TATIANE CRISTINA BARBOSA CÂNDIDO

BIOESTIMULANTES E VOLÁTEIS DE PLANTAS COMO FERRAMENTAS PARA O MANEJO DE *Dalbulus maidis* (DELONG & WOLCOTT) (HEMIPTERA: CICADELLIDAE) EM MILHO

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Tese apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós Graduação em Entomologia, área de concentração em Entomologia, para a obtenção do título de Doutor.

Profa. Dra. Maria Fernanda Gomes Villalba Peñaflor
Orientadora

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BIOSTIMULANTS AND PLANT VOLATILES AS TOOLS FOR THE MANAGEMENT OF *Dalbulus maidis* (DELONG & WOLCOTT) (HEMIPTERA: CICADELLIDAE) IN MAIZE

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DEDICATÓRIA

Ao meu filho Murilo, a fonte da minha resiliência e força diária para superar obstáculos e buscar sempre me tornar uma pessoa melhor.

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RESUMO

A crescente demanda agrícola intensificou o uso de produtos fitossanitários, cujo emprego excessivo e inadequado tem causado impactos significativos nos ecossistemas. Nesse contexto, torna-se essencial desenvolver sistemas produtivos mais sustentáveis, especialmente em culturas como o milho (*Zea mays* L.), amplamente afetado pela cigarrinha-do-milho, *Dalbulus maidis* (DeLong & Wolcott, 1923) (Hemiptera: Cicadellidae), uma das principais pragas dessa cultura. Diante desse cenário, a presente tese buscou investigar a aplicação e a eficácia de diferentes bioinsumos como estratégias de manejo para *D. maidis*. Neste estudo, avaliamos os efeitos do silício (Si) e de substâncias húmicas (SH), aplicados individualmente ou em combinação, sobre o crescimento das plantas, colonização e estabelecimento de *D. maidis*, por meio de análises comportamentais e biológicas, além da avaliação de mecanismos de defesa das plantas sob condições controladas. Os bioestimulantes não influenciaram o crescimento da parte aérea, embora as SH isoladas tenham promovido o desenvolvimento radicular — efeito que foi suprimido quando combinadas com Si. Os tratamentos com Si e Si+SH reduziram a aceitação da planta hospedeira para oviposição, sem afetar negativamente os parâmetros biológicos do inseto. Particularmente o tratamento Si+SH acelerou o desenvolvimento do primeiro ínstar ninfal da cigarrinha na planta de milho. Embora o tratamento com Si tenha promovido um aumento discreto na resistência da planta de milho à cigarrinha, este não está associado ao aumento dos níveis de compostos fenólicos totais. O Si, isoladamente ou combinado com SH, apresentou efeito protetor contra o estresse oxidativo induzido pela praga, reduzindo as atividades das enzimas superóxido dismutase (SOD) e catalase (CAT). Também foram avaliados os efeitos dos compostos orgânicos voláteis (COVs) mirceno, linalol, salicilato de metila (MeSA) e jasmonato de metila (MeJA) sobre a preferência de oviposição de *D. maidis*. Em bioensaios com chance de escolha, o mirceno a 20 ng μL^{-1} reduziu significativamente a oviposição, enquanto MeSA a 2 ng μL^{-1}, mirceno a 200 ng μL^{-1} e linalol a 200 ng μL^{-1} aumentaram a quantidade de ovos depositados. O MeJA, por sua vez, não influenciou o comportamento de oviposição em nenhuma concentração testada. Esses resultados demonstram respostas comportamentais dose-dependentes da praga a VOCs específicos, com o mirceno atuando como repelente em dose moderada, enquantoMeSA, mirceno (em alta concentração) e linalol atuaram como atrativos a *D. maidis*. Em conjunto, os achados destacam o potencial de bioestimulantes e dos COVs como ferramentas promissoras para o manejo integrado da cigarrinha-do-milho, oferecendo alternativas sustentáveis capazes de modular o comportamento de oviposição de *D. maidis*.

Palavras-chave: Silício; Substâncias Húmicas; semioquímicos; cigarrinha-do-milho; defesas das plantas; respostas olfativas.

ABSTRACT

The growing agricultural demand has intensified the use of phytosanitary products, whose excessive and improper application has caused significant impacts on ecosystems. In this context, it becomes essential to develop more sustainable production systems, especially in crops such as maize (*Zea mays L.*), which is heavily affected by the corn leafhopper, *Dalbulus maidis* (DeLong & Wolcott, 1923) (Hemiptera: Cicadellidae), one of the main pests of this crop. Given this scenario, the present dissertation aimed to investigate the application and effectiveness of different bioinputs as management strategies for *D. maidis*. In this study, we evaluated the effects of silicon (Si) and humic substances (HS), applied individually or in combination, on plant growth, colonization, and establishment of *D. maidis* through behavioral and biological analyses, as well as the assessment of plant defense mechanisms under controlled conditions. The biostimulants did not influence shoot growth, although HS alone promoted root development—an effect that was suppressed when combined with Si. Treatments with Si and Si+HS reduced host plant acceptance for oviposition, without negatively affecting the insect's biological parameters. Notably, the Si+HS treatment accelerated the development of the first nymphal instar of the leafhopper on maize plants. Although Si treatment slightly enhanced maize resistance to the pest, this effect was not associated with increased levels of total phenolic compounds. Si, whether applied alone or in combination with HS, exhibited a protective effect against pest-induced oxidative stress by reducing the activities of superoxide dismutase (SOD) and catalase (CAT). We also evaluated the effects of the volatile organic compounds (VOCs) myrcene, linalool, methyl salicylate (MeSA), and methyl jasmonate (MeJA) on oviposition preference of *D. maidis*. In choice bioassays, myrcene at 20 ng μL^{-1} significantly reduced oviposition, while MeSA at 2 ng μL^{-1}, myrcene at 200 ng μL^{-1}, and linalool at 200 ng μL^{-1} increased the number of eggs laid. MeJA, however, did not influence oviposition behavior at any of the tested concentrations. These results demonstrate dose-dependent behavioral responses of the pest to specific VOCs, with myrcene acting as a repellent at moderate doses, while MeSA, high-dose myrcene, and linalool acted as attractants to *D. maidis*. Altogether, the findings highlight the potential of biostimulants and VOCs as promising tools for the integrated management of the corn leafhopper, offering sustainable alternatives capable of modulating the oviposition behavior of *D. maidis*.

Key words: Silicon; Humic Substances; semiochemicals; corn leafhopper; plant defenses; olfactory responses.

INDICADORES DE IMPACTO

Os resultados desta pesquisa evidenciam o potencial de bioinsumos e compostos orgânicos voláteis de plantas como ferramentas inovadoras para o manejo da cigarrinha-do-milho, *Dalbulus maidis*, uma das principais pragas da cultura do milho (*Zea mays* L.) no Brasil. Diante do aumento da demanda agrícola e da intensificação do uso de produtos fitossanitários, que frequentemente resultam em impactos ambientais e riscos à sustentabilidade dos agroecossistemas, o estudo buscou avaliar estratégias alternativas baseadas na indução de defesas vegetais e na modulação do comportamento do inseto. Os experimentos demonstraram que a aplicação de silício (Si) e de substâncias húmicas (SH), isoladamente ou em combinação, não promoveu alterações significativas no crescimento da parte aérea das plantas de milho, embora as SH isoladas tenham estimulado o desenvolvimento do sistema radicular, sugerindo potencial contribuição para o fortalecimento fisiológico das plantas. Observou-se também que os tratamentos contendo Si reduziram a aceitação da planta hospedeira para oviposição de *D. maidis*, indicando que esse elemento pode atuar como um fator modulador da interação inseto-planta. Além disso, o Si, aplicado isoladamente ou em associação com SH, apresentou efeito protetor contra o estresse oxidativo induzido pela herbivoria, evidenciado pela redução da atividade das enzimas superóxido dismutase (SOD) e catalase (CAT), sugerindo um possível papel desse elemento na mitigação de danos fisiológicos causados pela praga. Paralelamente, a avaliação do papel de compostos orgânicos voláteis (COVs) revelou respostas comportamentais dose-dependentes de *D. maidis*, destacando o mirceno na concentração de 20 ng μL^{-1} como potencial repelente ao reduzir significativamente a oviposição do inseto, enquanto o salicilato de metila (MeSA), o linalol e o mirceno em concentrações mais elevadas atuaram como compostos atrativos. Esses achados demonstram que determinados voláteis vegetais podem atuar como mediadores químicos capazes de influenciar a seleção do hospedeiro pela praga, abrindo novas perspectivas para o desenvolvimento de estratégias baseadas na manipulação do comportamento de insetos. Em conjunto, os resultados reforçam a importância da compreensão das interações planta–inseto e da utilização de bioinsumos como alternativas sustentáveis no manejo integrado de pragas (MIP), contribuindo para a redução do uso de inseticidas químicos e para o fortalecimento de sistemas agrícolas mais resilientes. Do ponto de vista tecnológico e econômico, a pesquisa fornece bases científicas para o desenvolvimento de novas estratégias de manejo aplicáveis à cultura do milho, podendo beneficiar produtores rurais, técnicos agrícolas e o setor do agronegócio em regiões produtoras. Os impactos também se inserem nas áreas temáticas da Política Nacional de Extensão em “Tecnologia e Produção”, “Meio

Ambiente" e "Educação", ao promover inovação tecnológica e práticas agrícolas mais sustentáveis. Ademais, o estudo está alinhado aos Objetivos de Desenvolvimento Sustentável (ODS) da Organização das Nações Unidas, especialmente o ODS 2 (Fome Zero e Agricultura Sustentável), o ODS 12 (Consumo e Produção Responsáveis) e o ODS 15 (Vida Terrestre), ao contribuir para o desenvolvimento de soluções científicas voltadas à sustentabilidade da produção agrícola e à conservação dos ecossistemas.

