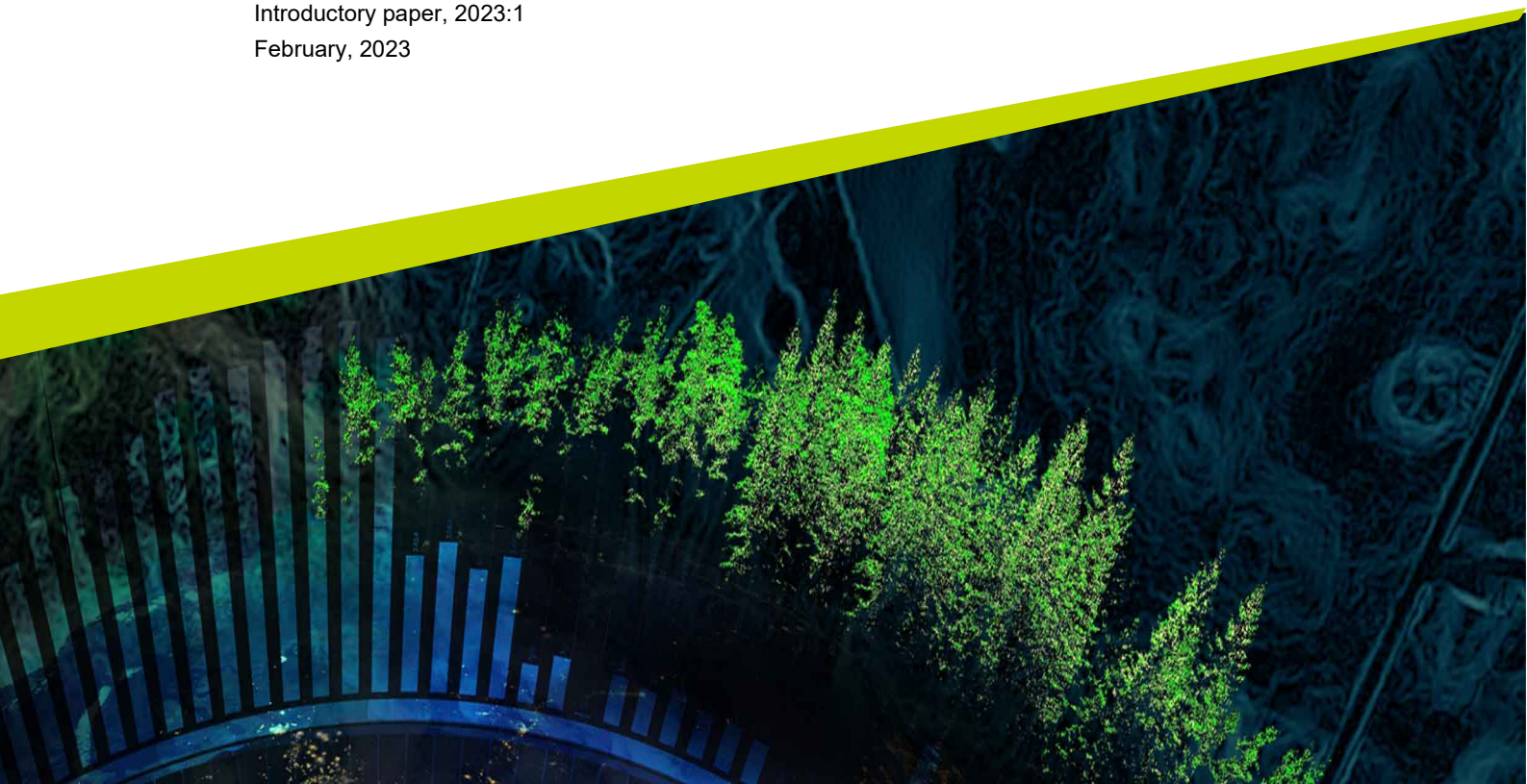
Onion storage diseases and their headspace volatiles

Isabella Kleman

Swedish University of Agricultural Sciences, SLU
Faculty of Landscape Architecture, Horticulture and Crop Production Science
Introductory paper, 2023:1
February, 2023



Onion storage diseases and their headspace volatiles

Isabella Kleman, https://orcid.org/0000-0002-0476-4820, Swedish University of Agricultural Sciences, Department of Biosystems and Technology,

Publisher:	Swedish University of Agricultural Sciences, Faculty of Landscape Architecture, Horticulture and Crop Production Science, Department of Biosystems and Technology
Year of publication:	2023
Place of publication:	Alnarp
Copyright:	All featured images are used with permission from the copyright owner.
Title of series:	Introductory paper at the Faculty of Landscape Architecture, Horticulture and Crop Production Science
Part number:	2023:1
DOI:	https://doi.org/10.54612/a.602791tdo5
Keywords:	onion, storage, plant pathogens, volatile compounds, headspace

Abstract

Onion, *Allium cepa,* is one of the world's most commonly produced and consumed vegetables. In order to be available year round in temperate climates onions must be stored for several months. During this time parts of the harvested weight of bulbs are lost to storage diseases, sprouting and respiration leading to loss of carbohydrates and water. Diseases developing in storage may be difficult to spot at early stages as bulbs are typically stored in large bins. However, storage diseases can change the volatile metabolite profile of the infected onions. Electronic sensors that detect the concentration of specific volatile compounds in the air could be deployed in storage facilities to detect these changes. This would provide an early warning system that could detect diseases developing in storage bins before it becomes obvious to a human observer. In this way, some of the losses that occur during storage of onions could be prevented. This introductory paper discusses some of the available literature on the facets of onion production that are connected to storage disease development and the detection of said storage diseases using headspace sampling and analysis. The focus of the paper is mainly on onion production and storage of long day cultivars in relatively cold, temperate climates, as the use of short day cultivars and warm storage in warmer climates comes with different challenges and diseases.

Table of contents

Abbreviations

CA	Controlled Atmosphere
FOC	*Fusarium oxysporum* f. sp *cepae*
GC	Gas Chromatography
HPLC	High Performance Liquid Chromatography
MH	Maleic Hydrazide
NSC	Nonstructural Carbohydrates
SPME	Solid Phase Microextraction

1. Introduction

1.1 Aim

This review focuses on onion storage and especially on storage diseases, their prevention and the volatiles released by diseased onions. The aim is to review currently available literature on volatile organic compounds found in the headspace of onions and the connection to infection by storage disease-causing pathogens. This information is expected to be useful for future studies and in practical application for prevention of storage waste.

1.2 Onions, background

1.2.1 Production and use

The genus *Allium* in the *Amaryllidaceae* family contains several important horticultural crops, including onion (*A. cepa* L.), garlic (*A. sativum* L.), leek (*A. porrum* L.) and chives (*A. schoenoprasum* L.). The most widely produced of the *Allium* species is the onion, *A. cepa*. Almost 100 million tons of dry onion bulbs were produced commercially worldwide in 2019, which makes onions one of the most commonly grown vegetable crops. It is second only to tomatoes with 180 million tons produced, and ahead of cucumbers and gherkins of which almost 88 million tons were produced (FAOSTAT, 2021). As the world population grows, so does the demand for food, and with it the production of onions which has been steadily increasing for the last several decades (Figure 1). *Allium cepa* is a biennial plant, growing a bulb in its first year, and using the stored carbohydrate resources to flower and produce seeds the following year. As a crop it is usually cultivated for its bulb and harvested in the same year it was sown or planted. It is a versatile vegetable, and yellow, red and white onion varieties are used cooked, pickled or raw in many different cuisines all over the world. This paper pertains to *A. cepa* harvested at maturity (dry bulbs).

Figure 1. Graph of the worldwide production of dry onion bulbs from the year 1961 to 2020. (Data from FAOSTAT 2022)

1.2.2 Cultivar types

Onion cultivars are divided into short, intermediate, long and very long day varieties, depending on the day length required for bulb initiation, which varies between 11-12 hours for short day and over 16 hours for long day varieties. While short day varieties can be produced year-round in tropical climates, long and very long day varieties are typically required to be long-storing. This is due to cold winter temperatures in the temperate climates in which they are grown making wintertime harvest of onions impossible (Brewster 2008). Onion cultivars meant to be stored for a long time typically have a higher dry weight and more pungent flavor than so called sweet onions which are less pungent and can only be stored for short periods of time.

1.2.3 Onion bulb dormancy

As a biennial plant, the onion naturally has a dormant period when conditions for growth are unfavorable, e.g. during a cold winter, before sprouting and flowering in its second year of growth. Dormancy can be described as the period of lower metabolic activity between harvest and the start of the internal sprouting process some time later (Yasin & Bufler 2007). At bulb maturity cell division in

the bulbs shoot apex ceases almost completely but slowly starts up again as early as two weeks into storage at 16°C, as activities shift from scale formation to leaf formation (Pak et al. 1995). The length of the dormancy period is dependent on a combination of factors, including genetics, cultivation methods and external influences during storage. For example, bulbs with a low dry matter content are less suited to long periods of storage as they use up their stored carbohydrates sooner.

1.2.4 Sprouting

As dormancy breaks sprouting starts in response to internal and external factors. Sprouting is defined as the visible emergence of the stem apex through the neck of the onion bulb (Sharma et al. 2016). Sprouting is considered undesirable in bulbs meant to be marketed as food as it uses up the carbohydrates of the bulb to produce an onion plant that is ready to flower. Histone 2A is a protein involved in the mitosis required for sprouting to take place. A study showed that histone 2A expression is at its lowest in the bulb shoot apex in the time leading up to harvest, after which it slowly increases in concentration ahead of visible sprouting in spring (Carter et al. 1999).

1.3 Cultivation and storage of onions

1.3.1 Bulb storability

Sufficient post-harvest longevity of onion bulbs is necessary to create year-round availability of domestically grown onions where wintertime cultivation is not possible. If not infected by pathogens, properly cured onion bulbs can typically be stored for several months with little quality loss.

Genotype is an important determining factor for onion storability. Certain cultivars are bred to maintain their quality during long periods of storage, while others are meant to be consumed soon after harvest. For how long a bulb can be stored also varies greatly depending on the various pre- and post-harvest conditions it has been exposed to.

While the dormant onion bulb is a storage organ that has a low rate of respiration compared to many other vegetables, some respiration still takes place which leads to loss of carbohydrates and water (Brewster 2008).

1.3.2 Preharvest

Many of the diseases affecting onion bulbs in storage begin their infection process earlier, either during active growth in the field or during lifting and curing. Damage caused by machinery, weather or insects feeding on above or below ground tissue can provide enhanced opportunities for infection by various pathogens

(Schwartz & Mohan 2007). More on this in the sections regarding each storage disease.

