*International Journal of Environment and Climate Change*

***Volume 14, Issue 9, Page 124-138, 2024; Article no.IJECC.122277***
***ISSN: 2581-8627***
*(Past name: British Journal of Environment & Climate Change, Past ISSN: 2231–4784)*

# The Role of Volatile Organic Compounds (VOCs) in Determining Seed Physiological Quality: A Review

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***Article Information***

DOI: https://doi.org/10.9734/ijecc/2024/v14i94398

**Open Peer Review History:**
This journal follows the Advanced Open Peer Review policy. Identity of the Reviewers, Editor(s) and additional Reviewers, peer review comments, different versions of the manuscript, comments of the editors, etc are available here:
https://www.sdiarticle5.com/review-history/122277

***Review Article***

***Received: 13/08/2024***
***Accepted: 23/08/2024***
***Published: 28/08/2024***

## ABSTRACT

Volatile organic compounds (VOCs) emitted by seeds serve as promising biomarkers for assessing seed vigor, viability, and deterioration during storage. This review synthesizes current knowledge on the types and chemical classes of VOCs released by seeds, factors affecting their emission, and methods for their collection and analysis. VOCs indicate seed aging, with increased emissions of alcohols, aldehydes, and ketones associated with deterioration processes like lipid peroxidation. Volatile organic compounds (VOCs) associated with seed deterioration include alcohols like

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***Cite as:** Suresh, Karantothu, Chetna, Raj Kumar Mandal, Dasari Purna Prakash, Kakadi Akhil Dora, and J M Kavana. 2024. "The Role of Volatile Organic Compounds (VOCs) in Determining Seed Physiological Quality: A Review". International Journal of Environment and Climate Change 14 (9):124-38. https://doi.org/10.9734/ijecc/2024/v14i94398.*

ethanol, which can indicate fermentation, aldehydes such as hexanal, which is linked to lipid oxidation, and ketones like 2-heptanone, which can result from microbial activity and contribute to off-flavors and rancidity. The quantity and composition of VOCs correlate with the extent of seed deterioration, potentially offering a rapid, non-destructive alternative to traditional germination tests for evaluating seed quality. VOCs also mediate interactions between seeds and microorganisms, influencing germination and stress responses. Different research findings regarding volatile organic compounds (VOCs) in seeds indicate their potential as indicators of seed quality, which could lead to improved seed management strategies. By utilizing VOC profiling, farmers can make informed decisions on seed selection and treatment, ultimately enhancing crop yield and resilience in agricultural practices. While VOC analysis shows promise for integration into seed quality testing, challenges remain in standardizing protocols and identifying robust markers across different seed types, species and storage conditions. Advances in VOC research may ultimately lead to novel solutions for improving seed and crop productivity. Future research directions in VOC analysis for seed quality testing should focus on standardizing VOC profiles across diverse seed species, integrating VOC analysis with precision agriculture technologies, exploring environmental influences on VOC emissions, developing non-invasive testing methods, conducting longitudinal studies on seed storage, applying VOCs in breeding programs, and establishing links between VOC emissions and disease resistance.

*Keywords: Seed quality; germination; seed vigor; seed deterioration; volatile organic compounds.*

## 1. INTRODUCTION

Volatile organic compounds (VOCs) are small signaling molecules with low molecular weight (<300 g/mol) and high vapor pressure that are emitted by plants, bacteria, and fungi [1]. In recent years, there has been increasing research interest in understanding the diverse roles VOCs play in mediating plant growth, development, and responses to biotic and abiotic stresses.

Metabolic changes in seeds during imbibition and germination liberate quantities of gaseous and volatile metabolites known as VOCs [2]. These VOCs emitted by germinating seeds have been found to have important effects on the physiological quality and performance of the seeds. For example, studies have shown that certain VOCs can stimulate seed germination and seedling growth in various plant species [3,4]. Exposure to VOCs released by some rhizobacteria increased the biosynthesis of essential oils and growth parameters in peppermint (*Mentha piperita*) [1]. VOCs emitted by Bacillus species promoted the germination and root elongation of lettuce seeds [4].

VOCs appear to be the prime seeds defense mechanisms, enabling enhanced resistance or tolerance to upcoming stresses [5]. VOCs have been implicated in quenching reactive oxygen species and inducing physiological changes that improve stress tolerance, though the mechanisms are not yet fully elucidated [5]. Some VOCs may also have allelopathic effects, inhibiting the germination and growth of competing plant species, and potentially providing a competitive advantage [5].

While most studies on seed VOCs to date have been conducted under controlled laboratory conditions, there is growing interest in exploiting VOCs to enhance seed quality and performance in agricultural field settings [5]. However, more research is needed to fully characterize the diverse VOCs emitted by seeds, elucidate their biological functions and mechanisms of action, and develop practical strategies for harnessing VOCs to improve crop productivity.

The current state of knowledge on the role of VOCs in determining seed physiological quality, identify key gaps in understanding, and highlight promising directions for future research and applications in agriculture. Understanding the complex functions of seed VOCs may ultimately enable new approaches to enhance the quality, stress tolerance, and yield of crop plants.