IMPACT INDICATORS

The results of this research highlight the potential of bioinputs and plant volatile organic compounds as innovative tools for the management of the corn leafhopper, *Dalbulus maidis*, one of the main pests of maize (*Zea mays* L.) in Brazil. In view of the increasing agricultural demand and the intensification of the use of phytosanitary products, which often result in environmental impacts and risks to the sustainability of agroecosystems, the study sought to evaluate alternative strategies based on the induction of plant defenses and the modulation of insect behavior. The experiments demonstrated that the application of silicon (Si) and humic substances (HS), either individually or in combination, did not promote significant changes in the shoot growth of maize plants, although HS applied alone stimulated root system development, suggesting a potential contribution to plant physiological strengthening. It was also observed that treatments containing Si reduced host plant acceptance for oviposition by *D. maidis*, indicating that this element may act as a modulating factor in the insect–plant interaction. In addition, Si applied alone or in combination with HS showed a protective effect against oxidative stress induced by herbivory, evidenced by the reduction in the activity of the enzymes superoxide dismutase (SOD) and catalase (CAT), suggesting a possible role of this element in mitigating physiological damage caused by the pest. Furthermore, the evaluation of the role of plant volatile organic compounds (VOCs) revealed dose-dependent behavioral responses of *D. maidis*, highlighting myrcene at the concentration of 20 ng μL^{-1} as a potential repellent by significantly reducing insect oviposition, whereas methyl salicylate (MeSA), linalool, and myrcene at higher concentrations acted as attractant compounds. These findings demonstrate that specific plant volatiles can function as chemical mediators capable of influencing host selection by the pest, opening new perspectives for the development of strategies based on the manipulation of insect behavior. Overall, the results reinforce the importance of understanding plant–insect interactions and the use of bioinputs as sustainable alternatives in integrated pest management (IPM), contributing to the reduction of chemical insecticide use and to the strengthening of more resilient agricultural systems. From a technological and economic perspective, this research provides scientific support for the development of new management strategies applicable to maize crops, potentially benefiting farmers, agricultural technicians, and the agribusiness sector in producing regions. The impacts of this study are also aligned with the thematic areas of the National Extension Policy, particularly “Technology and Production,” “Environment,” and “Education,” by promoting technological innovation and more sustainable agricultural practices. Moreover, the study is

aligned with the United Nations Sustainable Development Goals (SDGs), especially SDG 2 (Zero Hunger and Sustainable Agriculture), SDG 12 (Responsible Consumption and Production), and SDG 15 (Life on Land), as it contributes to the development of scientific solutions aimed at sustainable agricultural production and ecosystem conservation.

SUMÁRIO

PRIMEIRA PARTE

1 INTRODUÇÃO GERAL

A alta demanda agrícola levou ao uso intensivo de diversos produtos fitossanitários para o controle de plantas daninhas e pragas. Entretanto, o emprego intensivo e inadequado desses produtos acarreta diversos impactos nos ecossistemas adjacentes às áreas de cultivo, incluindo a degradação do solo, a poluição ambiental, a redução de populações de insetos benéficos — inclusive inimigos naturais das pragas — e efeitos adversos à saúde humana (Tahat et al., 2020). Diante desse cenário, a principal necessidade atual do setor agrícola é estabelecer um sistema produtivo e sustentável, capaz de garantir continuidade na produção e reduzir os impactos sobre o meio ambiente. Entre as práticas agrícolas adotadas em sistemas de cultivo mais sustentáveis destaca-se o Manejo Integrado de Pragas (MIP), que combina diferentes estratégias para reduzir ou substituir o uso de inseticidas sintéticos, por meio do monitoramento contínuo, do uso de limiares de ação, da integração de táticas de controle e de ajustes no agroecossistema (Muhie, 2022).

A utilização de bioinsumos integrada ao MIP contribui para manter a produtividade, melhorar a qualidade do solo e reduzir os impactos ambientais (Barbosa et al., 2025). Conforme a Lei Nacional de Bioinsumos (Lei nº 15.070/2024), esses produtos e tecnologias têm origem biológica — vegetal, animal, microbiana ou mineral — e são utilizados para favorecer o desenvolvimento das plantas e auxiliar no controle de pragas e doenças (BRASIL, 2024). Assim, os bioinsumos também englobam produtos resultantes de processos biotecnológicos, como biofertilizantes, condicionadores de solo, bioestimulantes, semioquímicos, metabólitos, macromoléculas e agentes de controle biológico (Barbosa et al., 2025).

Entre essa classe de produtos agrícolas destacam-se os bioestimulantes, substâncias ou microrganismos capazes de favorecer a absorção de nutrientes pelas plantas e aumentar sua tolerância a estresses abióticos (Du Jardin, 2015). Além disso, os bioestimulantes podem intensificar ou induzir as defesas das plantas, elevando sua resistência a pragas (Pereira, 2021), em parte por meio do efeito *priming*, que promove a ativação antecipada dos mecanismos de defesa, resultando em respostas mais rápidas e eficientes a estresses bióticos e abióticos, com menor custo energético para a planta (Nephali et al., 2020).

Outra classe de produtos agrícolas que merece destaque são os semioquímicos, compostos capazes de modular o comportamento dos insetos (Shashank, 2024). Os semioquímicos produzidos pelas plantas podem ser classificados em diferentes categorias, entre as quais se destacam os hormônios vegetais, os aleloquímicos, os fitoquímicos e os exsudatos radiculares (Serdo, 2024). Os aleloquímicos vegetais, por sua vez, são metabólitos secundários envolvidos na defesa contra herbívoros; essas substâncias químicas liberadas pelas plantas interferem no crescimento, desenvolvimento ou comportamento de outros organismos e desempenham papel essencial na comunicação intraespecífica (Tlak Gajger & Dar, 2021; Arora, Husain, Prasad, 2024). Os fitohormônios constituem componentes essenciais das vias de resposta ao estresse nas plantas, desempenhando papel central na regulação das defesas vegetais, modulando os compostos de defesa diante do ataque de insetos herbívoros e alguns compostos orgânicos voláteis COVs (Serdo, 2024).

O milho (*Zea mays* L.), pertencente à família Poaceae, é uma das principais *commodities* agrícolas do Brasil, que se mantém em posição de destaque no cenário mundial, ocupando o terceiro lugar no ranking global de produção, com estimativa de aproximadamente 115 milhões de toneladas em 2024 (IBGE, 2025). Devido ao elevado volume de produção, o cultivo do milho em duas safras é uma prática comum, o que favorece o aumento da incidência de insetos herbívoros — especialmente da cigarrinha-do-milho, *Dalbulus maidis* (DeLong & Wolcott, 1923) (Hemiptera: Cicadellidae) — considerada uma das pragas mais problemáticas e de difícil controle na cultura (Oliveira & Frizzas, 2022).