1.3.3 Harvest

Onions destined for storage are harvested at the end the growing season at a point when a certain share of the plants have reached "maturity". Maturity occurs when the leaves of the onion plants start folding over, so called tops down. The timing of the harvest has an effect on the bulbs quality and storability. A study found that onions harvested late, at 100% tops down, had a more appealing darker color, while onions harvested at 50% tops down had a higher number of intact dry outer skins and were better suited for long term storage (Wright et al. 2001). However, these onions were topped before storage, and the results could be different for onions that are stored intact. Another study found similar results, onions harvested later generally had fewer intact dry skins but were also less likely to succumb to pathogen infections later during storage (Wright 1997). The authors of that paper recommended lifting at 70-90% tops down and letting the leaves become as dry as possible before topping.

1.3.4 Curing

After the onions are lifted they must be cured in order to develop the characteristics necessary to maintain acceptable quality throughout a storage period. These characteristics include a sufficient number of dry and intact outer skins, a closed and dry neck and desirable color. Curing is the drying of bulbs, either passively in the field or using active methods such as forced air and heating. In climates where the harvest season is likely to be wet, such as the UK, a standard method is curing for 3-6 weeks in an enclosed space at 28°C and 65-75% RH (Downes et al. 2009). However, curing for long periods of time or at high temperatures (>35°C) has been found to increase the severity of storage rot in bulbs infected with *Burkholderia* spp. (Schroeder et al. 2012). In cases where a bacterial infection is likely it may therefore be a good idea to cure for a shorter period of time or at lower temperatures. Curing without topping can help reduce weight loss, sprouting and diseases in storage when compared to curing already topped bulbs (Nabi et al. 2013). Fast curing, i.e. curing at 30°C and high humidity, in this case 98% RH, can provide an alternative for better quality and storability of onion bulbs grown in hot and dry climates, where field curing does not result in sufficient quality (Eshel et al. 2014).

1.3.5 Control of bulb dormancy

Chemical control

The length of the dormant period can be manipulated using chemical or physical methods, such as applying maleic hydrazide (MH) or irradiating the bulbs. MH is typically applied before harvest and works by disrupting cell division in the meristem, thus preventing root and shoot growth during storage. MH is taken up through the leaves and transported into the bulb, where trace amounts can remain for long periods of time, preventing sprouting (Ilic et al. 2011). Post-harvest application can also produce the desired effect of lowering respiration and associated catabolic activity and prolonging the storability (Benkeblia 2004). However, the use of MH has been questioned, as there are concerns about traces remaining in the bulbs when they reach consumers and also about runoff contaminating drinking water. This causes a need to find alternative methods for sprouting inhibition (Downes et al. 2010).

Irradiation

Gamma radiation is sometimes used to irradiate bulbs ahead of storage. This method of sprouting inhibition is widely used in among others many Asian countries and the USA (Ihsanullah & Rashid 2017). Like MH application, gamma radiation works by disrupting cell division in the meristem, in this case by causing radiation damage (Benkeblia et al. 2000). Bulbs treated with appropriate levels of gamma radiation may better retain their firmness and weight and be less likely to rot (Sharma et al. 2020). Irradiated onions have also been recorded to have respiration rates that decrease with longer storage times, rather than increasing as is typical for untreated onions (Benkeblia et al. 2002).

1.3.6 Storage methods

Temperature

Successful onion storage limits the respiration rate of the onions to delay weight loss and sprouting. Onions are typically stored in climate controlled storage facilities. To keep the bulbs dormant and prevent root and shoot development temperatures need to be kept close to 0˚C, as temperatures between 5-15˚C tend to accelerate catabolism and sprouting (Abdalla & Mann 1963). Storage at 25-30˚C is also a possibility as it inhibits dormancy breaking, but it is not optimal for long term storage as it accelerates disease progression and water loss through respiration (Petropoulos et al. 2017). Warm temperatures are best used for short term storage in climates where the increased cost of cooling the storage facility is prohibitive.

Humidity

Relative humidity in onion storage is also an important factor that must be controlled in order to maintain good quality. It has been known for a long time that high humidity as well as high temperatures in storage promotes sprouting and root growth, while low humidity and high temperatures can increase weight loss due to transpiration in the bulbs that remain dormant (Wright et al. 1935). High humidity in combination with low temperatures tends to cause condensation on bulbs and other surfaces. This may promote growth of a variety of onion pathogens including *Fusarium oxysporum* f. sp *cepae* (FOC), the causal organism behind Fusarium basal plate rot (Schwartz & Mohan 2007). All in all, storage at temperatures close to but not below the freezing point and a relatively low humidity, e.g. 65-75% (Islam et al. 2015), is usually what is considered desirable.

Controlled atmosphere

Controlled atmosphere (CA) storage, where onions are stored in modified air with low levels of O_2 and higher levels of CO_2 in a sealed chamber, is also an option for storage. The temperature and humidity in the chamber can also be controlled. Concentrations 0.5 to 2% O_2 and 3% CO_2 has the potential to almost completely stop sprouting (Adamicki 2005). While CA is useful for the prevention of sprouting it may not stop the development of disease in the bulbs. In one variety trial Botrytis neck rot completely ruined batches of several of the tested varieties of sweet onion after 4.5 months in CA storage (Boyhan et al. 2005). Maleic hydrazide is widely used in many countries, but in countries where its use is banned, CA storage may provide an opportunity to prolong the season for domestically grown onions. When compared to traditional storage methods, CA storage can both prolong the time bulbs can be stored with quality intact and reduce storage losses (Põldma et al. 2011). One study found that onions stored in CA could retain marketable quality for as long as a full year (Tanaka et al. 1996).

1.3.7 Losses during storage

In addition to bulbs breaking their dormancy and sprouting, a percentage of the bulbs put into storage will eventually become diseased due to infections by one or more phytopathogenic fungi or bacteria. Infections by certain pathogens may lead to increased respiration (Wang et al. 2016), further increasing the rate of weight loss in stored bulbs. While bulbs that have externally visible sprout or root growth are often still edible they are not in an acceptable condition to be marketed, according to the Agricultural Quality Standards of the United Nations Economic Commission for Europe (UNECE 2019). According to the same standards, visible signs of rot or mold are also unacceptable. This means that onions that sprout or

become diseased in storage are not marketable and must be discarded, resulting in food waste and economic losses for growers. Reducing these losses would therefore be in the interests of growers and beneficial for the environment. About 13% of onions harvested in Sweden are lost during storage (Franke, 2013). Internationally losses can be even higher, especially when suboptimal storage methods are used, greatly increasing the weight loss and number of bulbs sprouting in storage (Ilić et al. 2009; Anbukkarasi et al. 2013).

1.3.8 Bulb composition and its connection to bulb storability

Nonstructural carbohydrates

Being a storage organ, the onion bulb contains a variety of nonstructural carbohydrates (NSC) such as fructans, sucrose, glucose and fructose that it uses when it starts growing again after a period of dormancy. No matter the dry matter content a large percentage of a bulbs dry weight consists of these NSC, in one study values between 83 and 88% were found (Darbyshire & Henry 1979). This means the difference in content of NSC between low and high dry matter content onions cultivars is dependent mostly on water content. A high content of sugars such as fructose at harvest has been shown to have a connection to bulbs having potential to store well for a longer period of time (Rutherford & Whittle 1982). It is also known that the relative contents of the various NSC found in a bulb changes during storage, and that larger oligosaccharides are broken down into simpler sugars that are then consumed as sprouting progresses. In particular, it has been shown that the fructan concentration decreases over time in storage and that the ratio between di- and monosaccharides can be used to distinguish between onions that are sprouting and onions that are still dormant (Chope et al. 2012). Larger bulbs tend to have poorer storability, likely due to being less firm and having lower dry matter content (Ko et al. 2002) and therefore a lower content of NSC.

Pyruvate

Among other flavor giving substances, pyruvate is a molecule whose concentration in onion tissue has a strong connection to the perceived pungency of flavor (Wall & Corgan 1992). The content of pyruvate and thus the pungency can be increased with sulfur fertilization during the growing season but does not seem to have any effect on storability (Forney et al. 2010). Sweet onions have relatively low concentrations of pyruvate when compared to pungent long-storing cultivars, but the pyruvate concentration tends to rise with time in storage, affecting the flavor (Abayomi & Terry 2009). The sharp flavor is not necessarily considered desirable, depending on the intended use of the onion.

1.4 Fungal storage diseases

1.4.1 Blue mold (*Penicillium* spp.)

Blue mold is the collective name for storage diseases caused by *Penicillium* species. The diseases are typically characterized by yellowish, reddish or watery stains and lesions, with moldy spots bearing blue or blue-green conidia. Later stages of infection may cause bulbs to start breaking down completely. There are a number of *Penicillium* species capable of infecting *A. cepa*, including *albocoremium*, *allii*, *aurantiogriseum*, *citrinum*, *digitatum*, *expansum*, *funiculosum*, *hirsutum*, *tulipae*, *radicicola*, *oxalicum*, *polonicum* and *venetum* (Overy et al. 2005; Vikram et al. 2005; Schwartz & Mohan 2007; Dugan et al. 2014). The specific species or strain of *Penicillium* infecting any given bulb is typically not known as many of them cause similar symptoms. *Penicillium* infections are problematic not only because of the decay they cause in onion bulbs, but also because several of the species that infect onions produce mycotoxins such as citrinin and penitrem A (Overy & Frisvad 2003). Citrinin is a polyketide that has a strong antibacterial effect (Subramani et al. 2013), but is also toxic to mammals and can affect the heart, liver, kidneys and reproductive system (Filho et al. 2017). Penitrem A is an indole diterpenoid that can increase the production of reactive oxygen species in human cells and thus cause harm to tissues, including the brain (Berntsen et al. 2017). These toxins could potentially be harmful to consumers, but heavily infected bulbs are unlikely to be eaten. The pathogenic *Penicillium* spp. that infect onions usually grow at temperatures between 15-32 ˚C and preferably in moist conditions (Schwartz & Mohan 2007). *Penicillium* species are usually found in the soil and often invade plants through previously damaged tissue, but can sometimes infect healthy bulbs (ibid.). Therefore, blue mold infections are best prevented by avoiding mechanical damage to the bulbs and with storage at appropriate temperatures and humidity levels.

