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Induced plant volatiles allow sensitive monitoring of plant health status in greenhouses

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A novel approach to support the inspection of greenhouse crops is based on the measurement of volatile organic compounds emitted by unhealthy plants. This approach has attracted some serious interest over the last decade. In pursuit of this interest, we performed several experiments at the laboratory-scale to pinpoint marker volatiles that can be used to indicate certain health problems. In addition to these laboratory experiments, pilot and model studies were performed in order to verify the validity of these marker volatiles under real-world conditions. This paper provides an overview of results and gives an outlook on the use of plant volatiles for plant health monitoring.

Introduction

This paper provides a synthesis of our research on the use of induced plant volatiles for sensitive monitoring of plant health status in greenhouses. The main research objective of this research was to investigate whether plant-emitted volatiles can be used to detect a *Botrytis cinerea* infection in a large-scale greenhouse. The pathogenic fungus *B. cinerea* and the plant species tomato (*Lycopersicon esculentum*) were selected as model organisms. Based on this choice, three main research questions were formulated: (1) What is the effect of a *B. cinerea* infection on the emission of volatiles from tomato? (2) Are *B. cinerea* induced emissions of tomato specific for the infection with this pathogen? (3) Are *B. cinerea* induced concentrations of volatiles detectable in large-scale greenhouses?

Effect of a *Botrytis cinerea* Infection on the Emission of Volatiles from Tomato

Severe *B. cinerea* infections resulted in a large increase in the emission of alcohols and aldehydes a few hours after inoculation and mild infections resulted in a small increase in the emissions of alcohols and aldehydes several hours after inoculation.[1] Once the emission of these type of volatiles reached their maxima, they reduced to values below detection limits within a few hours.

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The alcohols and aldehydes were undetected in experiments on *B. cinerea* infected leaves,[2] possibly because the 22 h delay between inoculation of the detached leaves and collection of headspace samples excluded the detection of a burst of alcohols and aldehydes. A second explanation arises from the physicochemical properties of volatiles. Alcohols and aldehydes are water soluble; maybe they dissolved in the water present in the Petri dishes to prevent dehydration of the leaves. A third option to consider is the sorbent used during sampling since the choice of sorbent is crucial for ensuring efficient concentration of volatiles.[3] In experiments on detached leaves, part of the samples were obtained using Tenax, a sorbent commonly used to concentrate the alcohols and aldehydes of interest.[4] However, most of the samples were obtained by the use of poly-dimethylsiloxane (PDMS) as solid sorbent. This type of sorbent is suitable for concentrating non-polar semi-volatile compounds, but not for the polar alcohols and aldehydes.[5]

Besides emissions of alcohols and aldehydes, severe *B. cinerea* infections resulted in the increased emission of mono- and sesquiterpenes from whole tomato plants.[1] This was not the case when whole plants showed mild symptoms of an infections by *B. cinerea*. This was also not the case for detached leaves upon infection,[2] possibly because the severity of infection was insufficient to alter the emission of these terpenes considerably; an opinion supported by the work of Mithöfer et al.[6] who showed that the emission of the monoterpenes ocimene and linalool from detached lima bean (*Phaseolus lunatus*) leaves correlates with the extent of damage.[6]

The sesquiterpene α-copaene was the one exception which proved to be predominantly emitted from infected tomato leaves.[2] In contrast to the increased emission of the sesquiterpene α-copaene from infected leaves, the results showed mixed findings in the case of infected whole plants. Whole plants, non infected as well as infected did not show a consistent change in emission of α-copaene. In some cases it increased, sometimes it decreased or remained constant despite a constant temperature and light regime. This difference might have been caused by the use of whole plants. Such differences between detached leaves and whole plants were described before,[7] and this confirms that the results of assays using excised tissues should be cautiously interpreted when considering whole-plant models.

Besides alcohols, aldehydes, monoterpenes and sesquiterpenes, *B. cinerea* infections affected the emission of the ester-substituted phenol methyl salicylate.[1] Non infected plants showed a small but increasing emission of methyl salicylate during the three days period, probably as a result of stress due to enclosure of plants.