A cigarrinha-do-milho é um inseto sugador que se alimenta do floema das plantas (Davis, 1966; Todd, Madden & Nault, 1991). Seu ciclo de vida dura cerca de 25 a 30 dias, e as fêmeas depositam os ovos de forma endofítica na nervura central ou nas lâminas foliares (Waquil et al., 1999). Tanto a alimentação quanto a oviposição provocam danos significativos às plantas, especialmente pela redução de biomassa (Virla, Coll Araoz & Luft, 2021). Além disso, essa praga transmite fitopatógenos responsáveis pelos enfezamentos e pela virose da risca. Os enfezamentos são causados por molicutes: o espiroplasma (*Spiroplasma kunkelii*) provoca o enfezamento pálido, enquanto o fitoplasma (*maize bushy stunt phytoplasma*) causa o enfezamento vermelho (Avila et al., 2021). Ambos resultam em sérios prejuízos às plantas, como encurtamento dos entrenós, redução da altura, diminuição do tamanho das espigas e falhas na granação. O enfezamento pálido também provoca estrias cloróticas paralelas às nervuras, enquanto o enfezamento vermelho leva ao avermelhamento e à seca das folhas, iniciando pelas bordas em direção ao centro (Avila et al., 2021). A virose da risca (*Maize rayado*

fino virus – MRFV), por sua vez, causa pontuações cloróticas que podem evoluir para riscas ao longo das nervuras, além de reduzir o tamanho das plantas, das espigas e dos grãos (Avila et al., 2021).

O sistema agrícola envolvendo o milho e a cigarrinha-do-milho insere-se em um cenário de uso intensivo de produtos fitossanitários para o controle de pragas. Estudos relatam gastos elevados com inseticidas — muitas vezes pouco eficazes — no manejo dessa praga, concentrando-se em poucas classes químicas, o que favorece o desenvolvimento de resistência do inseto (Moritz et al., 2025). Já foram observados casos de redução da suscetibilidade de *D. maidis* a piretroides e neonicotinoides no Brasil (Machado et al., 2024). Além disso, há registros de limitações na eficiência de microrganismos entomopatogênicos para seu controle, devido à baixa adesão dos conídios, atribuída à camada proteico-lipídica dos brocossomas e ao comportamento de autolimpeza do inseto (Lopes, Faria & Oliveira, 2025).

Diante desse cenário, torna-se evidente a necessidade de desenvolver e incorporar novas táticas ao Manejo Integrado de Pragas (MIP) para o controle da cigarrinha-do-milho, visando reduzir a dependência de inseticidas sintéticos. Assim, a presente tese teve como objetivo investigar a aplicação e a eficácia de diferentes bioinsumos como estratégias de manejo para *D. maidis* em plantas de milho. Para isso, foram conduzidos bioensaios destinados a avaliar a biologia e o comportamento do inseto, bem como os mecanismos de defesa química das plantas, considerando a aplicação combinada de dois bioestimulantes e da utilização de semioquímicos sintéticos. Espera-se que os resultados obtidos contribuam para aprimorar as táticas de controle dessa praga e para o avanço de uma agricultura mais sustentável.

2 REFERENCIAL TEÓRICO

2.1 Bioinsumos no controle de pragas

2.1.1 Substâncias Húmicas

As substâncias húmicas (SH) — constituídas por huminas, ácidos húmicos e ácidos fúlvicos — são componentes naturais originados da decomposição química e biológica da matéria orgânica (Trevisan et al., 2010). Além de promoverem o crescimento e a produtividade das plantas, também atuam como indutoras de defesas, desempenhando papel relevante na resistência vegetal (Pereira et al., 2021). Matérias orgânicas no geral, incluindo as SH, promovem aproximadamente 75% de controle de doenças fúngicas e 67% de controle de pragas (da Silva & Canellas, 2022). Quando aplicadas, as SH ativam respostas fisiológicas das vias de sinalização mediadas por fitormônios, como ácido abscísico, giberelinas e auxinas (Canellas et al., 2020). Além disso, estudos indicam que as SH modulam positivamente a sinalização do etileno, estimulam a síntese de ácido jasmônico (JA) e aumentam a expressão de genes relacionados à via do JA — fundamental para a resistência a estresses bióticos (da Silva et al., 2023).

A aplicação de SH estimula a atividade e a expressão da enzima fenilalanina (tirosina) amônia-liase (PAL/TAL), promovendo alterações na via metabólica dos fenilpropanoides — compostos secundários derivados da fenilalanina que desempenham papel central nos mecanismos de defesa das plantas (Schiavon, 2010; da Silva et al., 2023; da Silva et al., 2025). A ativação dessa via metabólica resulta no aumento da biossíntese de compostos fenólicos, uma vez que os fenilpropanoides originam, por meio de seus intermediários, a maior parte dos fenóis presentes nos tecidos vegetais. Diversos estudos comprovam que a fertilização com SH eleva significativamente a produção de compostos fenólicos nas plantas (Conselvan et al., 2017; Gholami et al., 2018). Entre esses compostos destacam-se os ácidos hidroxicinâmicos — como o ácido clorogênico, o ácido ferúlico e o ácido p-cumárico — que já foram reportados como redutores importantes da alimentação da cigarrinha-do-milho (Dowd & Vega, 1996).

As SH podem agir como potencializadoras de sinais aos estresses, que são mediados através da via de sinalização dos fitohormônios, marcadores de estresse e sinalização celular. Atuando assim, como um agente *priming,* que prepara a planta antes da ocorrência do estresse*,* atenuando seus efeitos (Canellas et al., 2020; da Silva et al., 2023).

2.1.2 Silício

Embora o silício (Si) seja considerado um elemento benéfico — e não essencial — para a maioria das plantas, sua aplicação proporciona inúmeros benefícios agronômicos. Diversos estudos demonstram que o Si pode estimular o crescimento e o desenvolvimento vegetal, aumentar a produtividade e mitigar os efeitos negativos decorrentes de estresses bióticos e abióticos (Debona et al., 2017). O efeito do silício depende diretamente da fisiologia de cada espécie vegetal, especialmente de sua capacidade de absorver, translocar e acumular esse elemento nos tecidos. De acordo com esse critério, as plantas podem ser classificadas quanto ao teor de Si acumulado na matéria seca em três categorias: espécies não acumuladoras (ou excludentes), que apresentam teor < 0,5%, como tomate e café; espécies intermediárias, com teor entre 0,5% e 1,0%, como cucurbitáceas e soja; e espécies acumuladoras, cujo teor é > 1,0%, como milho e arroz (Reis et al., 2007; Mitani-Ueno & Ma, 2020). Essa distinção é essencial, pois determina o potencial de resposta das plantas à suplementação com silício e influencia diretamente a magnitude dos benefícios relacionados ao crescimento, à mitigação de estresses bióticos e abióticos e à ativação de mecanismos de defesa contra insetos herbívoros.

O silício pode atuar na defesa das plantas contra insetos por meio de dois mecanismos principais: (i) barreiras físicas ou mecânicas e (ii) mecanismos químicos associados à ativação das vias metabólicas de defesa vegetal (Alhousari & Greger, 2018). As defesas físicas e mecânicas resultam da deposição de silício nos espaços intracelulares na cutícula das folhas, o que aumenta a rigidez, a dureza e a abrasividade dos tecidos vegetais (Bakhat et al., 2018). Além disso, a elevada concentração de silício nos tecidos foliares reduz a palatabilidade e a digestibilidade para insetos herbívoros, afetando negativamente parâmetros importantes do seu desempenho e comportamento, como alimentação, desenvolvimento e sobrevivência (Alhousari & Greger, 2018; Bakhat et al., 2018). Adicionalmente, a presença de Si pode interferir nos sistemas de desintoxicação dos insetos, dificultando a metabolização de compostos tóxicos, incluindo inseticidas, o que contribui para a redução de sua performance biológica (Wang et al., 2020).

A ativação de defesas químicas nas plantas suplementadas com silício ocorre por múltiplos mecanismos. O Si é capaz de estimular vias de sinalização associadas à resistência contra herbívoros, incluindo as vias do ácido salicílico (AS), do ácido jasmônico (AJ) e do etileno (Bakhat et al., 2018; Verma et al., 2021; Lin et al., 2022). Além disso, a fertilização com Si promove o aumento da atividade de importantes enzimas relacionadas à defesa. Entre elas,

destaca-se a fenilalanina amônia-liase (PAL), cuja indução intensifica a síntese de compostos fenólicos (Verma et al., 2021). O Si também estimula enzimas do sistema antioxidante, como ascorbato peroxidase (APX), catalase (CAT), glutationa redutase (GR) e superóxido dismutase (SOD), contribuindo o aumento da tolerância das plantas ao estresse biótico (Verma et al., 2021). O silício também intensifica as defesas das plantas por meio do efeito *priming*, um processo que prepara previamente os mecanismos defensivos antes mesmo da ocorrência do estresse. Como resultado, quando a herbivoria acontece, a planta é capaz de ativar suas respostas de defesa de forma mais rápida, intensa e eficiente, reduzindo os danos ocasionados pelo inseto (Lin et al., 2022; Samal et al., 2024).