1.4.2 Neck rot (*Botrytis allii* and *Botrytis aclada*)

Several different species of *Botrytis* are capable of infecting onions, with symptoms appearing either in the field or in storage. The diseases can affect several different parts of the onion plant. *Botrytis allii* or *B. aclada*, which were considered to be synonyms until 2003 (Steentjes et al. 2021), are the main pathogens causing neck rot, a disease that often occurs in storage and causes decay starting at the neck and progressing throughout the entirety of the bulb. The disease is characterized by the neck part of the scales becoming translucent and decaying and grayish mycelium growing in between the scales (Schwartz & Mohan 2007). Gray mold and sclerotia may also be visible on the outer scales of the bulb. The infection starts while the onion plants are still growing in the field, hyphae start growing in the

epidermis of the leaves but is usually not apparent until neck rot starts developing after harvest (Tichelaar 1967). The pathogens can also be seedborne (Schwartz & Mohan 2007). Other *Botrytis* spp., including *B. byssoidea* and *B. squamosa* (causal organism of Botrytis leaf blight) are also capable of causing similar symptoms (Lorbeer et al. 2007) but are less common as causal agents of neck rot in storage. Neck rot caused by *B. allii* or *B. aclada* is one of the more important storage diseases of onion, with recorded losses that can be as high as 70% (Singh et al. 2021). The disease can often be prevented if onion bulbs are properly cured in a way that closes the neck, and stored dry after harvest (Schwartz & Mohan 2007).

1.4.3 Fusarium basal plate rot (*Fusarium oxysporum* f. sp. *cepae*)

The genus *Fusarium* contains several pathogens causing severe diseases in various crops (Thrane 2014). Among them are several *Allium* pathogens, such as *Fusarium oxysporum* f. sp *cepae* (FOC). FOC is a wide-spread pathogen that causes Fusarium basal plate rot in onions, a disease that can lead to economically significant losses in the field as well as in storage (Schwartz & Mohan 2007). Onions infected with FOC can also contain toxins such as fumonisins, beauvericin, and moniliformin which may be detrimental to the health of consumers (Rämö et al. 2021). Different isolates of FOC can vary greatly in their ability to infect and cause disease symptoms in onions (Wang et al. 2019a). FOC can start its infection process at any point during the growing season, and can cause plants to wilt fully or cause bulbs to rot more slowly, from the basal plate and out. The pathogen is frequently found in the soil and has a strong ability to invade the bulb unaided, but infection is promoted by previous damage (Schwartz & Mohan 2007). Fungicides and resistant cultivars can help combat problems caused by Fusarium basal plate rot.

1.4.4 Black mold (*Aspergillus niger*)

Black mold caused by *Aspergillus niger* can be seen both on the surface of infected onions as black mycelia and conidia in the neck region and between the outermost scales. It can also grow and be seen inside the bulb as dark discoloration expanding from the neck area. The spores of *A. niger* can be found in many places but rarely infect undamaged bulbs (Schwartz & Mohan 2007). As such it may be avoided by limiting the presence of other factors that may damage the bulbs.

1.4.5 Less common fungal storage diseases

Downy mildew (Peronospora destructor)

Downy mildew, caused by *Peronospora destructor*, is a disease primarily affecting the leaves of onion plants during the growing season. However, the infection can also become systemic and affect the bulbs which may then shrivel or sprout prematurely in storage if symptoms are not detected before harvest. Infections become more serious in wet and cold conditions (Schwartz & Mohan 2007). Downy mildew is prevented by use of fungicide treatments during the growing season and through good hygiene, as the pathogen can survive in onion left over from previous seasons. For the same reason, having a crop rotation is recommended.

Sclerotinia rot (Sclerotinia sclerotiorum)

Sclerotinia sclerotiorum can cause sclerotinia rot of onion bulbs. It is characterized by a watery rot and white mold that eventually forms black sclerotia and may appear in storage. Sclerotia may remain viable in the soil for many years. The pathogen thrives in cool and moist conditions and the occurrence of Sclerotinia rot has been found to be negatively correlated with temperature in carrot fields (Kora et al. 2005). However, it is not considered to be a common or serious threat to onion production (Schwartz & Mohan 2007).

Southern blight (Sclerotium rolfsii)

Southern blight, caused by *Sclerotium rolfsii* is a disease of onion bulbs that is uncommon in temperate climates. It causes a mushy rot and bulbs eventually dissolve fully and is characterized by round brown sclerotia. Unlike those of *Sclerotinia*, the sclerotia of *S. rolfsii* do not remain viable for years, but can survive for a few months in wet conditions in the field. Infection is more likely in warm and moist conditions, and can be limited by careful irrigation strategies and growing onions in an appropriate season (Schwartz & Mohan 2007).

Purple blotch (Alternaria porrii)

Another onion disease that is mostly found in hot and humid climates is purple blotch, caused by *Alternaria porrii*. The disease primarily affects the leaves, but can occasionally infect the bulbs, where it causes a yellowish rot that with time turns purplish and finally dark brown or black as the infected tissue dries (Schwartz & Mohan 2007).

1.5 Bacterial storage diseases

1.5.1 Bacterial soft rots

A number of different bacterial species cause similar symptoms of rot in onion bulbs. These species come from the genera *Pectobacterium* and *Dickeya* (syn. *Erwinia*, and will be referred to as such in this text), *Enterobacter* and *Pseudomonas*, among others. These bacteria can act as opportunistic pathogens or, in the case of *Erwinia carotovora* ssp. *carotovora* and *Erwinia chrysanthemi*, invade directly through the leaves and necks of undamaged bulbs (Schwartz & Mohan 2007). Typical for infections by both *Erwinia* species mentioned here are mushy rots starting at the neck of the onion and spreading down and out throughout the bulb, similarly to fungal infections such as neck rot. However, as these soft rots are caused by bacteria, mycelia is not present. *Erwinia* spp. of the carotovora group are responsible for large economic damage, infecting a wide variety of fruits and tubers and causing losses in storage and in the field (Dadaşoğlu & Kotan 2017). Bacterial soft rots, such as the one caused by *Erwinia carotovora* ssp. *carotovora* may be controlled with bulb dips containing copper oxychloride and streptomycin in the case of bulbs for seed production (Gore & Rakhonde 2020), but these types of treatments are likely not suitable in onions meant for consumption. Bulbs meant for consumption are less likely to succumb to bacterial soft rot in moist condition if they are topped or if the leaves are fully dry before the bulbs are exposed to the moisture (Wright & Triggs 2005).

1.5.2 Slippery skin (*Burkholderia gladioli* subsp. *alliicola*) and sour skin (*Burkholderia cepacia*)

Slippery skin, so called because affected bulbs tend to have their cores escape the outer scales through the top when squeezed, is another type of bacterial rot of onion. The disease, caused by *Burkholderia gladioli* subsp. *alliicola*, is characterized by individual scales inside the bulb becoming softened due to rot. Sour skin is caused by another *Burkholderia*, *B. cepacia*, and symptoms may be relatively similar to those of slippery skin. Individual inner scales will rot, often leaving the outer scales firm and the bulb looks to still be healthy.

B. gladioli subsp. *alliicola* infects primarily through wounds, either during the growing season or at harvest, but also during handling and storage after harvest. *B. cepacia* is somewhat less dependent on previous damage, and can invade an onion bulb if moisture levels are high enough (Schwartz & Mohan 2007). As mentioned previously, curing plays a big part in preventing disease development if bulbs have already been exposed to the pathogens, with short curing times at relatively low temperatures being preferable (Schroeder et al. 2012). As they are opportunistic pathogens and like moisture further disease prevention involves curing as soon as

possible after harvest, avoiding damage and storing bulbs at low temperatures that are not conducive to pathogen growth.

1.6 Control of storage diseases

1.6.1 Chemical methods of control of storage diseases

In addition to minimizing the occurrence of storage diseases by lifting at the right time, curing in a good way and having the right storage conditions, fungicides can be used. However, the availability of approved fungicides that are effective against storage diseases is limited in Sweden (*Lök* u.å.). Fungicides applied to the seed can help prevent infections, especially those that occur early on. It has been shown that fungal pathogens present in the soil or on the seed, such as *F. oxysporum* or *A. niger,* can be prevented from infecting the onion seedlings by applying one or a combination of fungicides to the seed ahead of sowing (Özer & Köycü 1998). Storage diseases caused by fungal pathogens that infect at later stages of growth, e.g. *Botrytis allii* or *B. aclada*, can be stopped from developing using fungicides sprayed during growth in the field (Chilvers et al. 2006). It has been found that natural salts can be effective as treatment of FOC infection, and in particular sodium metabisulfite can inhibit the growth well even when used at low concentrations (Muharrem 2013). Using this salt rather than traditional fungicides may lower the risk to the environment and also to consumers due to low toxicity to mammals.

1.6.2 Biological control of storage diseases

In the name of sustainable production, use of fungicides and other pesticides with potential toxicity or other harmful side effects on non-target organisms should preferably be limited. Biological control is an option that tends to have lower risks, and there have been some studies performed regarding biological control of onion storage diseases.

As well as pathogenic species, the genus *Penicillium* contains species that could be used as biocontrol against other storage diseases. Khokhar et al. (2012), investigated a number of such species and their antagonistic effect against *Aspergillus niger*. It was found that several of the species had an inhibitive effect on growth of *A. niger*, but also that the *Penicillium* cultures tended to overgrow the *A. niger* cultures. Visible growth of *Penicillium* on the onion bulbs would not be desirable, but it is possible that some of the metabolites released by the fungus could prove useful. Another study found that a specific isolate of *Streptomyces* could significantly reduce losses of bulbs already infected with *Botrytis allii* (Jorjandi et al. 2009). Many *Trichoderma* spp. are known to be beneficial symbionts of plants. A study found that *Trichoderma longibrachiatum* can be applied to onion seeds or

soil to modify the onions metabolism to enhance growth and increase resistance to FOC infection (Abdelrahman et al. 2016).

1.7 Analysis of onion headspace volatiles

Volatiles of infected onions

In recent years there has been some interest in and publications regarding the volatiles found in the headspace of diseased onions and their potential usefulness for detecting storage diseases at early stages. The purpose stated in these publications is typically the development of non-destructive methods for monitoring of onion quality in storage (Prithiviraj et al. 2004; Vikram et al. 2005; Li et al. 2011; Wang et al. 2016, 2019a; b; Sinha et al. 2018). The methods used in these studies vary, but findings typically indicate measurable differences between healthy and infected onions. These differences pertain either to the quantity of volatile compounds released or the presence or absence of specific compounds. For an overview, table 1 lists the compounds found in six studies investigating which headspace volatiles are released by uninfected onions and onions infected by several different storage diseases. It is clear that certain compounds are released mainly when there is pathogenic microbial activity in the bulbs while others are present in both uninfected and infected onions. A limited number of compounds are found only in the presence of one specific pathogen. These could therefore be of interest as key indicators of infection by the respective pathogen.

