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Review article

Climate change impacts on sugarcane smut disease and its management

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Abstract

Importance of the work: Environmental factors play an important role in the development of sugarcane smut disease caused by a basidiomycete fungus, *Sporisorium scitamineum*.

Objectives: To discuss the impact of climate change on the development of sugarcane smut and the opportunity to develop a disease management system.

Materials & Methods: A literature search and review was carried out relating to environmental factors (especially temperature and relative humidity) that can affect the development of sugarcane smut disease, which is favored by hot and dry conditions. This was related to an increase in temperature as one of the indicators of global climate change that could enhance the spread and development of sugarcane smut worldwide.

Results: Smut disease has resulted from interactions among sugarcane as the host plant, the fungal pathogen and environmental factors favorable for disease development. A change of climate, typically indicated by an increase in temperature, could have a major influence on the incidence of the disease. In addition, the characteristics of fungal teliospores that can be dispersed easily by the wind would also improve its ability to spread and cause new infection. Therefore, the use of resistant varieties is the most appropriate control method for the disease. Furthermore, management of sugarcane trash could be considered to maintain the humidity of the soil making it less suitable for the survival of the fungus.

Main finding: Resistant sugarcane varieties could be introduced supported by good cultivation practices, including the efficient use of fertilizer and incorporating sugarcane trash to the soil and decomposer amendment, to develop an integrated management approach to control sugarcane smut disease.

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Introduction

The world's focus has been on climate change, which has serious consequences, poses a major threat to agricultural production, and is expected to continue evolving in the future (Hijioka et al., 2014). Some regions have already been experiencing the effects of climate change, such as rainfall variability (seasonal or year-round variability), rising minimum and maximum temperatures, frequent droughts and floods and tropical cyclones, which have a direct impact on decreasing agricultural production through physiological changes in crops (Chakraborty et al., 2000; Anton et al., 2012; Chandiposha, 2013; Afghan and Ijaz, 2015; Debela and Tola, 2018). Increases in the air temperature and atmospheric CO_2, fluctuations of extreme weather (either in frequency or intensity), including heavy rainfall that could cause flooding, as well as drought conditions can have major effects on the emergence of plant diseases and the resistance of host plants to pathogenic infection. For example, Chandiposha (2013) stated that an increase in temperature fluctuation increases the prevalence of weeds, diseases and insects on sugarcane plants. In addition, depending on the degree of water stress, yield losses in the range 50–70% can occur in both tropical and subtropical regions when moisture stress is combined with high temperature and low humidity (Ganesh et al., 2017).

A recent statistical analysis (Food and Agriculture Organization of the United Nations, 2022) indicated that the increase in greenhouse gases from the agriculture, forestry and fisheries sectors has nearly doubled over the past 50 yr and will continue to rise by 30% if there is no implementation of mitigation strategies to cut emissions. Extreme weather events (51.8%), drought (54.9%) and floods (3.5%) were the major climatic factors besides temperature and precipitation (Luiz-Silva and Oscar-Júnior, 2022). Furthermore, Afghan and Ijaz (2015) reported that the Southeast Asian region experienced an average temperature increase of 0.3–0.8°C during the last century, with this trend predicted to continue at 1.5–2.0°C by 2050. The trend of increasing global temperature reaching 1.11±0.13 °C will cause major changes to the ecology, including the spreading of plant diseases (World Meteorological Organization, 2022).

Sugarcane smut disease is one of the plant diseases highly affected by increased temperature (Bhuiyan et al., 2009a). The disease is caused by a basidiomycete fungus (*Sporisorium scitamineum*) that is one of the most important diseases in sugarcane worldwide, being first recorded in Natal, South Africa in 1877 and since then, it has spread to other sugarcane-growing countries, including West, Central, and East Africa, Indonesia, the Philippines, South and Central America, Brazil, India, China, Pakistan and Australia (Alfieri et al., 1979; Hoy et al., 1986; Braithwaite et al., 2004; Sundar et al., 2012; Wada et al., 2016; Luzaran et al., 2017; Tegene et al., 2021). Until early 2016, Papua New Guinea and Fiji were believed to be free of smut disease; however, in August 2016, smut disease was detected in Papua New Guinea (Tom et al., 2017). Accordingly, only Fiji has remained smut-free to this day (Bhuiyan et al., 2021).