2.2 Semioquímicos no controle de pragas

2.2.1 Monoterpenos

Quando são expostas a condições adversas no ambiente, as plantas ativam uma série de mecanismos de defesa para mitigar os danos, entre os quais se destaca a síntese de metabólitos secundários (Kumar et al., 2023). Esses compostos orgânicos desempenham papel central na regulação das vias de sinalização de defesa, fortalecendo a resistência vegetal frente ao ataque de insetos herbívoros (Divekar et al., 2022).

Os metabólitos secundários são tradicionalmente classificados em quatro grandes grupos: terpenoides, fenólicos e compostos contendo nitrogênio ou enxofre (Divekar et al., 2022). De modo geral, os terpenos apresentam ampla atividade contra insetos, atuando como toxinas, repelentes alimentares ou interferindo negativamente no crescimento e desenvolvimento das pragas (Qasim et al., 2024).

Entre os terpenos, os monoterpenos destacam-se por sua relevância na defesa vegetal. Esses Compostos Orgânicos Voláteis (COVs) exercem diversos efeitos sobre os insetos, incluindo toxicidade direta, repelência, redução da alimentação e inibição do crescimento (Abdelgaleil et al., 2025). Além disso, muitos desses COVs contribuem para a resistência sistêmica adquirida, reforçando a capacidade da planta de responder de forma mais eficiente a estresses subsequentes (Qasim et al., 2024).

Os monoterpenos representam alternativas promissoras para o monitoramento e o controle de pragas agrícolas, uma vez que exercem múltiplos efeitos sobre diferentes grupos de insetos. Esses compostos apresentam ampla diversidade de atividades biológicas, incluindo toxicidade, repelência, inibição da alimentação e interferência no crescimento e

desenvolvimento dos herbívoros (Abdelgaleil et al., 2025). Devido ao seu modo de ação multifacetado, os monoterpenos dificultam o surgimento de resistência nas populações de insetos-praga, ampliando seu potencial de aplicação em estratégias sustentáveis de manejo (Abdelgaleil et al., 2025).

Além disso, alguns monoterpenos têm relevância direta em sistemas agrícolas específicos. No milho, por exemplo, compostos como linalol e mirceno são naturalmente emitidos pelos tecidos vegetais e desempenham funções defensivas, podendo ser explorados como ferramentas aplicadas em estratégias sustentáveis de manejo de pragas (Yactayo-Chang et al., 2024).

2.2.2 Compostos Orgânicos Voláteis (COVs) com ação hormonal

As plantas sintetizam diversos hormônios vegetais que são essenciais para lidar com estresses abióticos e bióticos, entre eles estão o ácido jasmônico, ácido salicílico, giberelinas, citocininas, ácido abscísico, etileno e auxina (Hu et al., 2024). Alguns fitohormônios desempenham papéis cruciais na regulação e ativação das vias de defesas das plantas frente ao ataque de insetos herbívoros (Serdo, 2024).

Entre eles destaca-se o papel de dois hormônios vegetais, o ácido jasmônico (AJ), ácido salicílico (AS). A sinalização mediada por JA constitui um eixo central na modulação das respostas defensivas das plantas frente à herbivoria (Hu et al., 2024). Uma das formas biologicamente ativas do ácido jasmônico (AJ) é o jasmonato de metila (MeJA), um composto orgânico volátil (COV) que atua como elicitor hormonal nas plantas, reconhecido por desencadear respostas de defesa por meio da ativação da via do jasmonato, promovendo a expressão de genes relacionados à resistência vegetal (Hu et al., 2024). Esse composto regula a atividade de enzimas associadas à defesa — incluindo enzimas antioxidantes — e estimula o acúmulo de metabólitos de defesa, como compostos fenólicos (Yu et al., 2019). Em função desses efeitos, o MeJA pode influenciar diretamente o comportamento e o desempenho de insetos herbívoros, constituindo um componente relevante na modulação das interações planta–inseto.

A sinalização mediada pelo ácido salicílico (AS) está associada à ativação da resistência sistêmica induzida em plantas (Filgueiras et al., 2019). As respostas defensivas também podem ocorrer por meio da produção de compostos químicos, como os fenólicos, que apresentam propriedades repelentes e tóxicas para diversos insetos herbívoros (Filgueiras et al., 2019). Uma

das formas biologicamente ativas do AS é o salicilato de metila (MeSA), um composto orgânico volátil (COV) que atua como elicitor hormonal, estimulando a expressão de genes de defesa e promovendo a emissão de voláteis associados à repelência, especialmente contra insetos sugadores (Erb, 2018). Além de impactar negativamente o desempenho dos herbívoros, o MeSA também pode modular seu comportamento — incluindo a oviposição — ao desencadear múltiplos mecanismos de defesa na planta hospedeira (Fang et al., 2025).

REFERÊNCIAS

Abdelgaleil, S. A. M., Gad, H. A., Ramadan, G. R. M., El-Bakry, A. M., & El-Sabrout, A. (2025). Monoterpenes for management of field crop insect pests. *Journal of Agricultural Science and Technology*, *25*(4), 769-784. DOI: 10.22034/jast.25.4.1

Alhousari, F., & Greger, M. (2018). Silicon and Mechanisms of Plant Resistance to Insect Pests. *Plants*, *7*(2), 33. DOI: https://doi.org/10.3390/plants7020033

Arora, S., Husain, T., & Prasad, S. M. (2024). Allelochemicals as biocontrol agents: Promising aspects, challenges and opportunities. *South African Journal of Botany*, *166*, 503-511. DOI: https://doi.org/10.1016/j.sajb.2024.01.029

Avila, C. J., de Oliveira, C. M., da Moreira, S. C., Bianco, R., & Tamai, M. A. (2021). A cigarrinha *Dalbulus maidis* e os enfezamentos do milho no Brasil.

Bakhat, H. F., Bibi, N., Zia, Z., Abbas, S., Hammad, H. M., Fahad, S., ... & Saeed, S. (2018). Silicon mitigates biotic stresses in crop plants: A review. *Crop Protection*, *104*, 21-34. DOI: https://doi.org/10.1016/j.cropro.2017.10.008

Barbosa, M. F., Sales, R. M. M., Galarza, F. A. D., Kruger, C. Q., Fávaro, L. C. D. L., & Quirino, B. F. (2025). Biological resources driving productivity: bioinputs for sustainable plant agriculture in Brazil. *Sustainable Microbiology*, *2*(3), qvaf011. DOI: https://doi.org/10.1093/sumbio/qvaf011

BRASIL. Lei n.15.070, de 23 DE DEZEMBRO de 2024. **Diário Oficial da União de 24/12/2024, p. 3, col. 2.** Brasília, DF: Presidência da República, 2024. **https://normas.leg.br/?urn=urn:lex:br:federal:lei:2024-12-23;15070** (27 november 2025, date last accessed).

Canellas, L.P., Canellas, N.O.A., da S. Irineu, L.E.S. *et al.* Plant chemical priming by humic acids. *Chem. Biol. Technol. Agric.* **7**, 12 (2020). DOI: https://doi.org/10.1186/s40538-020-00178-4

Conselvan, G. B., Pizzeghello, D., Francioso, O., et al. (2017). Biostimulant activity of humic substances extracted from leonardites. *Plant and Soil, 420*, 119–134. DOI: https://doi.org/10.1007/s11104-017-3373-z

da Silva, R. M., Olivares, F. L., Peres, L. E., Novotny, E. H., & Canellas, L. P. (2025). Humic substances promote the activity of enzymes related to plant resistance. *Agriculture*, *15*(15), 1688. DOI: **https://doi.org/10.3390/agriculture15151688**

da Silva, R.M., Canellas, N.A., Olivares, F.L. *et al.* Humic substances trigger plant immune responses. *Chem. Biol. Technol. Agric.* **10**, 123 (2023). DOI: https://doi.org/10.1186/s40538-023-00468-7

Davis, R. (1966). Biology of the leafhopper *Dalbulus maidis* at selected temperatures. DOI: **10.1093/jee/59.3.766**

Debona, D., Rodrigues, F. A., Rios, J. A., Nascimento, K. J. T., & Silva, L. C. (2014). The effect of silicon on antioxidant metabolism of wheat leaves infected by *Pyricularia oryzae*. *Plant Pathology, 63*(3), 581–589. DOI: **https://doi.org/10.1111/ppa.12119**