Compound	CAS	Uninfected (U)	Aspergillus niger (A)	Botrytis allii (B)	Burkholderia cepacia (C)	Erwinia carotovora subsp. carotovora (E)	Fusarium oxysporum f.sp. cepae (F)	Penicillium aurantiogriseum (P)	Yes	Yes and no	No
Styrene	9003-53-6	No [1,3,4] Yes [6]	Yes [1]	Yes [6] No [1]		Yes [1] No [6]	Yes [1,4] No [6]	No [1]	A	UBEF	P
1-Ethenyl-4-ethyl-benzene	3454-07-7	No [6]		Yes [6]		No [6]	No [6]		B		UEF
Acetic acid-hydrazide	1068-57-1	No [6]		Yes [6]		No [6]	No [6]		B		UEF
Z-Propanethial-S-oxide	32157-29-2	No [2]		Yes [2]	No [2]				B		UC
Thiirane	420-12-2	No [6]		Yes [6]		No [6]	No [6]		B		UEF
(E)-1-(methylthio)-1-propene	42848-06-6	Yes [3,4] No [2,6]		Yes [2,6]	No [2]	No [6]	Yes [4] No [6]		B	UF	CE
1-Bromo-1-propene	590-14-7	No [6]		Yes [6]		No [6]	No [6]		B		UEF
Propylcarbamate	627-12-3	No [6]		Yes [6]		No [6]	No [6]		B		UEF
3(2H)-Furanone, 2-octyl-5-methyl-	57877-72-2	No [2]		No [2]	Yes [2]				C		UB
2-Nonanone	821-55-6	No [2]		No [2]	Yes [2]				C		UB
3-Bromo-furan	22037-28-1	No [6]		No [6]		Yes [6]	No [6]		E		UF
4-Mercapto-3-(methylthio)-gamma-(thio-lactone)-crotonic acid	?	No [6]		No [6]		No [6]	Yes [6]		F		UBE
2-Heptanone	110-43-0	No [4]					Yes [4]		F		U
Propene	115-07-1	Yes [5] No [4]					Yes [4]		F	U	
3-Methyl-1-butanol	123-51-3	No [3,4]					Yes [4]		F		U
Methyl isopropyl sulfide	1551-21-9	No [4]					Yes [4]		F		U
Ethyl cyclobutane	4806-61-5	No [1]	No [1]	No [1]		No [1]	Yes [1]	No [1]	F		UABEP
(E)-1,3-pentadiene	504-60-9	No [4]					Yes [4]		F		U
1-Oxa-4,6-diazacyclooctane-5-thione	74804-37-8	No [6]		No [6]		No [6]	Yes [6]		F		UBE
Methanethiol	74-93-1	Yes [5] No [4]					Yes [4]		F	U	
3,3′-Dioxy-1,2-propanediol-tetranitrate	?	Yes [6]		No [6]		No [6]	No [6]		U		BEF
Methyl formate	107-31-3	Yes [5]							U		
2-Pentanone	107-87-9	Yes [5]							U		
Hexane	110-54-3	Yes [5]							U		
Pentanal	110-62-3	Yes [5]							U		
2,5-Dimethylfuran	625-86-5	Yes [5]							U		
Isopropyl alcohol	67-63-0	Yes [5]							U		
2-Methyl-2-propanol	75-65-0	Yes [5]							U		
4-(1,2-Dimethyl-cyclopent-2-enyl)-butan-2-one	?	No [2]		Yes [2]	Yes [2]				BC		U
N-Dodecane	112-40-3	No [2]		Yes [2]	Yes [2]				BC		U
1-Nonanol	143-08-8	No [2]		Yes [2]	Yes [2]				BC		U
Methyl propenyl disulfide	23838-19-9	No [2]		Yes [2]	Yes [2]				BC		U
Pentalene/aromadendrene	250-25-9/25246-27-9	No [2]		Yes [2]	Yes [2]				BC		U
2-Tridecanone	593-08-8	No [2]		Yes [2]	Yes [2]				BC		U
Dipropyl trisulfide	6028-61-1	No [2]		Yes [2]	Yes [2]				BC		U
2,5-Dimethylthiophene	638-02-8	No [2]		Yes [2]	Yes [2]				BC		U
Acetone	67-64-1	Yes [2,4,5] No [6]		Yes [2,6]	Yes [2]	No [6]	Yes [4] No [6]		BC	UF	E
Alpha-myrcene	1686-30-2	No [6]		Yes [6]		No [6]	Yes [6]		BF		UE

(Z)-1-(methylthio)- 1-propene	52195-40-1	Yes [4,5] No [2]	Yes [2,6]	No [2]	**Yes [4]**	B**F**	U	CE
Methyl hydrazine	60-34-4	No [6]	Yes [6]	No [6]	Yes [6]	BF		UE
Phenyl-butanedioic acid	635-51-8	No [6]	Yes [6]	No [6]	Yes [6]	BF		UE
Prop-1-enyl dithiopropanoate	67269-06-1	No [6]	Yes [6]	No [6]	Yes [6]	BF		UE
Alpha-(1-phenylaminoethyl)-benzenemethanol	?	No [6]	Yes [6]	No [6]	Yes [6]	BF		UE
Alpha,alpha-dimethyl-benzeneethanol	100-86-7	No [6]	No [6]	Yes [6]	Yes [6]	EF		UB
Heptanal	111-71-7	No [6]	No [6]	Yes [6]	Yes [6]	EF		UB
Dimethyl ether	115-10-6	No [6]	No [6]	Yes [6]	Yes [6]	EF		UB
1-Methyl-5-(1-methylethenyl)-, R-cyclohexene	1461-27-4?	No [6]	No [6]	Yes [6]	**Yes [6]**	E**F**		UB
2-Methyl-4,6-octadiyn-3-one	29743-33-7	No [6]	No [6]	Yes [6]	Yes [6]	EF		UB
2-Ethylidene[1,3]dithiane	51102-62-6	Yes [6]	Yes [6]	No [6]	No [6]	UB		EF
Alpha-4-dimethyl-benzenemethanol	536-50-5	Yes [6]	Yes [6]	No [6]	No [6]	UB		EF
Methyl 1-propenyl disulfide	5905-47-5	Yes [4,5,6]	**Yes [6]**	No [6]	**Yes [4]** No [6]	U**B**	F	E
4-Methylene-1-(1-methylethyl)-cyclohexene	99-84-3	Yes [6]	Yes [6]	No [6]	No [6]	UB		EF
1-[(4-Methoxyphenyl)methyl]-3,3-dimethyl-4phenyl-2-azetidinone	?	Yes [6]	No [6]	Yes [6]	No [6]	UE		BF
Allyl methyl sulfide	10152-76-8	Yes [4]			**Yes [4]**	U**F**		
Pentane	109-66-0	Yes [4,5]			**Yes [4]**	U**F**		
Ethyl formate	109-94-4	Yes [4]			Yes [4]	UF		
Propanal	123-38-6	Yes [4,5]			Yes [4]	UF		
Heptane	142-82-5	Yes [4,5]			**Yes [4]**	U**F**		
2,4-Dithiapentane	1618-26-4	Yes [4]			**Yes [4]**	U**F**		
Allyl propyl sulfide	27817-67-0	Yes [4]			**Yes [4]**	U**F**		
2-Ethylfuran	3208-16-0	Yes [4]			**Yes [4]**	U**F**		
Methyl propyl sulfide	3877-15-4	Yes [3,4,5]			Yes [4]	U**F**		
2,3-Butanedione	431-03-8	Yes [4]			Yes [4]	UF		
Carbonyl sulfide	463-58-1	Yes [4]			Yes [4]	UF		
(E)-2-methyl-2-butenal	497-03-0	**Yes [4]**			Yes [4]	**U**F		
2-Methylfuran	534-22-5	Yes [4,5]			**Yes [4]**	U**F**		
2,2-Bis(methylthio)propane	6156-18-9	Yes [4]			**Yes [4]**	U**F**		
Acetic acid	64-19-7	Yes [3,4,5]			Yes [4]	UF		
Hexanal	66-25-1	Yes [4,5]			Yes [4]	UF		
Methanol	67-56-1	Yes [4]			**Yes [4]**	U**F**		
Acetaldehyde	75-07-0	Yes [4,5]			**Yes [4]**	U**F**		
Carbon disulfide	75-15-0	Yes [4,5]			**Yes [4]**	U**F**		
Dimethyl sulfide	75-18-3	Yes [4]			**Yes [4]**	U**F**		
Isoprene	78-79-5	Yes [4,5]			**Yes [4]**	U**F**		
2-Butanone	78-93-3	Yes [4,5]			**Yes [4]**	U**F**		
Methyl vinyl ketone	78-94-4	Yes [4]			Yes [4]	UF		
Methyl acetate	79-20-9	Yes [4]			**Yes [4]**	U**F**		