The presence of smut disease has the potential to have a major impact on sugarcane production, both in terms of quantity and quality. Instead of growing normally, the infected sugarcane might become stunted and produce excessive side shoots, resulting in grass-like growth. When this symptom occurs, less healthy cane will be produced, with the subsequent yield loss varying, depending on the resistance of the sugarcane to smut fungus infection (Que et al., 2014). In susceptible varieties, the yield loss caused by smut disease could exceed 60% (Magarey et al., 2010). In China, it was reported that infected ratoon cane could reduce cane yield by 15–20% (Que et al., 2012; Xu et al., 2014). Hoy et al. (1986) found that a 1% increase in smut incidence resulted in a 0.6% decrease in yield, with the fungus affecting both the stalk yield and the sucrose content of the sugarcane.

Sugarcane smut disease is favored by dry and hot conditions, with disease incidence increasing in a temperature range of 30–35°C (Ganesh et al., 2017). Sugarcane smut disease can spread over long distances and is capable of withstanding hot and dry conditions for more than 6 mth (Bhuiyan et al., 2021), which results in much more rapid spread of the disease throughout sugarcane plantations. The increasing frequency of dry conditions caused by climate change can contribute to the spread of smut disease and its severity in sugarcane. Furthermore, the dry conditions could influences the survival of smut teliospores within the soil. Although wind is the primary mode of transmission for smut disease, the presence of teliospores in dry soil for an extended period may worsen disease infection because the teliospores of smut fungus can survive for more than 24 wk in dry soil; however, in saturated soil, the teliospores might only be able to survive for 4–12 wk (Hoy et al., 1993; Bhuiyan et al., 2009a). In addition, the teliospores could be a source of inoculum for the subsequent growing season, as well as the fungus persisting within plant materials in the cane field area.

This review article discusses the possible effects of climate change on the development of sugarcane smut disease, with a focus on tropical Indonesia and the opportunity to develop sugarcane smut disease management in response to inevitable climate change.

Effect of climate change on development of sugarcane smut disease

Sugarcane smut epidemics are multicomponent systems arising from the dynamic interactions of the pathogen, host plants and the physical environment (Magarey et al., 2004; Agrios, 2005; Sundravadana et al., 2011) constituting the so-called disease triangle concept, which highlights that three favorable factors must coexist to develop a disease problem. These three conditions are the existence of a pathogen, a susceptible host (plant) and suitable environmental conditions. The following sub-section discusses this triangle concept for smut disease in sugarcane with regard to climate change.

Pathogen of sugarcane smut disease

Sugarcane smut disease is caused by *S. scitamineum,* a basidiomycete fungus, with the fungus producing teliospores as the sexual and thick-walled resting spore of smut fungi, which can play a role in protecting the fungus from unfavorable environmental conditions (Agrios, 2005). Survival for more than 6 mth in dry and hot conditions has been reported and these air-borne teliospores serve as the primary source of inoculum (Bhuiyan et al., 2021) that can germinate and infect the host under favorable environmental conditions (Horton et al., 2005). *S. scitamineum* produces two haploid teliospore forms that complement one another (Croft and Braithwaite, 2006). When two complementary sporidia merge, a dikaryotic mycelium is produced, which then infects the meristematic tissue of the host by propagating systematically. During its development, the hypha infects sugarcane by penetrating the bud scales and infecting the meristem (Liu et al., 2017). Sundar et al. (2012) demonstrated the infection of sugarcane smut fungus was initiated with the formation of appressoria on the inner scale of the young buds and at the base of the emerging leaves following teliospore germination. Subsequently, the appressoria penetrated the bud meristematic tissue within 6–36 hr after teliospore deposition which then systematically colonized the apical meristem.

The primary infection is caused by soil-borne teliospores or the planting of diseased setts, while secondary infection is caused by air-borne fungal spores infecting a healthy crop that is already standing (Hoy et al., 1991a). Nkhabindze et al. (2022) reported that although there were morphological differences in isolates, the genetic variation among isolates for the Internal Transcribed Spacer (ITS) was very low.