## 2. VOLATILE ORGANIC COMPOUNDS ASSOCIATED WITH SEEDS

### 2.1 Types and chemical classes of VOCs released by seeds

#### 2.1.1 Alcohols

Methanol and ethanol are prevalent VOCs emitted by seeds, especially under humid storage conditions [6].

#### 2.1.2 Aldehydes

Volatile aldehydes are released by seeds and can be used to measure seedvigor [6].

#### 2.1.3. Ketones

Acetone and methyl-ethyl-ketone (MEK) are ketone VOCs detected in the headspace of stored seeds [6].

#### 2.1.4 Short-chain ethers or peroxides

Unidentified short-chain ethers or peroxides are emitted bydry-stored seeds of some species [6].

#### 2.1.5. Alkanes

Butane and pentane are alkane VOCs released by dry-stored seeds [6].

#### 2.1.6 Terpenoids

Many seeds emit volatile terpenes and terpenoids [6,7]. Though, these are often subtracted from total VOC measurements when studying VOCs related to seed quality [6].

#### 2.1.7 Nitrogen-containing compounds:

Some seeds release nitrogen-containing volatile compounds [7,8].

#### 2.1.8 Sulphur compounds

Certain plant orders like Brassicales emit volatile sulphur compoundsfrom their seeds [8].

### 2.2 Factors Affecting VOC Emission from seeds (seed type, storage conditions, aging, etc.)

#### 2.2.1 Seed type/species

Different seed species emit distinct types and quantities of VOCs, reflecting variations in their biochemical composition and metabolic processes [6]. For instance, caraway (*Carum carvi*) seeds emitted higher levels of total VOCs compared to lettuce (*Lactuca sativa*) and guar (*Cyamopsis tetragonoloba*) seeds under the same storage conditions [6].

#### 2.2.2 Storage conditions

The temperature, humidity, and gaseous environment during seed storage significantly influence VOC emission rates.

- **Temperature and humidity:** Higher storage temperature and humidity tend to increase VOC emission, particularly alcohols like methanol and ethanol, which are products of fermentation reactions [6,9]. Seeds stored under humid conditions emitted VOCs indicative of fermentation, with methanol and ethanol being predominant [6].
- **Desiccation:** Dry storage conditions or the use of desiccants and oxygen absorbers can substantially reduce VOC emission by limiting oxidation and fermentation reactions [6,9]. Ageing seeds in the presence of silica gel or oxygen absorbers generally decreased volatile emission by around twofold compared to control seeds [9].
- **Gaseous environment:** The composition of the storage atmosphere, particularly oxygen levels, modulates VOC emission [9]. Lower oxygen concentrations decrease VOC emission from seeds [9].
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#### 2.2.3 Seed aging/deterioration

As seeds age and deteriorate during storage, they typically emit higher levels of certain VOCs that serve as markers for degradative processes.

- **Aldehydes and alcohols:** Aged and deteriorated seeds tend to release greater amounts of aldehydes and alcohols, which are indicative of lipid peroxidation and fermentation reactions, respectively [1,6]. VOC emission generally increased with storage time as seeds lost viability [6].
- **Metabolic inactivation:** Very old or dead seeds may eventually cease emitting VOCs as they become metabolically inactive [6].

### 2.3 Methods for collecting and analyzing seed VOCs.

#### 2.3.1 VOC collection methods

*2.3.1.1 Solid-Phase Microextraction (SPME)*

The most common method for collecting VOCs from seeds is solid-phase microextraction (SPME) [6]. In this technique, an absorbent fiber is exposed to the headspace above the seeds in an airtight container for a set time. The VOCs are absorbed onto the SPME fiber, which is then directly injected into a gas chromatography-mass spectrometry (GC-MS) system for analysis. Key parameters like fiber type, coating, exposure time, and sample volume are optimized for maximum VOC absorption [6].

*2.3.1.2 Tedlar bags*

Another method is collecting headspace VOCs from seeds in Tedlar bags, followed by SPME extraction of the VOCs from the bag [6]. This allows for larger sample volumes and longer collection times.

*2.3.1.3 Direct sampling*

VOCs can also be directly sampled from seed "breath" during germination using a gas-tight syringe [6]. The sampling is timed to coincide with the plateau phase of CO2 release to capture VOCs from the alveolar portion of the seeds.

*2.3.1.4 Cryogenic trapping*

Cryogenic trapping or cryofocusing of VOCs is another collection approach mentioned in the papers [6]. This involves condensing VOCs at very low temperatures for pre-concentration before analysis.

#### 2.3.2 VOC analysis methods

*2.3.2.1 Gas Chromatography-Mass spectrometry (GC-MS)*

GC-MS is the primary analytical technique for separating, identifying and quantifying the collected VOCs [6,10]. Different GC column types are used, such as DB-624 or DB-1, with optimized temperature programs. VOCs are identified by comparing their retention times and mass spectra to known standards. Quantification is done by relating peak areas to calibration curves.

The types of VOCs commonly reported from seeds include alcohols (ethanol, methanol), aldehydes (acetaldehyde, hexanal), alkanes (pentane), ketones, carboxylic acids, esters and terpenes [6]. In general, VOC levels increase as seeds age and deteriorate during storage. The VOC profiles provide information about seed quality, vigor, membrane integrity and biochemical processes like lipid peroxidation [6].