Divekar, P. A., Narayana, S., Divekar, B. A., Kumar, R., Gadratagi, B. G., Ray, A., Singh, A. K., Rani, V., Singh, V., Singh, A. K., Kumar, A., Singh, R. P., Meena, R. S., & Behera, T. K. (2022). Plant Secondary Metabolites as Defense Tools against Herbivores for Sustainable Crop Protection. *International Journal of Molecular Sciences*, *23*(5), 2690. DOI: https://doi.org/10.3390/ijms23052690

Dowd, P. F., & Vega, F. E. (1996). Enzymatic oxidation products of allelochemicals as a basis for resistance against insects: effects on the corn leafhopper *Dalbulus maidis*. *Natural Toxins*, *4*(2), 85-91. DOI: **https://doi.org/10.1002/19960402NT5**

Du Jardin, P. (2015). Plant biostimulants: Definition, concept, main categories and regulation. *Scientia Horticulturae, 196*, 3–14. DOI: https://doi.org/10.1016/j.scienta.2015.09.021

Erb, M. (2018). Volatiles as inducers and suppressors of plant defense and immunity—origins, specificity, perception and signaling. *Current opinion in plant biology*, *44*, 117-121. DOI: https://doi.org/10.1016/j.pbi.2018.03.008

Fang X, Xie Y, Yuan Y, Long Q, Zhang L, et al. 2025. The role of salicylic acid in plant defense responses against biotic stresses. *Plant Hormones* 1 (1). DOI: 10.48130/ph-0025-0003

Filgueiras, C. C., Martins, A. D., Pereira, R. V., & Willett, D. S. (2019). The Ecology of Salicylic Acid Signaling: Primary, Secondary and Tertiary Effects with Applications in Agriculture. International Journal of Molecular Sciences, 20(23), 5851. DOI: https://doi.org/10.3390/ijms20235851

Gholami, H., Saharkhiz, M. J., Fard, F. R., Ghani, A., & Nadaf, F. (2018). Humic acid and vermicompost increased bioactive components, antioxidant activity and herb yield of chicory (*Cichorium intybus* L.). *Biocatalysis and Agricultural Biotechnology, 14*, 286–292. DOI: https://doi.org/10.1016/j.bcab.2018.03.021

Hu, C., Li, Y. T., Liu, Y. X., Hao, G. F., & Yang, X. Q. (2024). Molecular interaction network of plant-herbivorous insects. *Advanced Agrochem*, *3*(1), 74-82. DOI: https://doi.org/10.1016/j.aac.2023.08.008

Kumar, S., Korra, T., Thakur, R., Arutselvan, R., Kashyap, A. S., Nehela, Y., ... & Keswani, C. (2023). Role of plant secondary metabolites in defence and transcriptional regulation in response to biotic stress. *Plant stress*, *8*, 100154. DOI: https://doi.org/10.1016/j.stress.2023.100154

Lin, Y., Lin, X., Ding, C., Xia, M., Xue, R., Sun, Z., ... & Song, Y. (2022). Priming of rice defense against a sap-sucking insect pest brown planthopper by silicon. *Journal of Pest Science*, *95*(3), 1371-1385. DOI: https://doi.org/10.1007/s10340-021-01462-4

Lopes, R. B., Faria, M., & Oliveira, C. M. (2025). Susceptibility of *Dalbulus maidis* to insect-pathogenic fungi: Unveiling the protective role of brochosomes and self-cleaning behavior. *Journal of Pest Science, 98*, 759–768. DOI: https://doi.org/10.1007/s10340-024-01823-9

M. Tahat, M., M. Alananbeh, K., A. Othman, Y., & I. Leskovar, D. (2020). Soil Health and Sustainable Agriculture. *Sustainability*, *12*(12), 4859. DOI: https://doi.org/10.3390/su12124859

Machado, E. P., Souza, E. V., Dias, G. S., Sacilotto, M. G., & Omoto, C. (2024). Is insecticide resistance a factor contributing to the increasing problems with *Dalbulus maidis* (Hemiptera: Cicadellidae) in Brazil?. *Pest Management Science*, *80*(10), 5120-5130. DOI: **https://doi.org/10.1002/ps.8237**

Mitani-Ueno, N., & Ma, J. F. (2020). Linking transport system of silicon with its accumulation in different plant species. *Soil Science and Plant Nutrition, 67*(1), 10–17. DOI: https://doi.org/10.1080/00380768.2020.1845972

Moritz, E. O., Plassa, W., Bordin, I., Bianco, R., & Telles, T. S. (2025). Dynamics of expenditure on insecticides in the management and control of corn leafhoppers (*Dalbulus maidis*). *Pest Management Science*, *81*(10), 7077-7089. DOI: **https://doi.org/10.1002/ps.70058**

Muhie, S. H. (2022). Novel approaches and practices to sustainable agriculture. *Journal of Agriculture and Food Research*, *10*, 100446. DOI: https://doi.org/10.1016/j.jafr.2022.100446

Nephali, L., Piater, L. A., Dubery, I. A., Patterson, V., Huyser, J., Burgess, K., & Tugizimana, F. (2020). Biostimulants for Plant Growth and Mitigation of Abiotic Stresses: A Metabolomics Perspective. *Metabolites*, *10*(12), 505. DOI: https://doi.org/10.3390/metabo10120505

Oliveira, C. M. D., & Frizzas, M. R. (2022). Eight decades of *Dalbulus maidis* (DeLong & Wolcott)(Hemiptera, Cicadellidae) in Brazil: what we know and what we need to know. *Neotropical Entomology*, *51*(1), 1-17. DOI: 10.1007/s13744-021-00932-9

Pereira, R. V., et al. (2021). The effects of biostimulants on induced plant defense. *Frontiers in Agronomy, 3*, 630596. DOI: https://doi.org/10.3389/fagro.2021.630596

Qasim, M., Islam, W., Rizwan, M., Hussain, D., Noman, A., Khan, K. A., ... & Han, X. (2024). Impact of plant monoterpenes on insect pest management and insect-associated microbes. *Heliyon*, *10*(20). DOI: 10.1016/j.heliyon.2024.e39120

REIS, T. H. P. et al. **O silício na nutrição e defesa de plantas**. Belo Horizonte: EPAMIG, 2007. 120p. – (EPAMIG. Boletim Técnico, 82).

Samal, I., Bhoi, T.K., Mahanta, D.K. *et al.* Establishing the Role of Silicon (Si) in Plant Resistance To Insects: A Bibliometric Approach. *Silicon* **16**, 2119–2128 (2024). DOI: https://doi.org/10.1007/s12633-023-02821-9

Schiavon, M., Ertani, A., Nardi, S., & Varani, G. (2010). High molecular size humic substances enhance phenylpropanoid metabolism in maize (*Zea mays* L.). *Journal of Chemical Ecology, 36*, 662–669. DOI: https://doi.org/10.1007/s10886-010-9790-6

Serdo D. F. 2024. Insects' perception and behavioral responses to plant semiochemicals. *PeerJ* ,12, e17735. DOI: https://doi.org/10.7717/peerj.17735

Shashank, D. U., Sujatha, G. S., Teja, K. S. S., Hema, A. P., Mishra, R., Abinaya, S., ... & Kumar, G. A. (2024). A comprehensive review of advances in semiochemical exploitation for insect pest management. *Journal of Advances in Biology & Biotechnology*, *27*(9), 845-863. DOI: https://doi.org/10.9734/jabb/2024/v27i91357

Silva, R. M. & Canellas L. P. (2022). Organic matter in the pest and plant disease control: A meta-analysis. *Chemical and Biological Technologies in Agriculture*, *9*(1), 70. DOI: https://doi.org/10.1186/s40538-022-00332-0

Silva, R. M., Peres, A. N., Peres, L. E., Olivares, F. L., Sangi, S., Canellas, N. A., ... & Canellas, L. P. (2023). Humic substances isolated from recycled biomass trigger jasmonic acid biosynthesis and signalling. *Plants*, *12*(17), 3148. DOI: **https://doi.org/10.3390/plants12173148**

Tlak Gajger, I., & Dar, S. A. (2021). Plant Allelochemicals as Sources of Insecticides. *Insects*, *12*(3), 189. DOI: https://doi.org/10.3390/insects12030189

Trevisan, S., Francioso, O., Quaggiotti, S., & Nardi, S. (2010). Atividade biológica de substâncias húmicas na interface planta-solo: de aspectos ambientais a fatores moleculares. *Plant Signaling & Behavior* ,*5* (6), 635–643. DOI: https://doi.org/10.4161/psb.5.6.11211

Verma, K. K., Song, X.-P., Tian, D.-D., Guo, D.-J., Chen, Z.-L., Zhong, C.-S., Nikpay, A., Singh, M., Rajput, V. D., Singh, R. K., Minkina, T., & Li, Y.-R. (2021). Influence of Silicon on Biocontrol Strategies to Manage Biotic Stress for Crop Protection, Performance, and Improvement. *Plants*, *10*(10), 2163. DOI: https://doi.org/10.3390/plants10102163