Table 1. Volatile organic compounds emitted from whole, intact tomato plants or detached leaves and the biotic and/or abiotic stresses responsible for the increase in VOC emissions

Volatiles	Biotic and abiotic stresses that increase VOC emissions from tomato
ALCOHOLS	
(Z)-3-hexenol	*Botrytis cinerea*,[1] *Spodoptera littoralis*,[12] *Liriomyza huidobrensis*,[13] *Spodoptera exigua*,[14] *Manduca sexta*,[15] *Macrosiphum euphorbiae*,[16] ozone,* *Helicoverpa armigera*[5]
ALDEHYDES	
(E)-2-hexanal	*Botrytis cinerea*,[1] *Spodoptera littoralis*,[12] *Liriomyza huidobrensis*,[13] *Spodoptera exigua*,[14] *Manduca sexta*,[15] ozone,* *Helicoverpa armigera*[5]
MONOTERPENES	
linalool	*Spodoptera littoralis*,[12,17] *Tetranychus urticae*[18]
α-pinene	*Botrytis cinerea*,[1] *Spodoptera littoralis*,[12,17] *Spodoptera exigua*,[14] *Macrosiphum euphorbiae*,[16] *Oidium neolycopersici*,[19] *Manduca sexta*,[19,15] ozone*
α-terpinene	*Botrytis cinerea*,[1] *Spodoptera littoralis*,[12,17] *Spodoptera exigua*[8]
	Oidium neolycopersici,[19] *Manduca sexta*,[19,15] ozone*
SESQUITERPENES	
β-caryophyllene	*Spodoptera littoralis*,[12,17] *Spodoptera exigua*,[14] *Aphidius erui*,[16] *Manduca sexta*,[15] ozone*
α-copaene	*Botrytis cinerea*,[2] *Spodoptera littoralis*[12]
HOMOTERPENES	
(E,E)-4,8,12-trimethyl-1,3,7,11-tridecatetraene	*Botrytis cinerea*,[1] *Tetranychus urticae*,[18,20] *Liriomyza huidobrensis*,[13] *Manduca sexta*,[15] ozone*
PHENOLICS	
methyl salicylate	*Botrytis cinerea*,[1] *Spodoptera littoralis*,[12] tobacco mosaic virus,[21] *Tetranychus urticae*,[18,20] *Manduca sexta*,[14,15] *Macrosiphum euphorbiae*,[16] ozone*

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Infected plants showed a larger increase in the emission of methyl salicylate compared to non infected plants.[8] No obvious correlation between the severity of infection and the increase in methyl salicylate could be established. Methyl salicylate was undetectable or present in trace amounts in the experiments on detached leaves.[2] This compound can be efficiently trapped on PDMS[9] and the sampling procedure itself could therefore not be the reason for the absence or low presence. Maybe, methyl salicylate was dissolved into water or differences between detached leaves and whole plants caused this difference.

Finally, *B. cinerea* infections affected the emission of the homoterpene (*E,E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene (TMTT).[1] Non infected plants showed a small but increasing emission of TMTT during the three days period, probably as a result of stress due to enclosure of plants. Infected plants showed a larger increase in the emission of TMTT than non infected plants. Similar to methyl salicylate, no obvious correlation between the severity of infection and the increase in TMTT emissions could be established. TMTT was undetectable or present in trace amounts in the experiments on detached leaves.[2] It is unclear whether this compound can be efficiently concentrated on PDMS but likely the compound TMTT was concentrated and then incorrectly identified as squalene,[9] and the sampling procedure itself could therefore not be the reason for the absence or low amounts.

In short, the emission of several volatiles increased upon infection of whole plants but not upon infection of detached leaves and vice versa. But, given the thorough study on whole plants, we regard the presence of alcohols and aldehydes as reliable indicators of a *B. cinerea* infection. On these grounds, increasing mono- and sesquiterpene emissions, apart from α-copaene, and increasing methyl salicylate and TMTT emissions were also regarded as reliable indicators of a *B. cinerea* infection. Furthermore, compared to research on detached leaves, the study on whole plants resembled conditions more comparable to greenhouse horticulture.

As mentioned before, the results obtained during the laboratory tests on whole plants were regarded as reliable and therefore served as basis for follow up studies. No time was spent on the inspection of data obtained from greenhouse air after infection of plants with *B. cinerea* in order to search for novel compounds. But, it can be questioned whether this was a good strategy since plants in a greenhouse may emit additional compounds due to e.g., differences in light intensity and/or differences in plant age.