SPME-GC-MS with headspace sampling is the most widely used approach for measuring VOCs from seeds as markers of quality and deterioration. The studies provide detailed protocols for collection, separation, identification and quantification of seed VOCs to enable standardized analysis.

## 3. VOCS AS MARKERS OF SEED QUALITY AND VIABILITY

### 3.1 Relationship Between VOC Profiles and Seed Germination, Vigor and Viability

- The quantity of VOCs emitted when seeds commence metabolic activity during germination depends on their vigor status and the amount of storage reserves [11]. Seeds with higher vigor tend to emit more VOCs.
- Metabolic changes in seeds during imbibition and germination release gaseous and volatile metabolites known as VOCs [2]. These VOCs can potentially serve as markers to predict seed vigor and viability.
- A study compared VOCs between artificially aged (AA) and non-aged (NA) sweet corn seeds and constructed Partial Least Squares Regression (PLS-R) models based on the VOC data to predict seed vigor [12]. This suggests VOC profiles could be used to assess seed quality.
- Researchers propose that VOC fingerprinting could enable quick assessment of the vigor status of seeds [11]. But standard protocols still need to be developed for this VOC fingerprinting approach.
- Plant growth-promoting rhizobacteria can modulate root system architecture in Arabidopsis thaliana through emission of VOCs **[**13]. This indicates VOCs play a role in regulating plant growth and development.

### 3.2 Important VOC Biomarkers Indicative Of Seed Physiological Status

#### 3.2.1 Aldehydes as markers of seed deterioration

Aldehydes such as hexanal, pentanal, and butanal accumulate in seeds during storage as a result of lipid peroxidation, which is a major cause of seed deterioration. Higher levels of these aldehydes are indicative of reduced seed viability and vigor.

In a study on lettuce seeds, hexanal levels increased as seed germination decreased from 75% to 50% during storage [6]. Similar trends were observed in caraway and wallflower seeds [6]. Aldehyde accumulation is initiated by autoxidation or enzymatic oxidation of unsaturated fattyacids in seeds [11].

#### 3.2.2 Alcohols and ketones associated with germination metabolism

Alcohols like ethanol and methanol, as well as ketones like acetone, are produced as a result of increased metabolic activity during seed imbibition and early stages of germination [11,6]. It is found that ethanol, methanol and acetone were prominent VOCs emitted from germinating lettuce seeds under humid conditions [6]. The levels of these compounds correlated with the seed germination potential. It is also reported that the emission of ethanol and acetone during early germination of soybean seeds [12].

#### 3.2.3 Experimental methods for voc profiling

Gas chromatography (GC) and GC-mass spectrometry (GC-MS) are commonly used techniques to analyze the VOC profiles emitted by seeds [11,12]. Seeds are typically stored at different moisture levels, and VOC emissions are measured at different germination percentages using headspace sampling [6].

The VOC data is then correlated with results from standard seed viability tests such as tetrazolium staining. This allows identification of specific VOC biomarkers associated with different physiological states of the seeds.

Key VOC biomarkers including aldehydes, alcohols and ketones can provide valuable information about the physiological status of seeds. Aldehydes like hexanal are indicative of seed deterioration, while alcohols and ketones are associated with germination metabolism. GC and GC-MS based VOC profiling methods, combined with seed viability assays, are effective experimental approaches for identifying these biomarkers. Establishing crop-specific VOC fingerprints can enable quick and non-destructive assessment of seed vigor and viability.

### 3.3 Using VOCs to Predict and Monitor Seed Deterioration During Storage

The VOCs emitted by seeds are thought to be products of various chemical reactions occurring within the seeds during storage. Many of these VOCs are reactive and potentially toxic to the seeds themselves. Their accumulation perpetuates further damaging reactions that lead to seeddeterioration [6, 11,12].

#### 3.3.1 Relationship between VOCs and seed deterioration

Studies have shown that the quantity of total VOCs emitted by seeds is positively correlated with the degree of seed deterioration [11,14,15]. As seeds age and lose viability during storage, the strength and diversity of VOCs released increases.

In one study on groundnut seeds, a significant decrease in seed germination, vigor and other physiological qualities was observed when the total VOC emission levels reached over 50% of initial values. The highest reductions in seed quality occurred when VOC levels reached 92% of the initial amounts [14,15].

The VOC profile also changes as seed deterioration progresses. Methanol and ethanol tend to be the predominant VOCs released by seeds stored at high moisture contents, while dry seeds emit higher proportions of hydrocarbons like pentane and butane [6]. Certain compounds like an unidentified short-chain ether/peroxide seem to be markers of seed aging in dry storage across multiple species [6].

### 3.4 Using VOCs as Predictive Markers of Seed Quality

Given the close association between VOC emissions and seed deterioration, VOCs have great potential to be used as sensitive, early indicators of seed quality during storage [11,12,14,15]. By monitoring the total quantity and composition of VOCs, it may be possible to detect seed aging before germination or other physiological changes become apparent.