Virla, E. G., Coll Araoz M. V., Luft Albarracin E. (2021). Estimation of direct damage to maize seedlings by the corn leafhopper, *Dalbulus maidis* (Hemiptera: Cicadellidae), under different watering regimes. *Bulletin of entomological research*, *111*(4), 438-444. DOI: https://doi.org/10.1017/S0007485321000079

Wang, J., Xue, R., Ju, X., Yan, H., Gao, Z., Elzaki, M. E. A., … & Song, Y. (2020). Silicon-mediated multiple interactions: simultaneous induction of rice defense and inhibition of larval performance and insecticide tolerance of chilo suppressalis by sodium silicate. Ecology and Evolution, 10(11), 4816-4827. DOI: https://doi.org/10.1002/ece3.6235

Waquil, J. M., Viana, P. A., Cruz, I., & Santos, J. P. (1999). Aspectos da biologia da cigarrinha-do-milho, *Dalbulus maidis* (DeLong & Wolcott)(Hemiptera: Cicadellidae). *Anais da Sociedade Entomológica do Brasil*, *28*, 413-420. DOI: 10.1590/S0301-80591999000300005

Yu X, Zhang W, Zhang Y, Zhang X, Lang D, Zhang X. (2019) The roles of methyl jasmonate to stress in plants. *Functional Plant Biology* 46, 197–212. DOI: https://doi.org/10.1071/FP18106

SEGUNDA PARTE

Artigo 1- Combined use of the biostimulants Silicon and Humic Substances in the resistance of maize plants to the corn leafhopper *Dalbulus maidis*

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ABSTRACT

Maize (*Zea mays* L.) is one of the main agricultural crops in the Americas, and its productivity has been compromised by the corn leafhopper, *Dalbulus maidis* (DeLong & Wolcott, 1923) (Hemiptera: Cicadellidae), a highly relevant pest due to its efficiency in transmitting phytopathogens. The limited efficacy of chemical and biological control strategies highlights the need for sustainable management alternatives. In this study, we evaluated the effects of silicon (Si) and humic substances (HS), applied individually or in combination, on plant growth, colonization, and establishment of *D. maidis* through behavioral and biological analyses, as well as the assessment of plant defense mechanisms through the levels of total phenolic compounds and oxidative stress enzymes, under controlled conditions. The biostimulants did not influence shoot growth, although HS alone promoted root development—an effect suppressed when combined with Si. Treatments with Si and Si+HS reduced host acceptance for oviposition without negatively affecting the insect's biological parameters; however, Si+HS accelerated the molt from the first to the second instar. A moderate resistance effect was observed in Si-treated plants, which was not associated with total phenolic compound levels. Si, alone or combined with HS, exhibited a protective effect against pest-induced oxidative stress by reducing the activities of superoxide dismutase (SOD) and catalase (CAT) enzymes. These findings highlight the need for further research on the mechanisms underlying induced plant defenses, chemical interactions between the biostimulants, and potential adaptations of *D. maidis*, as well as the evaluation of these treatments under field conditions and in new combinations aimed at integrated pest management.

Keywords: Induced resistance; plant–insect interaction; oviposition behavior; plant defense mechanisms.

INTRODUCTION

Maize (*Zea mays* L.) is a monocotyledonous species of the Poaceae family and holds significant economic importance due to its broad versatility of use, including human consumption, formulation of animal feed and other livestock products, applications in high-technology industries, and biofuel production (Veljković et al., 2018; Erenstein et al., 2022; Poole, Donovan & Erenstein, 2021). The Americas concentrate some of the world's largest maize producers, notably the United States, Brazil, and Argentina (FAOSTAT, 2023). Brazil stands out among the leading global producers and exporters, ranking third worldwide, with an estimated production of approximately 115 million tons in 2024 (IBGE, 2025).

Several factors affect maize crops and compromise their productivity. In Brazil, the expansion of planting seasons — which allows maize to be grown almost year-round — contributes to population outbreaks of insect pests, among which the leafhopper *Dalbulus maidis* (DeLong & Wolcott, 1923) (Hemiptera: Cicadellidae), known as the corn leafhopper, is particularly important (Oliveira & Frizzas, 2022). This pest can cause different types of damage to maize plants, including direct injury to leaves resulting from sap feeding. However, the main economic impact is associated with its ability to transmit phytopathogens, especially microorganisms belonging to the mollicutes (class *Mollicutes*, kingdom *Bacteria*) and the *Maize Rayado Fino Virus* (MRFV) (Nault, 1990). Over the past 11 years, the impact caused by the corn leafhopper has intensified, becoming an important phytosanitary problem due to the transmission of the maize stunt complex (Oliveira & Frizzas, 2022).

The spiroplasma *Spiroplasma kunkelii* and the phytoplasma known as *maize bushy stunt phytoplasma* are associated with pale stunt and red stunt diseases of maize, respectively. In general, affected plants exhibit reduced growth and development, shortened internodes, sprouting from leaf axils, reddish coloration of stems and leaves, chlorosis, as well as proliferation and malformation of ears, which often become unproductive. Additionally, stem weakening is observed, which favors fungal infection and increases susceptibility to lodging (Whitcomb et al., 1986; Nault, 1980). Plants infected by the maize rayado fino virus, in turn, develop fine chlorotic streaks along leaf veins and experience delayed vegetative development (Gámez, 1973).

The corn leafhopper is a pest restricted to tropical and subtropical regions of the American continent (Oliveira & Frizzas, 2022), due to the strong influence of temperature on its development (Van Nieuwenhove et. al, 2016). In addition to the expansion of planting

seasons and the adoption of different cropping systems, several factors contribute to the difficulty of controlling this pest, such as its high migratory capacity, survival on volunteer plants, and rapid population growth (Oliveira et al., 2013; Oliveira et al., 2020; Oliveira & Frizzas, 2022). Furthermore, many products used for chemical control— the main method applied both in seed treatment and foliar sprays—have proven ineffective, due to the pest's high resistance to insecticides and because their application does not prevent feeding or pathogen transmission (Machado et al., 2024). Biological control is also part of the integrated management of the corn leafhopper, primarily through the use of entomopathogenic microorganisms. However, the effectiveness of this strategy is limited by the low adherence of conidia, caused by the protein–lipid layer of the brochosomes and by the insect's grooming behavior (Lopes et al., 2025).

Biostimulants have gained prominence as more sustainable alternatives for agriculture, amid soil degradation and climate change, as they can mitigate the effects of abiotic stresses on plants, reducing losses and contributing to the maintenance of agricultural productivity (Yakhin et al., 2017; Bhupenchandra et al., 2022). Biostimulants are substances of natural or synthetic origin, or microorganisms, that enhance nutrient uptake by plants and increase their tolerance to abiotic stresses, such as water deficiency (Brown & Saa, 2015; Du Jardin, 2015; Barbosa et al., 2025). In addition, biostimulants may also contribute to increasing plant resistance against herbivorous insects by inducing or intensifying plant defense mechanisms (Pereira et al., 2021). However, further studies are still needed to more deeply explore the interactions among plants, biostimulants, and herbivorous insects, in order to fill existing gaps in the literature. In particular, there is a lack of information regarding the chemical mechanisms involved in these interactions, as well as the potential synergistic effects resulting from the combined application of different biostimulants.

Among the various categories of biostimulants are Humic Substances (HS), which are natural constituents formed through chemical and biological processes involved in the transformation of plant and animal organic matter, as well as microbial metabolism. These substances are composed of humins, humic acids, and fulvic acids (Piccolo, 2002). They are ubiquitous in nature and, as such, are responsible for numerous reactions that occur in the soil (Hayes & Clapp, 2000). The use of humic-substance–based products is common in agriculture, as these products promote increased crop production. The most frequently reported effect is the stimulation of root system development, due to the induction of auxins (Canellas & Olivares, 2014; Maffia et al., 2025).

In addition to these benefits, HS play a role in the plant defense system by promoting phenylalanine ammonia-lyase activity, thereby increasing the concentration of phenolic compounds, which are crucial for activating plant defense responses (Lattanzio et al., 2006; Schiavon, 2010). Among these phenolic compounds, it is important to highlight that HS enhance the synthesis of phenylpropanoids and flavonoids due to their auxin-like induction capacity (Schiavon, 2010).