3-Methylfuran	930-27-8	Yes [4,5]					**Yes [4]**		U**F**		
2-Azabicyclo[3.2.0]hept-6-ene	?	No [1]	Yes [1]	No [1]		Yes [1]	No [1]	Yes [1]	AEP		UBF
1-Propanethiol	107-03-9	Yes [3,4,5] No [2,6]		Yes [2,6]	Yes [2]	Yes [6]	Yes [4] No [6]		BCE	UF	
4,4-Dimethyl-1,3-diphenyl-1-(trimethylsilyloxy)-1-pentene	?	No [6]		Yes [6]		Yes [6]	Yes [6]		BEF		U
3,7,7-Trimethyl-, [1S-(1 alpha,3 alpha ,6 alpha)]bicyclo[4.1.0]hept-4-en-3-ol	103063-10-1	No [6]		Yes [6]		Yes [6]	Yes [6]		BEF		U
1,1-Dimethylethyl-urea	1118-12-3	No [6]		Yes [6]		Yes [6]	Yes [6]		BEF		U
Heptanoic acid	111-14-8	Yes [2]		Yes [2]	Yes [2]				UBC		
Undecane	1120-21-4	Yes [2]		**Yes [2]**	**Yes [2]**				U**BC**		
2-Undecanone	112-12-9	Yes [2]		Yes [2]	Yes [2]				UBC		
2,4-Octanedione	14090-87-0	Yes [2]		Yes [2]	Yes [2]				UBC		
Propylpropenyl disulfide	23838-20-2	Yes [2]		Yes [2]	Yes [2]				UBC		
3(2H)-Furanone, 2-hexyl-5-methyl	33922-66-6	Yes [2]		Yes [2]	Yes [2]				UBC		
2-Methyl-5-(1-methylethyl)-bicyclo[3.1.0]hexan-2-ol	15537-55-0?	Yes [6]		Yes [6]		Yes [6]	No [6]		UBE		F
N,N-dimethyl-1-Butanamine	927-62-8	Yes [6]		Yes [6]		Yes [6]	No [6]		UBE		F
2-(Thiocarboxy)hydrazide-O-methyl ester-acetic acid	20184-99-0	Yes [6]		Yes [6]		No [6]	Yes [6]		UBF		E
1,3,5-Cycloheptatriene	544-25-2	Yes [6]		No [6]		Yes [6]	Yes [6]		UEF		B
2,3-Dimethyl-thiophene	632-16-6	Yes [6]		No [6]		Yes [6]	Yes [6]		UEF		B
Alpha-phellandrene	99-83-2	Yes [6]		No [6]		Yes [6]	Yes [6]		UEF		B
N-3-Aminophenyl acetamide	102-28-3	Yes [1]	No [1]	No [1]		Yes [1]	No [1]	Yes [1]	UEP		ABF
Dimethyl disulfide	624-92-0	Yes [3,4,5,6] No [1,2]	Yes [1]	Yes [1,2,6]	Yes [2]	**Yes [1]** No [6]	Yes [1,4,6]	No [1]	A**B**CF	UE	P
Ethanol	64-17-5	Yes [1,3,4] No [6]	Yes [1]	Yes [1,6]		Yes [1,6]	Yes [1,4,6]	No [1]	ABE**F**	U	P
1-Propanol	71-23-8	Yes [3,5] No [1,4]	Yes [1]	Yes [1]		Yes [1]	Yes [1,4]	No [1]	ABEF	U	P
2,3-Butanedionylidene bis(o-aminobenzyl alcohol)	?	Yes [1,6]	Yes [1]	Yes [1] No [6]		Yes [1,6]	Yes [1] No [6]	Yes [1]	UAEP	BF	
1-Phenoxy-2-propanone	621-87-4	Yes [1]	Yes [1]	No [1]		Yes [1]	No [1]	Yes [1]	UAEP		CF
1,3-Cycloheptadien-1-yl-methyl-ketone	?	Yes [6]		Yes [6]		Yes [6]	Yes [6]		UBEF		
2-Methyl-5-(1-methylethyl)-bicyclo[3.1.0]hexan-2-ene	?	Yes [6]		Yes [6]		Yes [6]	Yes [6]		UBEF		
3-Carene	13466-78-9	Yes [6]		**Yes [6]**		**Yes [6]**	**Yes [6]**		U**BEF**		
1-(4-Metylphenyl)-1-pentanone	1671-77-8	Yes [6]		Yes [6]		Yes [6]	Yes [6]		UBEF		
[1,3]Dithiane-2-thione	1748-15-8	Yes [6]		**Yes [6]**		Yes [6]	Yes [6]		U**B**EF		
1-Methyl-4-(1-methylethenyl)-acetate-cyclohexanol	26252-11-9	Yes [6]		Yes [6]		Yes [6]	Yes [6]		UBEF		
2-(Dimethylamino)-1-phenyl-3-heptanone	27820-08-2	Yes [6]		Yes [6]		Yes [6]	Yes [6]		UBEF		
2,3,5-Trimethyl-4-methylene-2-cyclopenten-1-one	29765-85-3	Yes [6]		Yes [6]		Yes [6]	Yes [6]		UBEF		
1-Methyl-2-(1-methylethyl)-benzene	527-84-4	Yes [6]		Yes [6]		Yes [6]	Yes [6]		UBEF		
Oxybis chloro-methane	542-88-1	Yes [6]		**Yes [6]**		**Yes [6]**	Yes [6]		U**BE**F		
Formic acid	64-18-6	Yes [6]		Yes [6]		Yes [6]	Yes [6]		UBEF		
2-Ethyl-5-chloro-1,3,4-thiadiazole	71859-81-9	Yes [6]		Yes [6]		Yes [6]	Yes [6]		UBEF		
1-Methyl-4-(1-methylethyl)-1,4-cyclohexadiene	99-85-4	**Yes [6]**		Yes [6]		Yes [6]	Yes [6]		**U**BEF		
1-Methyl-aziridine	1072-44-2	Yes [1]	No [1]	No [1]		Yes [1]	Yes [1]	Yes [1]	UEFP		AB
Methyl propyl disulfide	2179-60-4	Yes [1,3,4,5,6] No [2]	Yes [1]	Yes [1,2,6]	Yes [2]	Yes [1,6]	Yes [1,4,6]	No [1]	ABCE**F**	U	P
Alpha-2,5,7-Octatrienyl-N-propylbenzenemethanamine	57368-49-7	No [1]	Yes [1]	Yes [1]		Yes [1]	Yes [1]	Yes [1]	ABEFP		U

1,2-Dichloro-benzene	95-50-1	Yes [1]	Yes [1]	Yes [1]		No [1]	Yes [1]	Yes [1]	UABFP	E
Bis(1-methylethyl) disulfide	4253-89-8	Yes [1,6]	Yes [1]	Yes [1] No [6]		Yes [1,6]	Yes [1,6]	Yes [1]	**U**AEFP	B
3,4-Dimethylthiophene	632-15-5	Yes [1,4,5,6]	Yes [1]	Yes [1] No [6]		Yes [1,6]	Yes [1,4,6]	Yes [1]	UAE**F**P	B
Trichloroethylene	79-01-6	Yes [1]	Yes [1]	Yes [1]		Yes [1]	Yes [1]	Yes [1]	UABEFP	
O-Methyl 2-acetylhydrazinecarbothioate	?	Yes [1]	Yes [1]	Yes [1]		Yes [1]	Yes [1]	Yes [1]	UABEFP	
Endo-Bicyclo[3.3.1]nonan-3-ol	10036-10-9	Yes [1,6]	Yes [1]	Yes [1,6]		Yes [1,6]	Yes [1,6]	Yes [1]	UABEFP	
1,4-Dichloro-benzene	106-46-7	Yes [1]	Yes [1]	Yes [1]		Yes [1]	Yes [1]	Yes [1]	UABEFP	
Methane oxybis dichloro	20524-86-1	Yes [1]	Yes [1]	Yes [1]		Yes [1]	Yes [1]	Yes [1]	UABEFP	
2-Bromomethyl-1,3-butadiene	23691-13-6	Yes [1]	Yes [1]	Yes [1]		Yes [1]	Yes [1]	Yes [1]	UABEFP	
1,3-Dichloro-benzene	541-73-1	Yes [1]	Yes [1]	Yes [1]		Yes [1]	Yes [1]	Yes [1]	UABEFP	
Chloroform	67-66-3	Yes [1,6]	Yes [1]	Yes [1,6]		Yes [1,6]	Yes [1,6]	Yes [1]	UABEFP	
Dipropyl disulfide	629-19-6	Yes [1,2,6]	Yes [1]	Yes [1,2,6]	Yes [2]	Yes [1,6]	Yes [1,6]	Yes [1]	UA**BC**E**F**P	

Table 1. The presence of headspace volatiles in uninfected onions (U) and onions infected with Aspergillus niger (A), Botrytis allii (B), Burkholderia cepacia (C), Erwinia carotovora subsp. carotovora (E) (syn. Pectobacterium carotovorum subsp. carotovorum), Fusarium oxysporum f.sp. cepae (F) or Penicillium aurantiogriseum (P). Compounds are sorted by the number of infection types they were found in, with compounds unique to one infection status at the top. Bold text indicates the compound was found in at least 10 times higher amounts in the specific infection than in uninfected onions or onions infected with other pathogens in a particular study. Numbers indicate the source of the information, as follows: 1. Vikram, Hamzehzarghani and Kushalappa, 2005, 2. Li, Schmidt and Gitaitis, 2011, 3. Wang et al., 2016, 4. Wang et al., 2019, 5. Wang, Luca and Edelenbos, 2019, 6. Prithiviraj et al., 2004. For reference number 3 only the data for uninfected onions were used, as the infected onions contained mixes of pathogens.

Methods for volatile analysis of onions

The odors that are released when healthy onions are cut or otherwise damaged consist largely of thiosulfinates and their related compounds and breakdown products. Some of these compounds are heat unstable and may break down if analysis is attempted using gas chromatography (GC) (Block et al. 1992b). High performance liquid chromatography (HPLC) may give a more complete picture of the volatile and heat sensitive compounds present in onions (Block et al. 1992a). However, when headspace volatiles are of interest, methods such as solid phase microextraction (SPME), which do not allow for the use of HPLC, are often chosen. Other methods, such as headspace-single drop microextraction (HS-SPDME) are possible to use if headspace collections need to be run using HPLC (Rincón et al. 2011), but the choice of solvent may provide a skewed picture of the present compounds. However, Mondy et al. (2001) found GC-MS to produce satisfactory results when compared to HPLC for onion samples, but not for garlic samples where the content of heat sensitive allicin is an important factor in the odor and flavor profile. A gas sensor array, or e-nose, can also be used to identify onion volatiles and differentiate between onions of different origin and quality (Abbey et al. 2004). Russo et al. (2013) used an e-nose to discriminate between four different

cultivars of red onions and found that this could be done with high specificity by comparing the grouping of identified volatiles.

Several of these methods for analysis of headspace volatiles have been used in efforts to compare healthy and diseased onions to find key compounds indicating the presence of specific pathogens.

HAPSITE

One study investigated the headspace volatiles released by onions artificially infected with *Fusarium oxysporum*, *Botrytis allii*, *Erwinia carotovora* subsp. *carotovora*, *Aspergillus niger*, and *Penicillium aurantiogriseum* using HAPSITE, a portable GC-MS system (Vikram et al. 2005). It was found that dipropyl disulfide was present in higher amounts in all infected bulbs and in relatively low amounts in the control bulbs, meaning it could be useful as a general indicator of infections. A number of compounds were found in several, but not all of the different types of infection, and at differing abundancies. It could therefore be possible to differentiate between different types of pathogen infections by looking at the combination of volatiles present and their relative abundancies. Many compounds were found relatively inconsistently, and may be uncertain indicators of infection. Another study using HAPSITE to detect differences between different diseases in onions was performed by Prithiviraj et al. (2004). The onions were infected with *Erwinia carotovora* ssp. *carotovora*, *Fusarium oxysporum* or *Botrytis allii* and volatiles were collected and disease progression was measured at 3 and 6 days past infection. It was found that the amounts of sulfur-containing compounds were higher in infected onions when compared to healthy onions. *Botrytis allii*-infected onions had the highest levels, followed by *F. oxysporum* and *E. carotovora* ssp. *carotovora*. Certain compounds were found exclusively in one of the types of infection or at different relative concentrations and could enable the creating of a volatile fingerprint for the specific diseases.