Some researchers propose that unique VOC "fingerprints" could be developed for each crop and linked to specific vigor levels [11]. This would allow quick, non-destructive assessment of seed lot quality. Standard sampling and analysis protocols need to be established, and further research is needed to identify the specific marker compounds most indicative of seed deterioration in each species [11].

## 4. MECHANISMS OF VOC RELEASE AND ACTION IN SEEDS

### 4.1 Biochemical Pathways And Enzymes Involved In Voc Biosynthesis in Seeds

- **Terpenoid biosynthesis:** Volatile terpenoids, including monoterpenes, diterpenes, and sesquiterpenes, are synthesized via the mevalonic acid (MVA) and methylerythritol phosphate (MEP) pathways [16]. Key enzymes include terpene synthases, which convert phenyl diphosphate precursors into various terpenes [17].
- **Phenylpropanoid/benzenoid biosynthesis:** These VOCs are derived from the shikimate and arogenate pathways [16]. Important enzymes include those involved in phenylpropanoid and benzenoid biosynthesis, such as phenylalanine ammonia-lyase (PAL) and benzoic acid carboxyl methyltransferase (BAMT) [17].
- **Fatty acid derivative biosynthesis:** VOCs like green leaf volatiles (GLVs) and jasmonate (JA) are produced via the lipoxygenase (LOX) pathway from fatty acid precursors [16]. Enzymes such as lipoxygenases and hydroperoxide lyases are crucial for GLV formation [17].
- **Cytochrome P450 enzymes:** These versatile enzymes play a key role in modifying and diversifying VOCs from various pathways, especially those derived from fatty acids like the octadecanoid pathway [17].

The biosynthesis of VOCs in seeds is under tight spatial and temporal regulation, with production often peaking during specific developmental stages or in response to environmental cues [17,3]. Transcriptional control by transcription factors and epigenetic regulation via mechanisms like non-coding RNAs, DNA methylation, and histone modifications also modulate VOC biosynthesis [16].

**Table 1. VOC emissions and their impact on seed quality**

| Study | Seed Type | VOCs Analyzed | Physiological Effects Observed | Key Findings |
|---|---|---|---|---|
| 1 | Groundnut [14,15] | Alcohols, Aldehydes, Acids, Esters, Alkanes, Alkenes, Ketones, Ethers | Decreased germination, root and shoot length, dry matter production | Significant reduction in quality attributes when total volatile strength exceeded 50% |
| 2 | Rice (Co 51) [14,15] | 1-Hexanol, 1-Butanol, Ethanol, Hexanal, Acetic Acid | Reduced germination, increased electrical conductivity, lipid peroxidation | Highest reduction in quality at total volatile strength of 54.90% |
| 3 | Groundnut [14,15] | Various VOCs | Increased electrical conductivity, decreased enzyme activities | Notable biochemical changes with increased VOC emission strength |

**Table 2. VOC emission levels and physiological quality indicators**

| Study | Seed Type | Total Volatile Strength (%) | Physiological Indicators Affected | Biochemical Changes |
|---|---|---|---|---|
| 1 | Groundnut [14,15] | >50% | Germination rate,root/shoot length, vigour index | Increased lipid peroxidation, decreased catalase activity |
| 2 | Rice (Co 51) [14,15] | >40% | Germination, root/shoot length, dry matter | Increased lipoxygenase activity, decreased peroxidase activity |

### 4.2 Physiological Roles of VOCs in Seed Dormancy, Germination, and Stress Responses

Volatile organic compounds (VOCs) released by plants and microbes play important physiological roles in regulating seed dormancy, germination, and stress responses.

Certain long-chain hydrocarbons produced by bacteria, such as C21, C24, and C31 alkanes released by Bacillus sp. MH778713, have been shown to break seed dormancy and promote germination in mesquite seeds under chromium stress [18]. These VOCs likely act as signaling molecules that counteract the inhibitory effects of heavy metal stress on seed germination.

Plants also emit a diverse array of VOCs that can have allelopathic effects on the germination and growth of other plants [19]. For example, monoterpenes like 1,8-cineole, camphor, and β-pinene released by some plants inhibit seed germination and seedling growth. Other plant-derived VOCs such as hexanal, 1-hexanol, and 1-octanol have been found to stimulate seed germination [19].

Many plants increase VOC emissions, particularly green leaf volatiles and terpenes when exposed to stresses like drought, salinity, extreme temperatures, ozone, and herbivory [19]. These stress-induced VOCs can prime defense responses in neighboring plants, attract predators of herbivores, and act as antioxidants to mitigate oxidative damage [19].

### 4.3 VOC-Mediated Interactions Between Seeds and Microorganisms

Microbial volatile organic compounds (mVOCs) play a crucial role in mediating interactions between seeds, plants and microorganisms. Diverse bacteria and fungi produce an array of mVOCs that can promote plant growth, induce systemic resistance against pathogens, improve abiotic stress tolerance, and modulate plant hormone signaling pathways [20,21,22].