Silicon (Si) is widely recognized as a beneficial element for plants, although it is not classified as essential (Epstein, 1994). Several studies have demonstrated that its application exerts physiological effects similar to those of biostimulants, promoting plant growth, development, and increased crop productivity (Salim et al., 2021; Gopal et al., 2024; Idrees et al., 2024; Wadas & Kondraciuk, 2025). Si contributes to the mitigation of biotic and abiotic stresses by strengthening cell walls and promoting the deposition of amorphous silica in plant tissues, preventing lodging, as well as improving water and nutrient use efficiency (Ma & Yamaji, 2015; Coskun et al., 2019; Debona et al., 2017; Oliveira et al., 2023). Thus, although Si is not legally classified as a biostimulant under the European Union and Brazilian bioinput regulations—which define biostimulants as products capable of acting directly on plant metabolism—its physiological effects allow it to be considered a functional biostimulant due to its positive impacts on plant performance and resilience. Additionally, some approaches in the literature treat Si as a distinct category of biostimulants (Savant et al., 1999; Savvas & Ntatsi, 2015; Regulation EU 2019/1009; MAPA, 2021).

Moreover, Si acts as a mechanical barrier against herbivorous insects and also participates in the activation of induced chemical defenses; however, information about these effects in maize plants is still limited (Vilela et al., 2014; Cristofano, El-Nakhel & Rouphael, 2021). Si fertilization can strengthen the constitutive defenses of plants by stimulating defense-related enzymes and promoting the enhancement of physical barriers, such as the deposition of silicon in the leaf cuticle. This accumulation increases tissue rigidity and abrasiveness, reducing palatability and digestibility and causing greater wear on the mouthparts of herbivores (Reynolds et al., 2016; Alhousari & Greger, 2018).

In addition, Si application can modulate plants induced defenses by interfering with phytohormone-mediated signaling, particularly through the physical stimulus resulting from its accumulation in tissues, which activates the jasmonic acid (JA) signaling pathway (Hall et al., 2019). JA plays a central role in mediating and synthesizing induced defenses against

herbivorous insects (Wang et al., 2021). Si may also promote a transient increase in JA concentrations, triggering a priming effect that prepares the plant to respond more rapidly and strongly when herbivore attack occurs (Reynolds et al., 2016; Alhousari & Greger, 2018; Hall et al., 2019). Moreover, the use of silicon in plants triggers the activity of phenylalanine ammonia-lyase, increasing resistance to herbivores through the activation of secondary metabolites, mainly phenolic compounds (Yang et al., 2017a; Hawerroth et al., 2019).

When plants are exposed to biotic or abiotic stresses, oxidative stress occurs, characterized by the production of reactive oxygen species (ROS). In general, biotic stress conditions promote the accumulation of superoxide (O_2^-) and hydrogen peroxide (H_2O_2), whose elevated concentrations can alter plant metabolism and ultimately lead to cell death (Xie et al., 2019). To mitigate these effects, plants have developed antioxidant defense systems based on enzymes such as catalase (CAT) and superoxide dismutase (SOD), which are responsible for regulating and eliminating ROS and are widely used as markers of plant stress (Syman et al., 2024). Studies indicate that the application of silicon (Si) and humic substances (HS) can induce stress-defense responses, including increased activity of these antioxidant enzymes (Debona et al., 2017; Canellas, 2020).

Given this context, the objective of this study was to evaluate how Si and HS treatments, applied either individually or in combination, influence the growth and resistance of maize plants to the corn leafhopper *D. maidis*. We hypothesized that fertilization with HS and/or Si would promote adequate maize plant development and enhance their chemical defense mechanisms, total phenolic compounds and antioxidant metabolism, resulting in negative effects on the biology and behavior of the corn leafhopper. Additionally, we proposed that the combined application of the two biostimulants—Humic Substances (HS) and Silicon (Si)—would generate a synergistic effect, strengthening plant resistance to the pest. In this study, we conducted a series of behavioral and biological experiments with *D. maidis* on maize plants, as well as evaluated plant growth parameters, chemical defenses, and antioxidant metabolism.

MATERIALS AND METHODS

Cultivation of Plants and Treatments

Maize seeds (hybrid DKB390) were grown in a greenhouse without controlled light or temperature conditions (Lavras, Brazil; 21°13'35.1"S, 44°58'30.6"W) between June 2024 and January 2025. For sowing, 2-L polyethylene pots were filled with a mixture of red latosol (C

horizon, composition in the supplementary material), commercial substrate (SV Substrato Vegetal, Vida Verde Indústria e Comércio de Insumos Orgânicos Ltda, Mogi Mirim, Brazil), and fine sand, in a 1:1:1 proportion. Before planting, all seeds were treated with the fungicide Vitavax Ultra (Carboxin; Thiram, UPL do Brasil Indústria e Comércio de Insumos Agropecuários S.A., Ituverava, Brazil). Two seeds were sown per pot, and five days after seedling emergence, thinning was performed, leaving only one seedling per pot. During cultivation, plants received treatments with Humic Substances (HS)– and Silicon (Si)–based fertilizers applied via soil drench at the early seedling stage, on different days, following manufacturer recommendations and previous studies (De Souza et al., 2025; Pereira et al., 2025). The control consisted of plants that did not receive Si or HS. For HS, we applied a commercial organomineral fertilizer based on humic substances (Solohumics®, Class A; Solohumics Indústria e Comércio de Fertilizantes LTDA, Viana, Brazil; composition in the supplementary material), adding 50 mL of a 0.1% (v/v) aqueous solution to each pot. This concentration was defined from preliminary maize growth assays (Figure S1). The application of the HS solution in the HS and Si+HS treatments occurred when plants had two leaf pairs. In treatments that did not receive HS—control and Si alone—only 50 mL of distilled water was applied. To obtain Si-treated plants, silicic acid ($SiO_2 \cdot xH_2O$) (Vetec Química Fina, Duque de Caxias, Brazil) was used at 1%, at a dosage equivalent to 0.93 ton Si ha^{-1} (2 ton SiO_2 ha^{-1}) (1.5 g of $SiO_2 \cdot xH_2O$ dissolved in 150 mL of water). The application was performed on seedlings of the Si and Si+HS treatments five days after emergence. In the other treatments (HS and control), the same volume of distilled water was applied. Plants from all treatments (control, Si, HS, and Si+HS) remained in the greenhouse throughout the entire growth period, were fertilized with NPK 4-14-8, and irrigated as needed. In all experiments, Si plants approximately 25–30 days after emergence (V4, with four fully expanded leaves) were used. Plants were transferred to the laboratory one day before the experiments.

Insects

The colony of the corn leafhopper *D. maidis* was established from hundreds of adult insects collected in maize fields in Lavras, Brazil (21°12'51.1"S, 45°03'18.1"W). Field-collected adults were maintained in cages containing maize plants until oviposition. After egg collection, the field adults were discarded to eliminate the possibility of maintaining infected adults within the colony. Insects were kept under controlled laboratory conditions (25 ± 2 °C,

70 ± 10% RH, and a 14 h photophase) in voile cages (23 × 45 × 93 cm) containing healthy maize plants. Plants were replaced whenever necessary; however, leaves containing eggs were retained, and nymphs were transferred to the new plants (Oliveira & Lopes, 2004).

Plant Growth

The influence of HS and Si fertilization, applied individually or in combination, was evaluated on maize plant growth by measuring fresh weight and the length of the shoot and root system. Shoot height was measured with a measuring tape, from the soil surface to the apex of the plant. The shoot was then cut at the base, and excess soil was removed from the root system, after which root length was also measured. Fresh shoot and root weights were determined using an analytical balance. To obtain dry weight, both parts were dried separately in a forced-air oven at 60 °C for 48 h. Each replicate consisted of one plant, and nine replicates were conducted for each treatment.

Host Acceptance and Oviposition Preference by D. maidis

We evaluated whether fertilization with HS and Si, applied individually or in combination, affects host acceptance and oviposition preference by *D. maidis* in no-choice and choice assays. In the host acceptance assay (no-choice), egg deposition was assessed on a single maize plant from one of the treatments, kept inside a fine-mesh–covered cage (55 × 55 × 52 cm). Oviposition preference was assessed in a choice assay containing one plant from each treatment (control, HS, Si, and Si+HS) within the same cage. Both assays were conducted under laboratory conditions (25 ± 2 °C, 70 ± 10% RH, 14 h photophase), with six 7-day-old *D. maidis* adult females released per cage; females had been previously kept with males to ensure mating. After 48 h, females were removed, and plants were maintained for an additional five days, during which eggs become white with red ocelli, facilitating counting (Oliveira et al., 2024). Plants were then examined under a stereomicroscope (7–45×) for egg counting. Each cage represented one replicate, with 12 replicates per treatment.