E-nose

Using a gas sensor array, also called electronic nose or e-nose is one possibility to detect infected onions in storage. Li et al. (2011) used an e-nose to detect differences between healthy onions and onions infected with either *Botrytis allii* or *Burkholderia cepacia*. They found that onions infected with *B. allii* could easily be separated from healthy onions and that onions infected with the two pathogens had relatively similar odor profiles when compared to the healthy onions, but could still be distinguishable. Another study used a relatively cheap custom gas sensor array and could demonstrate a high success rate in detecting sour skin infections as early as 4 days after infection when infected onions were incubated at 30°C (Konduru et al. 2015).

Field asymmetric ion mobility spectrometry

Another method to analyze headspace volatiles of diseased onions used by Sinha et al. (2018) is field asymmetric ion mobility spectrometry or FAIMS. The study investigated the release of a number of compounds (dimethyl disulfide, dipropyl disulfide, methyl propyl disulfide, undecane and 2-undecanone) present in both healthy onions and onions infected by *B. cepacia*. The amount of these compounds released by the infected bulbs was higher than in control bulbs, and infected bulbs could therefore be identified with relatively high accuracy as the disease progressed.

Solid phase microextraction

Wang et al. (2016) used solid phase microextraction (SPME) to collect volatiles from healthy and diseased onions taken from storage and divided them into soft rot and blue mold infections although a combination of pathogens was present in most bulbs. They reported that the soft rot group of onions contained high levels of ethanol, 1-propanol, 1-propanethiol, acetic acid, and 3-methyl-1-butanol and particularly that high contents of acetic acid, ethanol and 3-methyl-1-butanol marked the soft rot onions apart from both healthy and *Penicillium*-infected onions. In 2019, Wang et al. (Wang et al. 2019a) reported on investigations using SPME regarding the volatiles released by onions infected by two different strains of *F. oxysporum* with different degrees of pathogenicity. The more severe infection caused by one of the strains correlated with higher amounts of headspace volatiles detected. In particular the contents of 1-Propanethiol, methyl propyl sulfide, and styrene could be connected to the degree of disease progression, with increased release coinciding with increased content of *Fusarium* DNA in the bulbs. Another study using SPME to compare the volatile compounds released by onions in storage, some of which were infected by *B. cepacia*, *F. oxysporum* or neck rot (*Botrytis* spp.) showed that the overall release of volatile compounds increased with time for the infected onions, but decreased for healthy onions (Wang et al. 2019b).

Volatiles of onion pathogens on artificial media

Studies of headspace volatiles of organisms that can occur as onion pathogens growing on artificial media are rarely done with onions storage diseases in mind, and as such often use strains isolated from other sources. Therefore these publications may not be the optimal source of information for the identification of onions storage disease markers, but could still be of some use. For example, Costa et al. (2016) used SPME and GCxGC-ToFMS (two-dimensional gas chromatography and time-of-flight mass spectrometry) to elucidate the headspace volatilome (the totality of volatile organic compounds found in the headspace) of *Aspergillus niger* at two different growing temperatures and solid and liquid media.

They found 428 different metabolites released by *A. niger*, 44 of which were found in every testing condition meaning they could be used to create a fingerprint headspace volatilome for the pathogen. Some of these compounds are likely also found when the pathogen is growing on onion tissue.

Additionally, the headspace of sclerotia of three different species of *Sclerotinia*, including the onion pathogen *Sclerotinia sclerotiorum* was investigated in a search for volatiles that may trigger germination of conidia in the sclerotial parasite *Sporidesmium sclerotivorum* (Fravel et al. 2002). No such compounds were found in the experiment using SPME. However, volatiles with antimicrobial properties were identified, possibly acting as a defense system against parasitism for the sclerotia.

2. Discussion

Onion is a widely produced crop that is subject to a variety of diseases, both during the growing season and in storage. Some of the losses caused by these diseases could likely be prevented with new and improved tools in culture and post harvest handling. Many of the diseases that affect onions during the growing season can be fully or partially prevented using resistant cultivars and clean seed or sets, crop rotation and other cultural practices. When needed, it is also possible to treat the crop or seed with pesticides (Schwartz & Mohan 2007). However, while infections occurring during cultivation can often be detected through visual cues, the storage of onions in large bins in storage facilities makes it difficult to spot bulbs that are starting to rot or grow mold, at least in the lower layers of the bin. Certain storage diseases, including sour skin and slippery skin may not be at all visible to the human eye until very late stages (Wang et al. 2009), which means diseased bulbs risk being sold to consumers or infecting other bulbs in storage.

This is where volatile detection could prove useful. As discussed previously, several studies have been performed on some of the most common onion storage diseases and the volatile compounds found in the headspace of infected bulbs. As has been shown in these publications, volatiles released by ongoing infections could be used to detect diseased onions in storage, potentially at fairly early stages. The specific volatile fingerprint of each storage disease differs between publications (Table 1), probably due to factors such as sampling method and conditions, onion cultivar and pathogen strain used. While the methods used have varied and the compounds found differ from study to study there are some general trends. For example, it seems to be true that onions with certain storage diseases release higher volumes of volatile compounds when compared to uninfected bulbs (Prithiviraj et al. 2004; Li et al. 2011; Wang et al. 2016). This seems likely to be because of an increase in metabolism in both onion tissue and pathogen. However other environmental factors, such as storage temperature, can also affect the amounts of volatiles released (Wang et al. 2019b). Differentiating between specific storage diseases may prove difficult, as compounds that are detected in high amounts for a certain disease in one study may not be detected at all in another. As many of the compounds found in the discussed publications were only identified based on a database search it is possible not all of the identifications are accurate. Additionally,

the studies and used different types of equipment and sampling techniques and as such the results of a study may not be comparable to another.

The use of e-noses could make continuous odor monitoring and early warnings possible. This type of detection system has shown promise for detecting quality and spoilage in onions (Abbey et al. 2004; Li et al. 2011; Konduru et al. 2015) and in several other types of foods, from meats to horticultural crops (Röck et al. 2008). Cost is a problem of many commercially available e-noses, but Konduru et al. (2015) demonstrated the plausibility of cheaper solutions constructed specifically for the task of monitoring onions in storage.

Sprouting is another quality problem that often occurs during storage. The sprouting process brings on various metabolic changes, including increased respiration, in the bulbs. There may therefore exist a possibility to use e-nose technology to detect early stages of sprouting in onion storage facilities. However, this topic does not seem to have been studied much, if at all.

With a growing population and a need for more sustainable production and consumption patterns, food waste minimization is a necessity. Using automatic sensors to detect quality problems developing in storage means the affected produce can be removed and made useful before quality has deteriorated.

3. Conclusions

The area of storage disease volatiles and their potential use to minimize food waste using automated system is a new one, and further studies and technological developments are needed before a marketable solution can be created. There is a need for further studies, particularly into how such a system would work in practice and be cost effective. Based on existing literature it seems like non-destructive methods of predicting sprouting is a relatively unexplored area of study. Given the metabolic changes connected to sprouting, it seems likely that there will be corresponding changes in headspace volatile release. An odor detection system simultaneously scanning for signs of disease and signs of sprouting could possibly be developed.

References

Abayomi, L.A. & Terry, L.A. (2009). Implications of spatial and temporal changes in concentration of pyruvate and glucose in onion (Allium cepa L.) bulbs during controlled atmosphere storage. *Journal of the Science of Food and Agriculture*, 89 (4), 683–687. https://doi.org/10.1002/jsfa.3502

Abbey, L., Joyce, D.C., Aked, J., Smith, B. & Marshall, C. (2004). Electronic nose evaluation of onion headspace volatiles and bulb quality as affected by nitrogen, sulphur and soil type. *Annals of Applied Biology*, 145 (1), 41–50. https://doi.org/10.1111/j.1744-7348.2004.tb00357.x

Abdalla, A.A. & Mann, L.K. (1963). Bulb development in the onion (Allium cepa L.) and the effect of storage temperature on bulb rest. *Hilgardia*, 35 (5), 85–112. https://doi.org/10.3733/hilg.v35n05p085

Abdelrahman, M., Abdel-Motaal, F., El-Sayed, M., Jogaiah, S., Shigyo, M., Ito, S. & Tran, L.-S.P. (2016). Dissection of Trichoderma longibrachiatum-induced defense in onion (Allium cepa L.) against Fusarium oxysporum f. sp. cepa by target metabolite profiling. *Plant Science*, 246, 128–138. https://doi.org/10.1016/j.plantsci.2016.02.008

Adamicki, F. (2005). EFFECTS OF PRE-HARVEST TREATMENTS AND STORAGE CONDITIONS ON QUALITY AND SHELF-LIFE OF ONIONS. *Acta Horticulturae*, (688), 229–238. https://doi.org/10.17660/ActaHortic.2005.688.31

Anbukkarasi, V., Paramaguru, P., Pugalendhi, L., Ragupathi, N. & Jeyakumar, P. (2013). Studies on pre and post-harvest treatments for extending shelf life in onion – A review. *Agricultural Reviews*, 34 (4), 256. https://doi.org/10.5958/j.0976-0741.34.4.011

Benkeblia, N. (2004). Effect of maleic hydrazide on respiratory parameters of stored onion bulbs (Allium cepa L.). *Brazilian Journal of Plant Physiology*, 16 (1), 47–52. https://doi.org/10.1590/S1677-04202004000100007

Benkeblia, N., Varoquaux, P., Gouble, B. & Selselet-Attou, G. (2000). Respiratory parameters of onion bulbs (Allium cepa) during storage. Effects of ionising radiation and temperature. *Journal of the Science of Food and Agriculture*, 80 (12), 1772–1778. https://doi.org/10.1002/1097-0010(20000915)80:12<1772::AID-JSFA700>3.0.CO;2-5

Benkeblia, N., Varoquaux, P., Shiomi, N. & Sakai, H. (2002). Storage technology of onion bulbs c.v. Rouge Amposta: effects of irradiation, maleic hydrazide and carbamate isopropyl, N-phenyl (CIP) on respiration rate and carbohydrates. *International Journal of Food Science & Technology*, 37 (2), 169–175. https://doi.org/10.1046/j.1365-2621.2002.00554.x

Berntsen, H.F., Bogen, I.L., Wigestrand, M.B., Fonnum, F., Walaas, S.I. & Moldes-Anaya, A. (2017). The fungal neurotoxin penitrem A induces the production of reactive oxygen species in human neutrophils at submicromolar concentrations. *Toxicology*, 392, 64–70

Block, Eric., Naganathan, Sriram., Putman, David. & Zhao, S.Hai. (1992a). Allium chemistry: HPLC analysis of thiosulfinates from onion, garlic, wild garlic (ramsoms), leek, scallion, shallot, elephant (great-headed) garlic, chive, and Chinese chive. Uniquely high allyl to methyl ratios in some garlic samples.