In the laboratory tests on whole plants, plants were infected by spraying them with a solution containing *B. cinerea* spores. However, in practice, infections in tomato are usually restricted to stem wounds[10] which generally originate from pruning and removal of side shoots. To mimic these conditions, it might have been better to infect tomato plants by making incisions into the stem.[11] Then, they inoculated the wounds with agar plugs containing a culture of *B. cinerea* after which the wounds were covered with tape to ensure high humidity. Besides a more realistic way of inoculation, this procedure has the advantage that it eliminates the need of a high air humidity. This is an advantage as the trapping of volatiles from moist air often results in technical problems in VOC analysis.

Specificity of Botrytis cinerea-Induced Emissions of Volatiles from Tomato

In the previous section, the effect of a *B. cinerea* infection on the emission of volatiles from tomato was discussed. However, throughout the study, it became obvious that other factors occur in tomato production greenhouses that also affect the emission of volatiles from tomato. These factors should be considered since a *B. cinerea* specific detection is only feasible if such an infection consistently results in the emission of unique volatiles. **Table 1** provides an overview of volatiles and references in which their emissions have been reported to increase upon biotic and/or abiotic stresses of intact tomato plants or detached tomato leaves. None of the volatiles listed in **Table 1** can be exclusively linked

to one particular stress of tomato. Therefore, it is improbable that the causal agent of plant stress can be identified as a *B. cinerea* infection based on these volatiles only.

The overview in **Table 1** shows that the most common stress-induced volatiles are unspecific. On the other hand, literature offers some evidence for specific signals in the volatile blend of stressed plant species. For instance, the ability of host-seeking insects to recognize and respond to certain volatiles and to differentiate them from background volatiles indicates that insect-damaged plants emit volatiles that are distinguishable from those emitted in response to other types of damage or those emitted from undamaged plants.[22] Probably, such specific signals are based on the temporal and spatial variations of volatiles at concentration levels far below the detection limits of commonly used analytical instruments including the instruments used in our experiments.

The overview in **Table 1** is perhaps not complete, but the fact that emissions of many of the same substances increase upon different stressors suggests a general plant response by similar underlying mechanisms. Some of these mechanisms are briefly discussed below.

B. cinerea infected plants emitted several alcohols and aldehydes. These volatiles are denoted as lipoxygenase products. They originate from the oxidative cleavage of C_{18}-fatty acids in the presence of oxygen and enzymes such as lipoxygenases. They are emitted upon damage of cell membranes (that contain fatty acids) and are known to us as the characteristic smell that appears after cutting grass. Many biotic stresses such as herbivore feeding may result in damage of cell membranes which clarifies the numerous herbivore induced increases in emissions of the lipoxygenase products (**Table 1**).

An additional source for lipoxygenase products that should be considered is plant debris such as excised shoots after pruning. Such debris is nearly always present in a greenhouse and may then increase the concentrations of lipoxygenase products due to drying. Also nearby field crops are expected to be sources of lipoxygenase products, especially upon harvest or stress. These events are extremely difficult to predict. Consequently, the emission of lipoxygenase products maybe not suitable for a specific detection of *B. cinerea* infections in tomato production greenhouses and probably also not suitable for the detection of a general stress response of the crop.

Severely *B. cinerea* infected tomato plants emitted larger quantities of mono- and sesquiterpenes compared to non infected plants. Also spraying with an aqueous solution containing *B. cinerea* spores resulted in an increase of mono- and sesquiterpene emissions.[23] The emissions peaked within one hour after spraying and returned to initial levels within two to three hour. This burst was attributed to the damage of glandular trichomes as a result of spraying by which water droplets smack onto the stems and leaves. These trichomes are outgrowths of the plant epidermis and collectively constitute the hairy appearance of the tomato plant. To study the importance of trichomes in more detail, we stroked the full length of the stem of one of the plants enclosed in the chamber. Also this treatment resulted in a large burst of mono- and most sesquiterpene emissions. These results were not provided in our previous paper.[1] However, this result confirmed the importance of trichomes as source of plant volatiles and supports the work described before[23] in which it was demonstrated that glandular trichomes of tomato store in their interior considerable amounts of mono- and sesquiterpenes.