Temperature and humidity are environmental factors that affect the development of sugarcane smut disease. A temperature of 30°C and a relative humidity of 65–70% are the optimal conditions for germination (Bhuiyan et al., 2009b; Mansoor et al., 2016). The survival of smut teliospores in the soil is affected by the soil moisture content; Abdou et al. (1990) discovered that in dry conditions, the germination rate of *S. scitamineum* may reach up to 70% after 200 d, whereas under moist conditions, the teliospores would germinate rapidly within 48 hr. The viability of teliospores of the smut fungus in saturated soil was only 4 wk (Hoy et al., 1993). Abdou et al. (1990) and Bhuiyan et al. (2009a) suggested that although teliospores may survive for a short period, they have a longer survival period in the remaining sugarcane stalks and in dry soil. Furthermore, Bhuiyan et al. (2009a) showed that teliospores would be able to survive for more than 24 wk under low soil moisture conditions but only for 12 wk when the moisture level increased to 30%.

Basically, sugarcane smut is a disease of meristematic tissues, with the pathogen propagating only in young, actively growing plant tissues and the formation of a whip-like structure at the plant tip is an obvious symptom of smut disease in sugarcane (Comstock, 2000). After 6–8 mth of infection, the whip can be found not only on the primary stalk but also on the side shoots (Croft and Braithwaite, 2006). The whip, which might reach a maximum length of 1.5 m, consists of smut teliospores enclosed in a thin, silvery, membranous sheath (Comstock, 2000). Initially, the whip was believed to be a modification of sugarcane inflorescence (Schaker et al., 2016). However, recent research has shown that the whip is not related to the flowering stage (as it was detected during the early vegetative phase) and the genes associated with the reproductive stage were not expressed during symptom formation (Glassop et al., 2014; Hidayah et al., 2021). Consequently, the whip is no longer thought to develop during the flowering stage; instead, it is considered a modification of the stalk (Marques et al., 2018).

Another factor contributing to the development of smut disease on sugarcane is the concentration of smut spores both within the soil and air, with high spore concentrations enhancing the possibility of infected cane buds (Bock, 1964). When the primary stem of the cane is infected by smut, there is an increased possibility that its tillers will suffer from smut incursion (Bock, 1964; Elston and Simmonds, 1988). Lee-Lovick (1978) suggested that the distribution of secondary infection of smut disease is highly influenced by tiller age, moisture, temperature and the number of smut spores.

Sugarcane plant as smut disease host

Simultaneous unfavorable conditions affect sugarcane plants in the field. For example, stress caused by abiotic factors, such as drought, high temperature and salinity, would change the plant's metabolic system, which involves oxidative stress and resistance to pathogen infection (Azevedo et al., 2011; Dossa et al., 2016). Sugarcane plants under stress, due to both biotic and abiotic factors, ultimately experience oxidative stress (Manimekalai et al., 2022), with heat severely affecting sugarcane growth, yield, quality and sugar content (Chohan, 2019). Physiologically, stressed plants are very susceptible to pathogen infection (Bashir et al., 2021). In addition, attention must be paid to the morphological properties of the bud scale during the vegetative growth phase of sugarcane, which is the entry point for pathogen infection (Hidayah et al., 2021). Consequently, one action to mitigate the effects of climate change is the development of cultivars with high temperature and low water availability resistance, as well as bud scale morphological characteristics that are resistant to *S. scitamineum* infection.

There are two types of sugarcane resistance to smut disease: external and internal (Elston and Simmonds, 1988; Heinze et al., 2001; Bhuiyan et al., 2013). External resistance occurs prior to the pathogen entering the plant tissue. This resistance derives from the plant's inherent structure, such as the shape of the bud, the presence of trichomes and the waxy layer on the sugarcane stem (Da Gloria et al., 1999; Łaźniewska et al., 2012; Serrano et al., 2014; Marques et al., 2018). Łaźniewska et al. (2012) discovered that resistant cultivars have more bud scales and a higher concentration of trichomes (leaf hairs) than susceptible cultivars. Their research revealed that SP70-1143 (a resistant cultivar) had 5.5 scales per bud, whereas NA56-79 (a susceptible cultivar) only had 4.4 scales per bud. In addition, the concentration of trichomes in the resistant variety might reach up to 316.6/mm^2, whereas the concentration in the susceptible variety might not even exceed 250/mm^2. In such circumstances, the presence of trichomes would prevent smut spores from colonizing sugarcane stalks. In addition, Łaźniewska et al. (2012) elaborated on certain trichome functions, which included their capacity to act as a physical barrier to prevent fungal spores from adhering to plant surfaces. They may also emit chemical compounds with antibacterial capabilities, which would limit the development of fungal infections and preserve leaf surface moisture, which is essential for spore germination. Waxy substances and cuticles are additional plant surface structures that can serve as plant pathogen barriers in addition to trichomes (Serrano et al., 2014). According to Łaźniewska et al. (2012), wax substrates, which cover the majority of plant surfaces, vary in chemical compounds and physical properties. These structures may be crucial not only for preventing pathogen adherence to plant surfaces, but also for preventing pathogen dispersal.