Some key VOCs involved in these interactions include 2,3-butanediol, acetoin, terpenes, benzothiazole, and dimethyl disulfide. These compounds are produced by beneficial microbes such as *Bacillus*, *Pseudomonas*, *Trichoderma*, and *Streptomyces* species [20,21,23]. The mechanisms by which mVOCs mediate their effects on plants are multifaceted. They can exhibit direct antimicrobial activity against plant pathogens, elicit plant defense responses, and modulate phytohormone pathways like auxin, cytokinin, salicylic acid, and jasmonic acid signaling [20,22,24].

For example, studies have shown that Bacillus-derived mVOCs can promote growth and salt stress tolerance in *Arabidopsis thaliana* by regulating auxin homeostasis [21]. Similarly, Trichoderma virens produces mVOCs that display antifungal activity against plant pathogens [21]. *Pseudomonas* and *Bacillus* species emit mVOCs that enhance seed germination, root and shoot growth, and overall yield in crops like tomato and mung bean [21,23].

mVOCs from *Pseudomonas fluorescens* WR-1 and *Bacillus amyloliquefaciens* have been found to restrict the growth and virulence of plant pathogens like *Ralstonia solanacearum* [21]. Endophytic bacteria such as *Pseudomonas stutzeri* and *Stenotrophomonas maltophilia* also produce antifungal mVOCs that can protect plants against diseases [21].

Microbial volatile organic compounds serve as important signaling molecules in the complex interactions between seeds, plants and their associated microbiota. By promoting growth, inducing resistance, and modulating stress responses, mVOCs can greatly benefit plant health and productivity. Harnessing these natural plant-microbe communication systems could lead to the development of sustainable agricultural practices with reduced reliance on chemical fertilizers and pesticides [24].

## 5. APPLICATIONS OF SEED VOC ANALYSIS

### 5.1 Rapid and Non-Invasive Techniques For Assessing Seed Quality Based on VOCs

Volatile organic compounds (VOCs) released by seeds have emerged as promising biomarkers for rapidly and non-invasively assessing seed quality and vigor. During storage and germination, seeds emit a diverse array of VOCs, including alcohols, aldehydes, alkanes, acids, and esters [14,15,25]. The composition and quantity of these VOCs are influenced by factors such as seed moisture content, storage conditions, and the extent of deterioration [14,15,6].

Studies have consistently shown a strong positive correlation between VOC emission and seed aging or deterioration. As seeds lose vigor, their VOC profiles change distinctively compared to high-quality seeds [14,15,25,2]. This makes VOC analysis a potential tool for quickly distinguishing between high and low-vigor seed lots.

Advanced analytical techniques like gas chromatography-mass spectrometry (GC-MS) enable precise profiling of seed VOCs [14,15,26,12]. Compounds commonly associated with seed deterioration include ethanol, methanol, acetaldehyde, hexanal, and pentane [6,25]. For example, in a study on groundnut seeds, the total VOC emission strength reached over 90% in heavily deteriorated samples that had lost most of their germinability [14,15].

The development of standardized VOC fingerprinting protocols and identification of specific marker compounds for different crop species could pave the way for practical applications of this approach in seed quality testing [11, 2]. VOC analysis offers the advantages of speed and non-destructive sampling compared to traditional germination and vigor tests [25,11].

Several studies across various crops like rice, sweet corn, tomato, and others have demonstrated the feasibility of using VOC profiling for vigor assessment [26,12,2]. However, more research is needed to establish robust crop-specific protocols and validate VOC markers against physiological and biochemical parameters of seed quality [25,11].

VOC fingerprinting holds great promise as a rapid and non-invasive technique for evaluating seed vigor. By harnessing the potential of VOC biomarkers, seed technologists could significantly improve the efficiency and precision of quality testing in the future [25,11].

## 5.2 Using VOCs for Early Detection Of Seed Pathogen Infection

Plants and microorganisms emit specific blends of volatile organic compounds (VOCs) that can serve as biomarkers for detecting pathogen infections in seeds and plants [27,28]. VOC profiles are often pathogen-specific, allowing for identification of the causal agent. For example, wheat infected with Fusarium head blight emitted higher levels of germacrene D and sativene compared to healthy plants, while wheat infected with *Septoria nodorum* blotch had increased emissions of mellein and heptadecanone [28].

Analytical techniques like gas chromatography-mass spectrometry (GC-MS) and electronic noses are commonly used to detect and characterize VOCs associated with pathogen infections [29,1,30]. GC-MS provides reliable, efficient, and selective measurement of hundreds of VOCs, while electronic noses can mimic the mammalian olfactory system to "sniff out" infections based on VOC profiles [1, 30].

Combining VOC analysis with physiological parameters can enable early diagnosis of seed infections before visible disease symptoms appear [30]. A study on potato found that monitoring both VOCs and physiological activity could feasibly detect fungal and bacterial infections during seed potato storage [30].

Some common VOCs identified as potential markers of pathogen infection include alcohols, ketones, terpenoids, sulfur compounds, and esters [27,28,21]. The abundance of specific marker VOCs often differs significantly between healthy and infected seeds and plants. For instance, potato tubers infected with various rot pathogens emitted distinct VOC profiles compared to healthy tubers [1].