A burst in mono- and sesquiterpene emission was also observed at greenhouse-scale when fruits were harvested, and side shoots were removed.[24] Almost certainly, every other crop operation will affect the emission of mono- and sesquiterpenes. Also temperature determines the emission of mono- and sesquiterpenes. Harvesting fruits, removal of side shoots, other crop operations and fluctuations in temperature occur often in greenhouse practice. Moreover, many biotic stresses such as herbivore feeding may result in damage of trichomes which clarifies the numerous herbivore induced increases in emissions of mono- and sesquiterpenes (**Table 1**). Consequently, an increase in the emission of mono- and sesquiterpenes may be not suitable for a specific detection of *B. cinerea* infections in tomato production greenhouses and probably also not suitable for the detection of a general stress response of the crop.

B. cinerea infected tomato plants emitted larger quantities of methyl salicylate. Such an increase was also reported upon stress of tomato as a result of at least seven different biotic and abiotic stressors (**Table 1**). Therefore, increased emissions of methyl salicylate are not specific for a *B. cinerea* infection. The slight increase in the emission of methyl salicylate from enclosed control tomato plants as reported,[1] was probably a result of stress due to enclosure. This effect was mentioned before,[25] providing additional evidence that increased emissions of methyl salicylate are not specific to a particular type of stress but rather a general stress response. However, the concentrations of methyl salicylate remained stable after stroking of stems, after removal of side shoots, and after picking fruits.[24] Three reasons may account for this: (1) *B. cinerea*-derived elicitors were absent in the above mentioned treatments. These elicitors may play an important role in the induction of methyl salicylate emission from tomato plants. (2) The damage to the plants was inflicted at one moment while *B. cinerea* infections probably results in a continuous type of damage. There is an increasing body of evidence suggesting that the time course of damage has an effect on the emissions of volatiles from plants.[6] (3) Volatiles were measured directly after the damage stopped. There are several examples in literature in which the emission of volatiles, such as methyl salicylate, increases, but with a time delay of several hours after the stress application.

The fact that stroking, removal of side shoots, and picking fruits did not affect the concentration of methyl salicylate is beneficial since then, methyl salicylate allows the discrimination between plant stress and crop operations. Ultimately, an increase in the concentration of methyl salicylate might serve as an effective warning sign for the presence of *B. cinerea* since the diversity of stress factors that occur in a tomato production greenhouse is often limited. However, it should be noted that methyl salicylate emission from tomato is also light dependent.[15, 26] As light will fluctuate in a greenhouse, this will have to be taken into account when correlating increased methyl salicylate concentrations in the greenhouse atmosphere to any type of plant stress.

The increased emission of the homoterpene TMTT after inoculation remains poorly understood due to the limited amount of information available and uncertainties about this information. For instance, few researchers indicate increased TMTT emissions from tomato upon stress, whereas others did not (**Table 1**). The interpretation of TMTT emission is also complicated by the fact that several researchers observed large amounts of TMTT in the headspace of control tomato plants while other researchers did not observe this compound at all, or possibly failed to identify it.

Detectability of Botrytis cinerea-Induced Concentrations of Volatiles in Large-Scale Greenhouses

To find out whether *B. cinerea* is detectable in large-scale greenhouses, it is important to know the *B. cinerea* induced increase in concentrations as well as the precision and detection limits of analytical instruments. Therefore, we developed a model to predict whether volatiles can be used to detect a *B. cinerea* infection in a large-scale tomato production greenhouse with a volume of 5×10^4 m^3 containing 2.2×10^4 plants.[27] The precision and detection limits of a gas chromatograph (GC) coupled to a mass spectrometer (MS) or flame ionization detector (FID) were compared with the *B. cinerea*-induced increase in concentration of the lipoxygenase product (*Z*)-3-hexenol, the trichome damage related volatiles α-pinene, α-terpinene and β-caryophyllene, and the volatile plant hormone methyl salicylate to determine the appropriateness of these instruments for measuring the increase. The model was used to predict the effect of the fraction of infected plants and the effect of the air exchange rate on the *B. cinerea*-induced increase in concentration.

Independent of the air exchange rate, the *B. cinerea*-induced increases in concentration of (*Z*)-3-hexenol is detectable in a large-scale tomato production greenhouse when 0.5% or more of the plants are infected. Independent of the air exchange rate and independent of the fraction of infected plants, the *B. cinerea*-induced increases in concentration of α-pinene, α-terpinene and β-caryophyllene are undetectable in a large-scale tomato production greenhouse. The *B. cinerea*-induced increase in concentration of methyl salicylate is detectable in a large-scale tomato production greenhouse when at least three conditions are met: (1) windows are fully opened, (2) the *B. cinerea*-induced increase in emission of methyl salicylate continues for at least 1 h and (3) 5% of the plants are infected. The *B. cinerea*-induced increase in concentration of methyl salicylate is also detectable when (1) windows are closed, (2) the *B. cinerea*-induced increase in emission of methyl salicylate continues for at least six hour and (3) 5% of the plants are infected.