Journal of Agricultural and Food Chemistry, 40 (12), 2418–2430. https://doi.org/10.1021/jf00024a017

Block, Eric., Putman, David. & Zhao, S.Hai. (1992b). Allium chemistry: GC-MS analysis of thiosulfinates and related compounds from onion, leek, scallion, shallot, chive, and Chinese chive. *Journal of Agricultural and Food Chemistry*, 40 (12), 2431–2438. https://doi.org/10.1021/jf00024a018

Boyhan, G.E., Purvis, A.C., Randle, W.M., Torrance, R.L., Cook, M.J., Hardison, G., Blackley, R.H., Paradice, H., Hill, C.R. & Paulk, J.T. (2005). Harvest and Postharvest Quality of Short-day Onions in Variety Trials in Georgia, 2000–03. *HortTechnology horttech*, 15 (3), 694–706. https://doi.org/10.21273/HORTTECH.15.3.0694

Brewster, J.L. (2008). *Onions and other vegetable alliums*. 2nd ed. Wallingford, UK ; Cambridge, MA: CABI. (Crop production science in horticulture series; 15)

Carter, C.E., Partis, M.D. & Thomas, B. (1999). The expression of histone 2A in onion (*Allium cepa*) during the onset of dormancy, storage and emergence from dormancy. *New Phytologist*, 143 (3), 461–470. https://doi.org/10.1046/j.1469-8137.1999.00484.x

Chilvers, M.I., Hay, F.S., Hills, J., Dennis, J.J.C. & Wilson, C.R. (2006). Influence of benzimidazole fungicides on incidence of Botrytis allii infection of onion leaves and subsequent incidence of onion neck rot in storage in Tasmania, Australia. *Australian Journal of Experimental Agriculture*, 46 (12), 1661–1664

Chope, G.A., Cools, K., Hammond, J.P., Thompson, A.J. & Terry, L.A. (2012). Physiological, biochemical and transcriptional analysis of onion bulbs during storage. *Annals of Botany*, 109 (4), 819–831. https://doi.org/10.1093/aob/mcr318

Costa, C.P., Gonçalves Silva, D., Rudnitskaya, A., Almeida, A. & Rocha, S.M. (2016). Shedding light on Aspergillus niger volatile exometabolome. *Scientific Reports*, 6 (1), 27441. https://doi.org/10.1038/srep27441

Dadaşoğlu, F. & Kotan, R. (2017). Identification and characterization of Pectobacterium carotovorum. *J Anim Plant Sci*, 27 (2), 647–654

Darbyshire, B. & Henry, R.J. (1979). The association of fructans with high percentage dry weight in onion cultivars suitable for dehydrating. *Journal of the Science of Food and Agriculture*, 30 (11), 1035–1038. https://doi.org/10.1002/jsfa.2740301103

Downes, K., Chope, G.A. & Terry, L.A. (2009). Effect of curing at different temperatures on biochemical composition of onion (Allium cepa L.) skin from three freshly cured and cold stored UK-grown onion cultivars. *Postharvest Biology and Technology*, 54 (2), 80–86. https://doi.org/10.1016/j.postharvbio.2009.05.005

Downes, K., Chope, G.A. & Terry, L.A. (2010). Postharvest application of ethylene and 1-methylcyclopropene either before or after curing affects onion (Allium cepa L.) bulb quality during long term cold storage. *Postharvest Biology and Technology*, 55 (1), 36–44. https://doi.org/10.1016/j.postharvbio.2009.08.003

Dugan, F.M., Lupien, S.L., Vahling-Armstrong, C.M., Chastagner, G.A. & Schroeder, B.K. (2014). Host ranges of North American isolates of Penicillium causing blue mold of bulb crops. *Crop Protection*, 64, 129–136. https://doi.org/10.1016/j.cropro.2014.06.013

Eshel, D., Teper-Bamnolker, P., Vinokur, Y., Saad, I., Zutahy, Y. & Rodov, V. (2014). Fast curing: A method to improve postharvest quality of onions in hot climate harvest. *Postharvest Biology and Technology*, 88, 34–39. https://doi.org/10.1016/j.postharvbio.2013.09.002

FAOSTAT (2021). *FAOSTAT*. *FAOSTAT Statistical Database*. http://www.fao.org/faostat/en/#data/QCL [2021-08-24]

Filho, J.W.G. de O., Islam, M.T., Ali, E.S., Uddin, S.J., Santos, J.V. de O., Alencar, M.V.O.B. de, Júnior, A.L.G., Paz, M.F.C.J., Brito, M. dos R.M. de, Sousa, J.M. de C. e, Shaw, S., Medeiros, M. das G.F. de, Dantas, S.M.M. de M., Rolim, H.M.L., Ferreira, P.M.P., Kamal, M.A., Pieczynska, M.D., Das, N., Gupta, V.K., Mocan, A., Andrade, T. de J.A. dos S., Singh, B.N., Mishra, S.K., Atanasov, A.G. & Melo-Cavalcante, A.A. de C. (2017). A comprehensive review on biological properties of citrinin. *Food and Chemical Toxicology*, 110, 130–141. https://doi.org/10.1016/j.fct.2017.10.002

Forney, C.F., Jordan, M.A., Campbell-Palmer, L., Fillmore, S., McRae, K. & Best, K. (2010). SULFUR FERTILIZATION AFFECTS ONION QUALITY AND FLAVOR CHEMISTRY DURING STORAGE., november 11 2010. 163–168. International Society for Horticultural Science (ISHS), Leuven, Belgium. https://doi.org/10.17660/ActaHortic.2010.877.14

Franke, U., Nordisk Ministerråd, & Nordisk Råd (2013). *Kartläggning av matsvinnet i primärproduktionen*. Kbh.: Nordisk Ministerråd : Nordisk Råd : [Eksp.] www.norden.org/order.

Fravel, D.R., Connick, W.J., Grimm, C.C. & Lloyd, S.W. (2002). Volatile Compounds Emitted by Sclerotia of *Sclerotinia minor* , *Sclerotinia sclerotiorum* , and *Sclerotium rolfsii*. *Journal of Agricultural and Food Chemistry*, 50 (13), 3761–3764. https://doi.org/10.1021/jf0117098

Gore, P.M. & Rakhonde, R.I.P. (2020). Management of bulb rot of onion caused by Erwinia carotovora pv. carotovora. *Journal of Pharmacognosy and Phytochemistry*, 9 (4), 3294–3301

Ihsanullah, I. & Rashid, A. (2017). Current activities in food irradiation as a sanitary and phytosanitary treatment in the Asia and the Pacific Region and a comparison with advanced countries. *Food Control*, 72, 345–359. https://doi.org/10.1016/j.foodcont.2016.03.011

Ilic, Z., Filipovic-Trajkovic, R., Lazić, S., Bursic, V. & Šunjka, D. (2011). Maleic hydrazide residues in the onion bulbs induce dormancy and hamper sprouting for long periods. *Journal of Food Agriculture and Environment*, 9, 113–118

Ilić, Z., Milenković, L., Djurovka, M. & Trajković, R. (2009). THE EFFECT OF LONG-TERM STORAGE ON QUALITY ATTRIBUTES AND STORAGE POTENTIAL OF DIFFERENT ONION CULTIVARS. *Acta Horticulturae*, (830), 635–642. https://doi.org/10.17660/ActaHortic.2009.830.92

Islam, M.N., Wang, A., Skov Pedersen, J. & Edelenbos, M. (2015). Microclimate tools to monitor quality changes in stored onions., 2015. 229–234

Jorjandi, M., Bonjar, G.S., Baghizadeh, A., Sirchi, G.S., Massumi, H., Baniasadi, F., Aghighi, S. & Farokhi, P.R. (2009). Biocontrol of Botrytis allii Munn the causal agent of neck rot, the post harvest disease in onion, by use of a new Iranian isolate of Streptomyces. *American Journal of Agricultural and Biological Sciences*, 4 (1), 72–78

Khokhar, I., Haider, M., Mukhtar, I. & Mushatq, S. (2012). Biological control of Aspergillus niger, the cause of Black-rot disease of Allium cepa L. (onion), by Penicillium species. *Journal of Agrobiology*, 29. https://doi.org/10.2478/v10146-012-0003-5

Ko, S.-S., Chang, W.-N., Wang, J.-F., Cherng, S.-J. & Shanmugasundaram, S. (2002). Storage Variability among Short-day Onion Cultivars under High Temperature and High Relative Humidity, and its Relationship with Disease Incidence and Bulb Characteristics. *Journal of the American Society for*