## 5.3 Potential of VOCs as Natural Fumigants for Seed Storage Pest Control

Volatile organic compounds (VOCs) derived from plants and microbes show promising potential as natural fumigants for controlling storage pests of seeds and grains. VOCs are considered environmentally benign alternatives to synthetic pesticides and have proven efficacy against major storage pests like beetles, moths, and nematodes [31,32].

Many plant-derived VOCs exhibit repellent and insecticidal effects. For example, limonene, β-ocimene, linalool, and methyl salicylate (MeSA) effectively repel whiteflies, beetles, and moths [31]. Slow-release dispensers of these VOCs can create a protective barrier around stored products. Also, essential oils from plants like *Carum carvi* [32] and *Artemisia annua* [32] have shown fumigant toxicity against storage pests like confused flour beetle and maize weevil.

Microbial VOCs also possess pest control properties. Dimethyl disulfide (DMDS) and S-methyl thioacetate (MTA) emitted by bacteria exhibit strong nematicidal activity against root-knot nematode *Meloidogyne incognita* [33]. The LC50 values were 8.57 and 1.43 μg/cm3 air for DMDS and MTA respectively, suggesting their potential as natural fumigants [33].

Besides direct toxicity, VOCs can induce plant defense responses against pests and pathogens. The exogenous application of MeSA upregulates salicylic acid signaling and antioxidant defense pathways, enhancing plant resistance [31]. Integrating repellent VOCs with defense elicitors could provide a multi-pronged approach for managing storage pests.

The efficacy of VOCs is often variable, likely influenced by factors like pest density, plant variety, and environmental conditions [31,32]. Optimizing formulation, delivery methods, and integrating with other IPM tactics is necessary for consistent pest control. While challenges remain, the use of VOCs as natural fumigants holds great promise for sustainable management of seed storage pests.

## 5.4 Implications for Seed Science and Technology

- **VOCs as biomarkers of seed quality:** VOCs emitted by seeds can serve as non-invasive indicators of seed viability, vigor, and physiological state during storage. Specific VOCs like alcohols (methanol, ethanol) and ketones are associated with deteriorating seed quality [6]. Monitoring VOC profiles could allow early detection of seed aging and quality issues.
- **VOCs influence seed germination and seedling growth:** Some VOCs, especially those produced by microbes, can promote seed germination, break dormancy, and enhance seedling growth. For example, VOCs from Bacillus and Pseudomonas species improved germination and growth parameters in various crops [34]. Understanding these effects could lead to applications of microbial VOCs as natural growth promoters.
- **VOCs in seed pathogen and pest defense:** Seeds emit VOCs that can defend against pathogens and pests. Conversely, VOCs from infected seeds may serve as early indicators of seed-borne diseases [30]. Harnessing defensive VOCs and monitoring disease-related VOCs could improve seed health and quality.
- **Optimizing seed production and storage:** In hybrid seed production, floral VOCs mediate pollinator attraction which is critical for effective pollination [35]. During seed storage, monitoring VOC profiles and minimizing VOCs associated with deterioration could help maintain seed quality and longevity [6,30]. Manipulating VOCs might also enhance seed viability and pathogen resistance.
- **VOCs as tools for assessing and sorting seeds:** Rapid and non-destructive analysis of seed VOCs using methods like GC-MS, PTR-MS and e-noses could allow quality testing and sorting of seed lots [26,12]. VOC-based markers could complement or replace traditional germination and vigor tests.
- **VOCs as indicators of seed deterioration during storage:** VOCs like alcohols (methanol, ethanol) and ketones emitted by seeds are associated with deteriorating seed quality and reduced longevity during storage [35,12]. Some VOCs may be toxic to seeds and perpetuate reactions that accelerate aging [12]. Monitoring VOC profiles could allow early detection and control of seed deterioration. Controlling storage conditions to remove certain VOCs could help maintain seed viability.
- **VOCs in seed disease diagnosis and management:** Seeds emit defensive VOCs that protect against pathogens and pests, while VOCs from infected seeds can serve as early indicators of seed-borne diseases [36,37]. Understanding these VOC markers could improve disease diagnosis and management to enhance seed health [37].
- **Microbial VOCs for seed pathogen resistance:** Certain microbial VOCs like benzothiazole, phenols, and pyrazines have antimicrobial activity and can induce plant defense responses in seeds [34]. Harnessing these microbial VOCs could be a strategy to enhance seed resistance against pathogens.
- **VOCs mediate pollinator attraction for seed production:** Floral VOCs are critical for attracting pollinators, which is essential for effective pollination and seed-set in many crops [35,38]. The specific VOC blend influences pollinator preference and

behavior [35]. Virus infections can alter floral VOC emissions and consequently impact pollinator visits [38].

- **VOCs as tools for assessing seed vigor:** The composition of VOCs emitted during seed imbibition and germination can indicate seed vigor and quality [2]. Analyzing these VOCs could provide a rapid, non-destructive method to evaluate seed lot performance.