Chemical substances, such as lignin, phenols, phenylpropanoids and glycosyl-flavonoids, can contribute to a plant's external resistance to *S. scitamineum* infection (Waller, 1970; Dean, 1982; Da Gloria et al., 1999; Fontaniella et al., 2002; Millanes et al., 2005; Millanes et al., 2008). A study on the resistance mechanisms of two different characters of sugarcane genotypes to *S. scitamineum* infection showed an increase in the lignin level in a resistant sugarcane genotype to smut disease (Hidayah et al., 2021). This result reflected the plant's response to infection by the fungus *S. scitamineum*. The lignin can play a role by limiting the flow of any toxins or enzymes produced by pathogens so they cannot enter plant tissues or by blocking the transport of nutrients from plants to pathogens, so the pathogens cannot flourish and cause infections in plants. Loyd and Pillay (1980) suggested that the buds of a resistant variety produce higher amounts of teliospore germination inhibitors, such as flavonoid compounds, than did susceptible varieties. A study of three sugarcane varieties with varying levels of resistance to smut disease—var. Mayari 5514 (resistant), Jaronu 60-5 (mid-resistant), and Barbados 42231 (highly susceptible)—revealed a significant accumulation of soluble polysaccharides and glycoproteins in the Mayari and Jaronu varieties in response to teliospore challenge. In contrast, these chemicals were infrequently detected in the variety Barbados 42231 (Martinez et al., 2000). These results suggested that soluble polysaccharides and glycoproteins are chemical metabolites responsible for the resistance of some sugarcane varieties to smut fungus infection.

Internal resistance occurs within plant tissues after the pathogen has overcome the plant's outward defenses. As a defense mechanism against pathogens, plants produce chemical substances that protect them from the inside (Aitken et al., 2012). Lao et al. (2008) found that the mechanisms of sugarcane resistance to smut are complex, involving numerous defense genes and secondary metabolic pathways, including an accumulation of phenolic compounds, oxidative burst, ethylene and auxin pathways, the pathogenesis-related (PR) protein pathway, cellular development, signal transduction and other metabolisms. After 72 hr of smut spore inoculation, peroxidase (ScSs36) activity was greatly elevated in the M31/45 genotype (known for its resistance to smut) but not in the Ja60-5, which is a known susceptible genotype (Lao et al., 2008). There was also an increase in *phenylalanine ammonia-lyase* (PAL) activity and the concentration of six pathogenesis-related (PR) proteins, including the polyphenol oxides, *phenylalanine ammonia-lyase*, *peroxidase*, *esterase*, *chitinase*, and *1,3 glucanase*, that were significantly higher in sugarcane-resistant varieties than in susceptible varieties (Esh et al., 2014). Other research findings revealed that some resistant characteristics, such as hydroxycinnamic and syringic acids, *phenylalanine ammonia-lyase*, and *peroxidase* activities, were highly correlated with plant resistance to smut disease (de Armas et al., 2007). Sugarcane varieties resistant to *S. scitamineum* infection enhanced the production of hydroxycinnamic acids as a result of increasing *phenylalanine ammonia-lyase* (PAL). Furthermore, there was an increase in *peroxidase* activity that could strengthen plant cell walls to create a barrier to smut infection. On the other hand, in the susceptible variety, enhancement of hydroxybenzoic acid in cane plants was not followed by the release of antifungal metabolites (Santiago et al., 2008).