Horticultural Science jashs, 127 (5), 848–854. https://doi.org/10.21273/JASHS.127.5.848
Konduru, T., Rains, G.C. & Li, C. (2015). Detecting sour skin infected onions using a customized gas sensor array. *Journal of Food Engineering*, 160, 19–27. https://doi.org/10.1016/j.jfoodeng.2015.03.025
Kora, C., McDonald, M.R. & Boland, G.J. (2005). Epidemiology of sclerotinia rot of carrot caused by Sclerotinia sclerotiorum. *Canadian Journal of Plant Pathology*, 27 (2), 245–258. https://doi.org/10.1080/07060660509507222
Li, C., Schmidt, N.E. & Gitaitis, R. (2011). Detection of onion postharvest diseases by analyses of headspace volatiles using a gas sensor array and GC-MS. *LWT - Food Science and Technology*, 44 (4), 1019–1025. https://doi.org/10.1016/j.lwt.2010.11.036
Lorbeer, J.W., Seyb, A.M., de Boer, M. & van den Ende, J.E. (2007). Botrytis Species on Bulb Crops. I: Elad, Y., Williamson, B., Tudzynski, P., & Delen, N. (red.) *Botrytis: Biology, Pathology and Control*. Dordrecht: Springer Netherlands. 273–294. https://doi.org/10.1007/978-1-4020-2626-3_15
Lök (u.å.). *LM Odla - Odlingsstrategier för lantbrukare*. https://www.odla.lantmannenlantbruk.se/grodor/friland/lok/ [2022-06-28]
Mondy, N., Naudin, A., Christides, J.P., Mandon, N. & Auger, J. (2001). Comparison of GC-MS and HPLC for the analysis ofAllium volatiles. *Chromatographia*, 53 (S1), S356–S360. https://doi.org/10.1007/BF02490356
Muharrem, T. (2013). Antifungal effect of various salts against Fusarium oxysporum f.sp. cepae, the causal agent of fusarium basal rot of onion. *Tarım Bilimleri Dergisi*, 19 (3), 178–187. https://doi.org/10.1501/Tarimbil_0000001243
Nabi, G., Rab, A., Bhutta, M., Farhatullah, D., Abbas, S. & Ali, A. (2013). Influence of curing methods and storage conditions on the post-harvest quality of onion bulbs. *Pakistan Journal of Botany*, 45, 455–460
Overy, D.P. & Frisvad, J.C. (2003). New Penicillium Species Associated with Bulbs and Root Vegetables. *Systematic and Applied Microbiology*, 26 (4), 631–639. https://doi.org/10.1078/072320203770865945
Overy, D.P., Frisvad, J.C., Steinmeier, U. & Thrane, U. (2005). Clarification of the agents causing blue mold storage rot upon various flower and vegetable bulbs: implications for mycotoxin contamination. *Postharvest Biology and Technology*, 35 (2), 217–221. https://doi.org/10.1016/j.postharvbio.2004.08.001
Pak, C., van der Plas, L.H.W. & de Boer, A.D. (1995). Importance of dormancy and sink strength in sprouting of onions (Allium cepa) during storage. *Physiologia Plantarum*, 94 (2), 277–283. https://doi.org/10.1111/j.1399-3054.1995.tb05312.x
Petropoulos, S.A., Ntatsi, G. & Ferreira, I.C.F.R. (2017). Long-term storage of onion and the factors that affect its quality: A critical review. *Food Reviews International*, 33 (1), 62–83. https://doi.org/10.1080/87559129.2015.1137312
Põldma, P., Moor, U., Merivee, A. & Tõnutare, T. (2011). Effect of controlled atmosphere storage on storage life of onion and garlic cultivars., 2011. 63–69
Prithiviraj, B., Vikram, A., Kushalappa, A.C. & Yaylayan, V. (2004). Volatile Metabolite Profiling for the Discrimination of Onion Bulbs Infected by Erwinia carotovora ssp. carotovora, Fusarium oxysporum and Botrytis allii. *European Journal of Plant Pathology*, 110 (4), 371–377. https://doi.org/10.1023/B:EJPP.0000021058.81491.f8
Rincón, A.A., Pino, V., Ayala, J.H. & Afonso, A.M. (2011). Headspace-single drop microextraction (HS-SDME) in combination with high-performance liquid

chromatography (HPLC) to evaluate the content of alkyl- and methoxy-phenolic compounds in biomass smoke. *Talanta*, 85 (3), 1265–1273. https://doi.org/10.1016/j.talanta.2011.05.046
Russo, M., di Sanzo, R., Cefaly, V., Carabetta, S., Serra, D. & Fuda, S. (2013). Non-destructive flavour evaluation of red onion (Allium cepa L.) Ecotypes: An electronic-nose-based approach. *Food Chemistry*, 141 (2), 896–899. https://doi.org/10.1016/j.foodchem.2013.03.052
Rutherford, P.P. & Whittle, R. (1982). The Carbohydrate Composition of Onions During Long Term Cold Storage. *Journal of Horticultural Science*, 57 (3), 349–356. https://doi.org/10.1080/00221589.1982.11515063
Rämö, S., Haapalainen, M. & Latvala, S. (2021). Development and Validation of a UHPLC-MS/MS Method for the Analysis of Fusarium Mycotoxins in Onion. *Food Analytical Methods*, 14 (8), 1524–1536. https://doi.org/10.1007/s12161-021-01992-8
Röck, F., Barsan, N. & Weimar, U. (2008). Electronic Nose: Current Status and Future Trends. *Chemical Reviews*, 108 (2), 705–725. https://doi.org/10.1021/cr068121q
Schroeder, B.K., Humann, J.L. & du Toit, L.J. (2012). Effects of Postharvest Onion Curing Parameters on the Development of Sour Skin and Slippery Skin in Storage. *Plant Disease*, 96 (10), 1548–1555. https://doi.org/10.1094/PDIS-02-12-0117-RE
Schwartz, H.F. & Mohan, S.K. (2007). *Compendium of Onion and Garlic Diseases and Pests, Second Edition*. The American Phytopathological Society. https://doi.org/10.1094/9780890545003
Sharma, K., Rok Lee, Y., Park, S.W. & Nile, S.H. (2016). Importance of growth hormones and temperature for physiological regulation of dormancy and sprouting in onions. *Food Reviews International*, 32 (3), 233–255. https://doi.org/10.1080/87559129.2015.1058820
Sharma, P., Sharma, S.R., Dhall, R.K. & Mittal, T.C. (2020). Effect of γ-radiation on post-harvest storage life and quality of onion bulb under ambient condition. *Journal of Food Science and Technology*, 57 (7), 2534–2544. https://doi.org/10.1007/s13197-020-04290-z
Singh, P., Ahmad, F., Bisht, V., Thakkar, N. & Sajjad, S. (2021). Early detection of onion neck rot disease in Manitoba. *Canadian Journal of Plant Science*, 101 (6), 919–932
Sinha, R., Khot, L.R., Schroeder, B.K. & Sankaran, S. (2018). FAIMS based volatile fingerprinting for real-time postharvest storage infections detection in stored potatoes and onions. *Postharvest Biology and Technology*, 135, 83–92. https://doi.org/10.1016/j.postharvbio.2017.09.003
Steentjes, M.B.F., Scholten, O.E. & van Kan, J.A.L. (2021). Peeling the Onion: Towards a Better Understanding of Botrytis Diseases of Onion. *Phytopathology®*, 111 (3), 464–473. https://doi.org/10.1094/PHYTO-06-20-0258-IA
Subramani, R., Kumar, R., Prasad, P. & Aalbersberg, W. (2013). Cytotoxic and antibacterial substances against multi-drug resistant pathogens from marine sponge symbiont: Citrinin, a secondary metabolite of Penicillium sp. *Asian Pacific Journal of Tropical Biomedicine*, 3 (4), 291–296. https://doi.org/10.1016/S2221-1691(13)60065-9
Tanaka, K., Matsuo, Y. & Egashira, J. (1996). Controlled atmosphere storage for onions., 1996. 669–674
Thrane, U. (2014). Fusarium. I: Batt, C.A. & Tortorello, M.L. (red.) *Encyclopedia of Food Microbiology (Second Edition)*. Oxford: Academic Press. 76–81. https://doi.org/10.1016/B978-0-12-384730-0.00141-5

Tichelaar, G.M. (1967). Studies on the biology ofBotrytis allii onAllium cep A. *Netherlands Journal of Plant Pathology*, 73 (5), 157–160. https://doi.org/10.1007/BF02000455

UNECE (2019). UNECE Standard FFV-25 concerning the marketing and commercial quality control of onions. UNITED NATIONS New York and Geneva. https://unece.org/fileadmin/DAM/trade/agr/standard/fresh/FFV-Std/English/25_Onions.pdf [2021-09-12]

Vikram, A., Hamzehzarghani, H. & Kushalappa, A.C. (2005). Volatile metabolites from the headspace of onion bulbs inoculated with postharvest pathogens as a tool for disease discrimination. *Canadian Journal of Plant Pathology*, 27 (2), 194–203. https://doi.org/10.1080/07060660509507216

Wall, M.M. & Corgan, J.N. (1992). Relationship between Pyruvate Analysis and Flavor Perception for Onion Pungency Determination. *HortScience HortSci*, 27 (9), 1029–1030. https://doi.org/10.21273/HORTSCI.27.9.1029

Wang, A., Casadei, F., Johansen, A., Bukman, H. & Edelenbos, M. (2016). Emission of volatile organic compounds from healthy and diseased onions. *Acta Horticulturae*, (1144), 333–340. https://doi.org/10.17660/ActaHortic.2016.1144.49

Wang, A., Islam, Md.N., Johansen, A., Haapalainen, M., Latvala, S. & Edelenbos, M. (2019a). Pathogenic Fusarium oxysporum f. sp. cepae growing inside onion bulbs emits volatile organic compounds that correlate with the extent of infection. *Postharvest Biology and Technology*, 152, 19–28. https://doi.org/10.1016/j.postharvbio.2019.02.010

Wang, A., Luca, A. & Edelenbos, M. (2019b). Emission of volatile organic compounds from yellow onion (Allium cepa L.) bulbs during storage. *Journal of Food Science and Technology*, 56 (6), 2940–2948. https://doi.org/10.1007/s13197-019-03764-z

Wang, W., Thai, C., Li, C., Gitaitis, R., W Tollner, E. & Yoon, S.-C. (2009). Detection of Sour Skin Diseases in Vidalia Sweet Onions Using Near-infrared Hyperspectral Imaging. *Proceedings of 2009 Reno, Nevada, June 21 - June 24, 2009*, St. Joseph, MI, 2009. St. Joseph, MI: ASABE. https://doi.org/10.13031/2013.28837

Wright, P.J. (1997). Effects of cultural practices at harvest on onion bulb quality and incidence of rots in storage. *New Zealand Journal of Crop and Horticultural Science*, 25 (4), 353–358. https://doi.org/10.1080/01140671.1997.9514026

Wright, P.J., Grant, D.G. & Triggs, C.M. (2001). Effects of onion (*Allium cepa*) plant maturity at harvest and method of topping on bulb quality and incidence of rots in storage. *New Zealand Journal of Crop and Horticultural Science*, 29 (2), 85–91. https://doi.org/10.1080/01140671.2001.9514166

Wright, P.J. & Triggs, C.M. (2005). Effects of curing, moisture, leaf removal, and artificial inoculation with soft-rotting bacteria on the incidence of bacterial soft rot of onion (Allium cepa) bulbs in storage. *Australasian Plant Pathology*, 34 (3), 355–359. https://doi.org/10.1071/AP05051

Wright, R.C., Lauritzen, J.I. & Whiteman, T.M. (1935). *Influence of storage temperature and humidity on keeping qualities of onions and onion sets*

Yasin, H.J. & Bufler, G. (2007). Dormancy and sprouting in onion (*Allium cepa* L.) bulbs. I. Changes in carbohydrate metabolism. *The Journal of Horticultural Science and Biotechnology*, 82 (1), 89–96. https://doi.org/10.1080/14620316.2007.11512203

Özer, N. & Köycü, N.D. (1998). Evaluation of seed treatments for controlling Aspergillus niger and Fusarium oxysporum on onion seed. *Phytopathologia Mediterranea*, 37 (1), 33–40