These findings are bases on the momentaneous concentrations of volatiles. In practice, volatiles are often pre-concentrated to achieve the detection limits of commonly applied analytical instruments. The period of time required for pre-concentration depends on the concentration of the volatiles of interest in the air. Also the separation of volatiles in the mixture requires a certain amount of time. A sensitivity analysis should include the separation and pre-concentration periods to determine the detectability of *B. cinerea*-induced increase in concentrations of volatiles in large-scale greenhouses. Such analysis should also include the period of time in which the *B. cinerea*-induced increase in emission of volatiles from a certain proportion of plants is above the baseline level emission of healthy plants. Furthermore, a sensitivity analysis should include the emission flux densities of methyl salicylate by healthy tomato plants. These values were obtained under laboratory conditions. It is doubtful whether laboratory conditions are suitable to determine methyl salicylate emissions from healthy plants since stress due to enclosure of tomato plants—a prerequisite for analysing plant emissions at the laboratory scale—also led to increased emissions of methyl salicylate.[25]

Analytical instruments based on GC-MS and GC-FID with a precision of 10% relative standard deviation and a detection limit of 1 nmol m^{-3} were used as a reference. These type of instruments are routinely used to detect air contaminants in field settings[28,29] and to monitor biogas tower reactors for the presence of potentially toxic volatiles.[30] Besides GC-MS and GC-FID, electronic noses (e-noses) are also widely used to detect plant-emitted volatiles in air.[31] In general, they are not useful for the identification and quantification of individual components.[32] However, the identification of the volatiles being emitted may not be needed if the comparison and recognition of patterns in the volatile profile are sufficient for crop health monitoring through the analysis of plant-emitted volatiles. Such a profile can be obtained through the use of sensor arrays, a technique used for the VOC based inspection of trees based on e-nose systems which rely on the recognition of fingerprints of volatiles released from them. For instance, a prototype device incorporating three metal oxide sensors was able to detect basal stem rot disease of oil palm (*Elaeis guineensis* Jacq.) infected by the fungus *Ganoderma boninense*.[33]

A combination of the marker-compound-approach with the e-nose technique can result in e-nose systems that have the ability to quantify VOC concentration in air as demonstrated for the differentiation of fresh and rancid butter based on volatiles.[34] This development seems to be quite promising. The remaining drawback of e-noses based on sensor arrays is that the threshold of determination of most of these systems is in the low ppmv-range. However, this drawback can be overcome by utilization of pre-concentration techniques. Such a combination of a gas-chromatographic system equipped with a pre-concentration unit and e-nose was successfully applied to detect plant emitted volatiles in a small cuvette.[31] However, the reported limits of detection for this instrument, see[36] are several orders of magnitude less than required for the in[28] predicted concentrations of *B. cinerea*-induced volatiles in a large-scale greenhouse.[27,35]

More recently, biosensors have been developed to identify and quantify low levels of volatiles in ambient air. A biosensor is a particular type of chemical sensor that uses the recognition properties of biological components in the sensitive layer. Today even whole animals or certain organs of animals are used in biosensors. Especially insects are seen as suitable model to develop biosensors for gas analysis. Several studies attempted to quantify the sensitivity of insects to certain volatiles. For instance, trained wasps responded to 3-octanone, myrcene, cadaverine

and putrescine at concentrations in the order of 10 ppbv,[36] and a biosensor based on insect antennae responded to (*Z*)-3-hexenol at a concentration of 10 ppbv.[37] These sensitivities are several orders of magnitude less than required for VOC detection in greenhouses. Besides the demand for an increase in sensitivity, there are numerous other methodological and biological hurdles that needs exploration before sensors based on insects could be used in horticultural practice.

Conclusions

The research summarized in this paper has led to the following conclusions.