The level of resistance, regardless of the mechanisms, seems to be affected by heat. Noel et al. (2022) verified that increased temperature for a long period reduced the level of the resistance of *Brassica napus* against *Leptosphaeria maculans* (the causal pathogen of stem canker). However, the resistance level of sugarcane against smut fungus has not been validated yet. An example case was the BL variety of Indonesia, which is a favorite among sugarcane farmers and has been widely planted since 2003 (Personal communication). Growing the BL variety over a long period could cause the outbreak of smut disease. The variety used to be categorized as a moderately resistant variety; however, since 2016, it has been almost 80% affected by *S. sporisorium*. The reduction in the resistance level could be due to a change in pathogen population or a change in the plant response to the pathogen and may be a result of the increase in average temperature that has occurred in the last 8 yr due to climate change (Velasquez et al., 2018).

According to Rameshsundar et al. (2015), there was a positive correlation among the levels of total phenolics, reducing sugars and total free amino acids with the resistance levels of sugarcane against smut. The higher the content of phenolic compunds, the higher the levels of resistance. During global warming, the increased temperature could decrease the levels of phenolic content since higher temperature increases the rate of phenolic loss (Choulitoudi et al., 2021).

Environmental factors affecting sugarcane smut disease development

The third aspect of the disease triangle is an accessible environment for the growth of a pathogen (Klopfenstein et al., 2009), which is represented by climatic factors, such as temperature, rainfall, humidity, dew, radiation and wind speed (Rott et al., 2013). Increases in temperature, humidity and precipitation may promote the growth of plant diseases because humid vegetation conditions provide an ideal habitat for plant pathogens. Increases in the carbon content and air temperature are detrimental to the smut pathogen. It is estimated that increasing CO_2 levels will increase the growth of leaves, stems and roots and even the numbers of tillers and the plant biomass, as well as nutritional quality, which will automatically increase production (Vu et al., 2001). The increased number of nodes will increase the likelihood of smut spores infecting the plant, resulting in a higher incidence of infection. Additionally, the rise in CO_2 heightens crop competition with weeds, which are also experiencing enhanced growth. This also increases the probability of the infection developing within another host. Although a rise in CO_2 levels can stimulate plant development, a rise in air temperature will increase evapotranspiration, causing plants to lose more water and experience water stress (Coakley et al., 1995; Velasquez et al., 2018). Generally, plants under stress are more susceptible to pathogen infection (Bashir et al., 2021).

Environmental conditions, primarily the temperature, are responsible for the development of smut disease in the field (Hoy et al., 1991). Akalach and Touil (1996) revealed that the incidence of smut disease in sugarcane plants increased when the temperature was 30–35°C. In contrast, low temperature (22°C) increased the latent periods and reduced the production of sori (Hoy et al., 1991). A temperature in the range 30–31°C is optimal for both the germination and infection of *S. scitamineum* on sugarcane plants (Millanes et al., 2005; Rupiah, 2017). According to Matthieson (2007) and Zhao and Li (2015), the prevalence of smut increased in hot environments. In addition, a rise in temperature will boost the photosynthetic capability of C4 plants (Matsuoka et al., 2001) which could influence the resistance mechanisms of plants toward pathogen invasion (Yang and Luo, 2021).

Furthermore an increase in temperature could interfere with some sugarcane metabolic processes, such as altering the cytoskeleton, which would then impact the vesicular transport and the formation of cell walls (Parrotta et al., 2016). However, when exposed to hot temperatures, the lignin content in the rinds of young and older internodes of sugarcane thickened (Santos et al., 2015), suggesting that the plant would be more difficult to infect. All these responses to a rise in temperature increase the vulnerability of sugarcane to insect and pathogen attack, as well as making it less competitive with weeds (Patterson, 1995). Overall, these increase the susceptibility to smut fungus, one of the most devastating pathogens of sugarcane.