## 6. CHALLENGES AND FUTURE PERSPECTIVES

### 6.1 Limitations and Technical Challenges In Seed VOC Research

- Experiments on VOC efficacy is often performed using concentrations far higher than those achievable in open-field conditions. Trials testing the antimicrobial activity of VOCs are frequently done in Petri dishes by applying pure liquid solution, without quantifying the actual VOC concentration in the headspace during the experiment [5].
- The high biodegradability of VOCs limits their persistence and activity, despite minimizing long-term non-targeted effects [5].
- There is limited information on the effects of plant VOCs on crop productivity [5].
- Accurate quantification of VOC production in seeds must account for sorption–desorption dynamics between solids and airspaces. More work is needed to accurately model the partitioning of VOC products [6].
- VOC analyses reflect the most prominent reaction types, but these may not be the most physiologically relevant. For example, high pentane production in aged seeds likely derives from lipid peroxidation, but may not directly impact seed viability [6].
- Developing effective and specific synthetic VOC blends can require 5-10 years for researchand development [5].
- High costs associated with formulation, mass production, registration and marketing of synthetic VOCs, along with scalability limitations, have slowed the use of VOCs in agriculture [5].
- VOCs are challenging to control in field trials [19]. Problems exist in managing VOC application in open fields where their effects cannot be controlled as effectively as in greenhouses [5].
- Sampling and analysis of VOCs is considered a technical challenge due to their special features, extreme complexity, diversification and significant spatial-temporal emission variation [39].

### 6.2 Knowledge Gaps and Areas for Further Investigation

Volatile organic compounds (VOCs) play an important role in determining seed physiological quality and deterioration during storage. Studies have shown that seeds release various VOCs including alcohols, aldehydes, acids, esters, alkanes, alkenes, ketones, and ethers during storage [5,14,15]. Increased emission of VOCs is associated with seed deterioration and loss of key physiological properties like viability, germination capacity, vigor, and biochemical processes [5].

High levels of VOC emission, especially when exceeding 50% of the total VOCs released, can significantly reduce important seed quality parameters. Experiments found that seeds with high VOC emission had lower germination rates, reduced root and shoot growth, decreased dry matter accumulation, and a lower overall vigor index compared to seeds with low VOC emission [5]. This indicates that VOCs are not just markers of seed deterioration, but their accumulation may directly impact the physiological performance of seeds. The composition of VOCs released can also provide insights into seed quality. Certain compounds like aldehydes have been identified as specific markers of poor seed quality and advanced stages of deterioration [14,15]. By analyzing the VOC profiles of seed samples, it may be possible to detect early signs of quality decline before physiological symptoms become apparent.

There are still some knowledge gaps in understanding the full role and potential applications of VOCs in seed science. The mechanisms by which seeds perceive and respond to different VOCs are not yet clear [5]. The effects of specific blends or ratios of VOCs need to be investigated further [14,15]. With more research, VOC analysis could be developed into a powerful tool for early detection of seed deterioration during storage, allowing timely interventions to maintain seed quality [5,14,15].

### 6.3 Prospects for Integrating VOC Analysis in seed Quality testing and Certification Programs

Volatile organic compound (VOC) analysis is emerging as a promising approach for rapid, non-destructive assessment of seed quality and vigor. VOCs released from seeds can provide valuable information about their physiological status and deterioration during storage [12]. Techniques such as headspace solid-phase microextraction (HS-SPME) coupled with gas chromatography-mass spectrometry (GC-MS) and electronic noses enable the detection and fingerprinting of complex VOC profiles from seeds [12,40].

Studies have shown that specific VOCs are associated with seed aging and loss of vigor. These include compounds related to alcoholic fermentation, lipid peroxidation, and Maillard reactions [12]. By identifying reliable VOC markers, it may be possible to predict seed storability and detect early signs of deterioration [12, 40].

Integrating VOC analysis into seed quality testing and certification programs still faces several challenges. Standardized sampling and analysis protocols need to be developed to ensure consistent and reproducible results [12]. Identifying robust VOC markers that are applicable across different seed species and storage conditions requires further research [12,40].

While VOC analysis holds great potential as a complementary tool to traditional seed testing methods, more validation studies are necessary to establish its effectiveness and Reliability [12, 40]. Future research should focus on correlating VOC profiles with seed germination, vigor, and field performance to demonstrate the practical utility of this approach [12].

VOC analysis is a promising technique for enhancing seed quality assessment, but further work is needed to standardize methodologies and integrate it into existing seed testing frameworks. With continued research and development, VOC analysis could become a valuable tool for seed producers, testing laboratories, and certification agencies to ensure the quality and performance of seeds in the future [12,40].

