compounds (VOCs), generated during the decomposition of organic matter, contribute to phytotoxicity. VOCs are a group of compounds of anthropogenic or biogenic origin characterized by a boiling point lower than 80°C (Komilis et al. 2004).

The VOCs most produced during composting are oxygenated compounds such as esters, acids, and ketones, but the dominant role is played by terpenes (β-pinene, D-limonene, α-pinene).

Additionally, the microorganisms living in the compost can produce terpens (inhibitors of seed germination and growth of several plant species); among these, the fungi *Aspergillus versicolor* and *Paecilomyces variotii* have been identified, which are present at mesophilic and thermophilic temperatures during composting. Although, the mechanisms by which terpenes can influence germination are not well known; some studies report that α-pinene diminishes mitochondrial respiration of soybean cotyledons and increases the rates of electron transport by the alternative oxidase pathway. The generation of mitochondrial ATP is important for macromolecule synthesis and takes part in other metabolic processes such as cellular division. Thus, the interference of terpenes with mitochondrial respiration could be the cause of the inhibition of germination and plant growth (Ryckeboer et al. 2003; Abrahim et al. 2000; Fischer et al. 1999).

The role of organic substances in the growth of plants has long been debated, largely due to microbial decomposition byproducts that can either stimulate or inhibit germination. In fact, according to some experiments, it has been demonstrated that some compounds such as fatty acids (butyric, formic, caproic, crotonic) negatively affect the growth of wheat plant roots, until inhibiting them (Mccalla and Haskins 1964).

Microorganisms responsible for producing such phytotoxic compounds are predominantly present in the initial phases of the composting process (Ryckeboer et al. 2003). Their phytotoxic action is caused by the production of molecules or spores deriving from metabolism and then released into the soil. Regarding spore-forming bacteria with inhibitory effects on plant growth, these are species such as *Bacillus subtilis, B. cereus, and B. brevis*. Certain unidentified bacteria and *Pseudomonas fluorescens*, also present in compost, have an herbicidal effect (Mccalla and Haskins 1964).

4 Conclusions

The antigerminative effects of some allelochemicals produced during the composting process have always been considered from a negative perspective, due to their impact on the production of annual crops. However, in tree crops, this could be considered a beneficial effect to be exploited to control weed growth in a more environmentally sustainable manner. An in-row soil management strategy based on the use of compost could be implemented considering, besides the mulching and fertilizing benefits, also its herbicide properties. In fact, we suggest that compost could be compared to an anti-sprouting herbicide to be used in pre-emergence of weeds.

It is necessary to explore the application of compost at different soil application rates and methods to harness the potential of the allelochemical compounds. Nevertheless, the composting process could be differently designed and implemented to produce different quality of amendments, depending on their optimal applications in different cropping systems (annual herbaceous plants or perennial trees). In this regard, further studies are necessary to enforce the process to valorize the antigerminative effects, avoiding environmental risks.

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Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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