Certain diseases can spread due to erratic rainy-dry seasons (Velasquez et al., 2018). on numerous sugarcane farms, the incidence of smut increased and spread substantially as a result of a lengthy dry season, a change from irrigated to rainfed areas and the prolonged plantings of the same variety. Teliospores of the smut fungus survived for almost 6 mth in nearly dry soil, but just 3 mth when the soil moisture was in the range 20–30% (Bhuiyan et al., 2009a). In 2016, there was an outbreak of smut in several sugarcane locations in Java and Sulawesi. Even the BL cultivar, which was previously tolerant to plant infection by the disease, was nearly 80% affected (personal observation). This variety has been established in Java for more than two decades and is the most favored sugarcane variety among sugarcane growers in Indonesia and especially on Java Island because it very adaptive and has high productivity, as well as a high sugar content if harvested at the right time (personal communication). According to Rott et al. (2013), sugarcane resistance to smut disease has remained nearly constant over several decades. However, long-term planting of a single sugarcane variety will result in new disease issues (Magarey et al., 2011). The use of the BL variety in Indonesia provides a useful of this issue. Since 2003, the BL variety has been the preferred variety among sugarcane farmers and has been widely planted. However, it appears that both climate change and pathogenic variation of *S. scitamineum* might influence the breakdown of the resistance of the BL variety to sugarcane smut.

Strategy for sugarcane smut disease management

Mitigation strategies to anticipate disease outbreaks related to climate change include: 1) the development of resistant or tolerant varieties to biotic and abiotic factors; 2) the enhancement of cultural practices and the efficient use of fertilizers; and 3) the introduction of decomposer or endophytic antagonistic fungi to sugarcane trash.

During climate change, unpredictable and extreme weather, such as drought and excessive rainfall, induce abiotic stress in sugarcane plants. The development of such resistant types could support sugarcane in surviving and thriving in these precarious conditions. Currently, sugarcane fields are established primarily in rain-fed areas without irrigation. In a global warming scenario, an increase in CO_2 could stimulate plant growth, but an increase in air temperature would increase evapotranspiration, leading to greater water loss by plants and an increase in water stress (Velasquez et al., 2018). These conditions prompted Indonesian scientists to produce the drought-resistant, transgenic sugarcane variety NXI-4T, which was launched in 2013 and followed by the release of many more types (Sugiharto, 2017). The variety is descended from BL, into which a beta gene cloned from the bacterium *Rhizobium meliloti* was added. The cultivars should be evaluated for resistance to infections that are anticipated to proliferate due to climate change.

According to Biggs et al. (2013), climate change will exacerbate the loss of nitrogen in the future. The efficient application of fertilizer could help prevent nitrogen loss by providing organic matter and returning sugarcane waste to the soil. Historically, sugarcane farmers have burnt their waste, which contributes to global warming since it emits smoke particles, CO_2 and other noxious substances. Returning sugarcane waste to the soil enhances the land's physical, chemical and biological properties, retains water and decreases evaporation. Nonetheless, it is asserted that a rise in temperature and CO_2 concentration might slow down the decomposition process (Amani et al., 2019). A decomposer, such as *Trichoderma* spp., could assist in accelerating the process as they are well-known as antagonists and are capable decomposers (Sharma et al., 2012). Cui et al. (2020) discovered that an endophytic bacteria isolated from sugarcane leaves, *Burkholderia gladioli*, generated antifungal toxoflavin against *S. scitamineum*. This bacterium could serve as a biocontrol agent against the smut fungus. Better smut management, including sanitation and the application of fungicide, could limit the spread and incidence of smut. Finally, monitoring weather fluctuations on a regular basis in collaboration with a climate station could aid in predicting the water requirement balance for sugarcane growth.

Future research

The use of resistant varieties is the most appropriate control for sugarcane smut. For further research work, there are some interesting areas that could be considered to mitigate smut outbreak under climate change:

1. Progressing a breeding program harnessing recent advances in biotechnology including molecular aspects; for example by using the genome editing technique to omit susceptible genes in sugarcane genotypes and the development of resistance markers to sugarcane smut.

2. Development of sugarcane varieties resistant to climate change; for example resistance to drought conditions.

3. Development of sugarcane varieties with hard bud scales to protect against pathogen infection.

4. Development of molecular markers to determine genetic diversity, particularly for biochemistry characters related to sugarcane smut pathogen interaction-related enzymes or other secondary metabolites. This marker could assist plant breeders to screen potential parents.

5. Improving cultivation system by applying silicon fertilizer to enhance the sugarcane plant immune system and returning sugarcane plant residues together with the addition of microbial antagonists to increase soil moisture. These conditions could promote the growth and development of antagonists and yet reduce the pathogen virulence and inoculum.

6. Study on interactions between plant trichomes as a part of the plant defense system with microbial (especially fungal) infection and survival.

Conflict of Interest

The authors declare that there are no conflicts of interest.

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