**Table 3. The significant role of VOCs in influencing seed physiological quality through various environmental interactions and biological processes**

| Study | Key Findings | VOCs Involved | Impact on Seed Quality |
|---|---|---|---|
| 1<br>[41] | VOCs can differentiate biological soil quality, influencing seed germination and growth. | Various VOCs from soil microbes | Enhanced seed germination rates and vigor. |
| 2<br>[42] | Cannabis plants emit VOCs that can affect air quality and may influence seed physiological traits. | β-myrcene, α-pinene, limonene | Potentially alters seed development and stress responses. |
| 3<br>[43] | VOCs in indoor environments can affect seed storage conditions, impacting seed viability. | Multiple VOCs from building materials | Reduced seed longevity and quality due to contamination. |
| 4<br>[44] | Biogenic VOCs contribute to ozone formation, affecting seed germination in urban areas. | Ethylene, toluene | Negative effects on seed germination and growth under high ozone levels. |
| 5<br>[45] | VOCs released during food processing can indicate seed quality and nutritional status. | Various food-related VOCs | Correlation between VOC profiles and seed quality metrics. |

## 7. SUMMARY OF IMPORTANT FINDINGS ON THE ROLE OF VOCS IN SEED PHYSIOLOGY

Volatile organic compounds (VOCs) emitted from seeds can serve as important biomarkers for assessing seed quality and deterioration during storage. Many VOCs produced by seeds are reactive and potentially toxic, perpetuating reactions that lead to seed aging and reduced viability. The quantity and composition of VOCs released correlates with the extent of seed deterioration.

Seeds undergoing aging and loss of vigor emit higher levels of VOCs like alcohols, aldehydes, ketones, alkanes, and acids. These are produced through processes such as lipid peroxidation, alcoholic fermentation, and Maillard reactions that occur as seeds deteriorate. Specific VOCs that tend to increase with seed aging include hexanal, pentane, ethanol, and methanol.

The VOC profile or "fingerprint" can provide a rapid, non-destructive way to evaluate seed physiological quality as an alternative to traditional germination tests. When total VOC emissions exceed a certain threshold (e.g. over 50% of initial levels), significant reductions in seed germination, vigor, and seedling growth are observed. Seed viability and vigor are lowest when VOC levels reach their maximum.

Factors like seed moisture content, storage temperature and humidity, and seed chemical composition influence the types and quantities of VOCs produced. Higher moisture, temperature, and humidity accelerate VOC emission and seed aging.

The VOCs released by seeds are closely linked to their physiological status and can be used to monitor deterioration during storage. Analyzing VOC profiles has potential as an early, non-invasive technique to assess seed quality in crop management. However, more research is needed to standardize VOC fingerprinting methods and thresholds for different seed types.

## 8. RECOMMENDATIONS FOR FUTURE RESEARCH DIRECTIONS

- **Develop VOC biomarkers for seed quality assessment:** Conduct more comprehensive profiling studies to identify specific VOCs or VOC patterns that reliably correlate with seed vigor, viability, and deterioration during storage. Validate these VOC biomarkers across different seed varieties, storage conditions, and time points to ensure broad applicability. Couple VOC analysis with rapid analytical techniques and chemometrics to enable high-throughput, non-destructive prediction of seed quality.
- **Elucidate the mechanisms of VOC effects on seed physiology:** Investigate the molecular pathways and gene expression changes underlying VOC-mediated influences on seed germination, dormancy, and early seedling development. Determine if VOCs act directly as signaling molecules or indirectly by altering seed biochemistry and metabolism. Explore potential interactions between VOCs and plant hormones in regulating seed physiological processes.
- **Exploit VOCs for enhancing seed performance and stress tolerance:** Test the efficacy of applying specific VOCs or VOC blends to prime seeds/seedlings for improved germination, growth, and resilience to abiotic and biotic stresses. Optimize VOC treatment protocols (e.g. concentration, timing, duration) for maximum benefit without phytotoxic effects. Evaluate if VOC priming can be a cost-effective, eco-friendly alternative or complement to other seed enhancement methods.
- **Establish VOCs as early indicators of seed pathogen infection:** Characterize the VOCs emitted by major seed-borne pathogens and identify unique marker compounds for each disease. Develop sensitive VOC detection methods for rapid, non-invasive diagnosis of seed health and infection status during storage. Assess if VOC analysis can detect diseases earlier than current visual and molecular diagnostic techniques.
- **Harness VOCs for controlling seed and seedling diseases:** Screen VOCs produced by beneficial microbes and plants for antimicrobial activity against common seed pathogens. Engineer VOC-based seed treatments or seed coatings for preventing pathogen growth and transmission. Integrate VOCs with other sustainable disease control strategies as part of an integrated pest management approach.

Future research should focus on expanding VOC profiling for seed quality prediction, unraveling VOC mechanisms of action, and applying VOCs to improve seed performance, health, and disease management. Advances in these areas can lead to novel, environmentally friendly solutions for enhancing seed and crop productivity.

## 9. CONCLUSION

The role of volatile organic compounds (VOCs) in determining seed physiological quality is increasingly recognized as significant, with research highlighting their effects on seed germination, growth, and stress responses. VOCs, which are emitted during seed imbibition and germination, can stimulate growth and enhance the seeds' defense mechanisms against biotic and abiotic stresses. Different seed species emit various VOCs influenced by factors like storage conditions and aging, with certain compounds serving as biomarkers for seed vigor and viability. While current studies predominantly focus on controlled laboratory settings, there is a growing interest in applying this knowledge to agricultural practices to enhance crop productivity. Future research should aim to further elucidate the mechanisms of VOC action, standardize profiling methods, and develop practical applications for utilizing VOCs in seed quality assessment and improvement, ultimately contributing to better crop yields and resilience in agricultural systems.

## DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of manuscripts.

## COMPETING INTERESTS

Authors have declared that no competing interests exist.

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