(1) Tomato plants emit different types and amounts of volatiles during infection by *B. cinerea*. The main effects are the burst of lipoxygenase products and the increase in emissions of monoterpenes, sesquiterpenes, methyl salicylate and TMTT. The burst of lipoxygenase products is probably the result of damage to cell membranes. The increase in emissions of monoterpenes and sesquiterpenes is probably the result of damage to glandular trichomes. The increase in emission of methyl salicylate and TMTT is not directly related to cell membrane or trichome damage but probably the result of a systemic plant response as a result of stress.

(2) Based on model predictions, the *B. cinerea*-induced increase in concentration of lipoxygenase products is detectable in a full-scale greenhouse when 0.5% of the plants are infected. However, many additional sources of lipoxygenase products exist including plant debris and nearby field crops especially upon harvest and stress. Plant debris is nearly always present and harvest and/or stress of nearby crops is extremely difficult to predict. Consequently, lipoxygenase products can probably not be used to detect a *B. cinerea* infection in a large-scale greenhouses.

(3) Based on model predictions, the *B. cinerea*-induced increase in concentration of mono- and sesquiterpenes cannot be detected in a full-scale tomato production greenhouse. Furthermore, crop operations will almost certainly affect the concentration of mono- and sesquiterpenes. These crop operation occur often. Consequently, mono- and sesquiterpenes can probably not be used to detect a *B. cinerea* infection in a large-scale greenhouses.

(4) Based on model predictions, the *B. cinerea*-induced increase in concentration of methyl salicylate is detectable in a large-scale tomato production greenhouse when at least three conditions are met: (a) windows are opened, and (b) the *B. cinerea*-induced increase in emission of methyl salicylate continues for at least one hour, and (c) 5% of the plants are infected. The *B. cinerea*-induced increase in concentration of methyl salicylate is also detectable when (a) windows are closed, and (b) the *B. cinerea*-induced increase in emission of methyl salicylate continues for at least six hour, and (c) 5% of the plants are infected. Consequently, methyl salicylate can probably be used to detect a *B. cinerea* infection in a large-scale greenhouses. However, the *B. cinerea*-induced increase in concentration of methyl salicylate is not specific for a *B. cinerea* infection of tomato. Therefore, it will be impossible to identify the stressor as *B. cinerea* based on methyl salicylate emissions only.

Outlook

In this research, much insight has been gained into volatile based crop monitoring. However, it is clear that this topic is in its infancy and far from being completely understood. Therefore research effort in the following areas is suggested.

Future research may involve low-molecular volatiles to monitor crop health at greenhouse scale. In this study, we focussed on the mid-molecular weights volatiles in the range of C_5-C_{24}. However, an infection of tomato plants with *B. cinerea* probably also affects the emission of low-molecular weight volatiles (<C_5). For instance, emissions of nitric oxide (NO), hydrogen peroxide (H_2O_2),ethylene (C_2H_4), ethane (C_2H_6), acetaldehyde (C_2H_4O) and ethanol (C_2H_5OH) from diverse plant species were found to increase upon stress exposure. Depending on the source- and sink strengths of these volatiles, they may be used as indicator of plants stress at greenhouse scale, but probably not to identify the stressor itself.

Due to the high costs, we are years away from having sensitive and precise analytical instruments in horticultural practice. But, the ongoing expansion and intensification of greenhouse production, and the concern among consumers about the potential intake of pesticide residues on fruits and vegetables will support the prospected application of plant health monitoring in a commercial setting. Another point for future research is therefore the development of sensitive, precise, but also affordable instruments, specifically designed for application in horticulture practice. Four steps should then be considered. First, the collection and pre-concentration of the plant emitted volatiles. Second, the separation of the plant emitted volatiles in the mixture. Third, the identification, and/or quantification of the separate volatiles. Fourth, the automatic processing of data. Colorimetric tubes based on a chemical reaction generating a colour change may offer an alternative cost-effective approach to measure the concentration of important stress associated volatiles such as methyl salicylate.

To determine the potential of volatile based crop monitoring, it is necessary to perform semi- and large-scale experiments. Care should then be taken because such experiments will be influenced by the inherent variability present in crops grown in practice. Especially the importance of VOC transfer into water should be studied, more specifically the role of condensation on dehumidifiers versus the role of condensation on the glass cover.

Finally, the effect of other stressors on the emission of volatiles from tomato and other plant species that are common in greenhouse horticulture should be studied. Especially infections by root pathogens seems an important plant health problem to study because the effect of these types of infection are difficult to see by the naked eye.

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