Biological Parameters of the First and Second Generations of D. maidis

It was evaluated whether feeding on maize plants treated with HS and Si, either individually or in combination, affects early and late biological parameters of *D. maidis*, such as the nymphal development of the first generation and the fecundity and egg viability of the second generation. For nymphal development, one maize plant from each treatment was placed in fine-mesh fabric-covered cages (55 × 55 × 52 cm) and infested with three first-instar nymphs. The development time to the second instar was assessed daily at the same time of day. To evaluate fecundity and viability, 40 females from the laboratory colony were evenly distributed into four voile cages (23 × 45 × 93 cm), each containing four maize plants per treatment. These cages were kept in a greenhouse, without light or temperature control but with similar ventilation and sunlight incidence across treatments. Rearing was conducted in this environment because, in the laboratory, it was not possible to ensure the same intensity and uniformity of light incidence for all cages. First-generation females remained for 48 h for oviposition, and the plants were maintained until the emergence of second-generation adults. Subsequently, six 7-day-old adult *D. maidis* females, previously held with males for mating, were released into each cage containing a maize plant from the same treatment in which they had developed and remained for 48 h in a controlled-environment room (25 ± 2 °C, 60 ± 10% RH, 12-h photophase). After female removal, the plants were kept for five days until the eggs turned white with red ocelli, allowing them to be counted on each plant (de Oliveira et al., 2024) under a stereomicroscope (7–45×). After 10 days, embryonic viability was determined by the proportion of hatched nymphs relative to the total number of eggs. The assays with the first and second generations were conducted in the laboratory (25 ± 2 °C, 70 ± 10% RH, 14-h photophase), and each cage constituted one replicate, with 12 replicates per treatment.

Total phenolic compounds

The effect of fertilization with HS and Si, individually or in combination, on maize plant chemical defenses was evaluated using constitutive and induced total phenolic compounds as a proxy. For herbivory induction, maize plants approximately 25 days after emergence, belonging to the four treatments (C, Si, HS, and Si+HS), were infested with six female maize leafhoppers. Each plant was kept individually in a voile cage and remained infested for seven days. The two youngest leaves from maize plants of each treatment were cut and immediately frozen in liquid nitrogen. Subsequently, these leaves were lyophilized (LÍOTOP, model L101) at –50 °C for approximately 24 h. After this period, the fully dried samples were individually ground to obtain a fine powder. The samples were then weighed and placed in 3-mL microtubes for analysis. After grinding and obtaining the fine powder, a 30-mg aliquot was placed in a microtube

containing 1.5 mL of 80% methanol. The microtubes were placed on a rotary shaker for 15 h, in the dark and at room temperature. The suspension was centrifuged at 12,000 g for 5 min. The supernatant was transferred to a new microtube for total phenolic analysis. The method developed by Spanos and Wrolstad (1990), with some modifications, was used to determine the concentration of total soluble phenolic compounds. In microplates, 15 µL aliquots of the methanolic extract were mixed with 15 µL of 80% methanol and 30 µL of 0.25 N Folin–Ciocalteu reagent for 5 min, homogenized with 30 µL of 1 M Na2CO3 for 10 min, and diluted with 110 µL of distilled water at room temperature for 1 h. Absorbance values were measured at 725 nm in an ELISA spectrophotometer and calculated based on a chlorogenic acid standard curve. Total phenolic compounds were expressed as µg of chlorogenic acid equivalent per milligram of dry mass.

Antioxidant metabolism enzymes

The effect of fertilization with HS and Si, individually or in combination, on the mitigation of oxidative stress caused by herbivory was evaluated by measuring the activity of two antioxidant metabolism enzymes: superoxide dismutase (SOD) and catalase (CAT). To induce herbivory, maize plants from the four treatments (C, Si, HS, and Si+HS) were infested with six female corn leafhoppers and kept individually in a voile cage, remaining infested for seven days, and subsequently the pair of youngest leaves from these plants was cut at the base of the stem, immediately wrapped in aluminum foil, and frozen in liquid nitrogen. The samples were ground in liquid nitrogen using a mortar and pestle until a fine and homogeneous powder was obtained. After this process, 180 mg of each sample was placed into a microtube with 2.0 mL. This entire procedure was performed while keeping samples at low temperature. A buffer solution was added to the microtubes containing 100 mM potassium phosphate (pH 7.8), 0.1 mM EDTA, 10 mM ascorbic acid, and distilled water. Immediately after, the samples were centrifuged at 13,000 × g for 10 min at 4 °C, and the supernatants were used for protein quantification and enzymatic assays (Biemelt et al., 1998). Total protein concentration was determined using the Bradford method (1976). Coomassie Blue G-250, H3PO4, ethanol, and bovine serum albumin (BSA) (2.5 mg/mL) were used as reagents. After preparation, the reagents were placed overnight under constant agitation and filtered. Final concentrations were 0.01% Coomassie, 8.5% phosphoric acid, and 4.7% ethanol. After adding the reagents to the microtubes containing the sample supernatants, the tubes were vortexed and the absorbance

was measured at 595 nm with a spectrophotometer. Superoxide dismutase (SOD) activity was determined according to Giannopolitis and Ries (1977). The reaction mixture consisted of soluble plant protein extract, 100 mM potassium phosphate buffer (pH 7.8), 70 mM methionine, 10 μM EDTA, distilled water, 1 mM nitro blue tetrazolium (NBT), and 0.2 mM riboflavin. The plates containing the samples were exposed to light for 20 minutes and subsequently read in a spectrophotometer at 595 nm. Catalase (CAT) activity was determined according to Havir and McHale (1987). The buffer solution (200 mM potassium phosphate, pH 7.0, and distilled water) was kept in a water bath at 30 °C and then added to the plate containing the soluble plant protein extract. Before the readings, 250 mM H_2O_2 was added to the plate. Spectrophotometer readings were taken at 240 nm every 15 seconds for 3 minutes. CAT activity was assessed by monitoring the rate of H_2O_2 decomposition.

Data Analyses

Statistical analyses were conducted considering the different response variables evaluated in maize plants treated with humic substances (HS), silicon (Si), HS + Si, and control (C), under infestation by *D. maidis*. The variables plant height, length, fresh weight, and biomass were evaluated individually. Initially, residual normality was assessed using the Shapiro–Wilk test and homogeneity of variance using Levene's test, with the *car* package. When assumptions were met, data were analyzed using generalized linear models (GLMs) with Gaussian distribution. When the assumptions of normality and homoscedasticity were not met, GLMs with Gamma distribution and log-link function were applied.

The mean time for instar transition and the mean number of eggs laid by *D. maidis* were analyzed following the same procedures: normality verification using the Shapiro–Wilk test and homogeneity via Levene's test, followed by fitting GLMs with Gamma distribution and log-link function.

For the choice assay (with opportunity for choice), the number of eggs laid per plant was initially fitted using a Poisson GLM. Due to overdispersion, a Negative Binomial model was adopted using the *glm.nb* function from the *MASS* package.

Concentrations of total phenolic compounds and the activities of SOD and CAT enzymes, evaluated under constitutive and herbivory-induced conditions, were also subjected

to residual normality tests. According to variable behavior, GLMs with Gaussian or Gamma (log-link) distributions were fitted.

Fecundity (total number of eggs per plant) was initially analyzed with a Poisson GLM; however, due to overdispersion, a Negative Binomial model was used. Viability (proportion of hatched nymphs) was evaluated using a Binomial GLM and subsequently adjusted to a Quasipoisson model for the same reason.

Model validation included comparison of information criteria (AIC) and assessment of overdispersion using the *performance* package. Pairwise comparisons among treatments were performed using the *glht* function from the *multcomp* package with Tukey adjustment ($\alpha = 0.05$), and estimated marginal means (EMMs) were obtained with the *emmeans* package. All statistical analyses were conducted in R software, version 4.4.1 (R Core Team, 2024).

RESULTS

Plant Growth

Plants treated with HS showed superior performance in root development. This treatment resulted in greater root fresh weight and higher root biomass compared to the other treatments (Table 1). The HS treatment stood out as the most effective in promoting root growth, presenting significantly higher values of fresh weight and biomass. Conversely, none of the tested biostimulants produced significant changes in the other morphometric parameters of maize plants evaluated. Stem height, total height, root length, shoot fresh weight, and shoot biomass did not differ among treatments (Table 1).

Table 1. Morphometric parameters of maize plants (*Zea mays*). Plants without fertilization (C) and fertilized with the biostimulants humic substances (HS), silicon (Si), and their combination (HS + Si). Means within columns followed by different letters differ significantly according to Tukey's test ($P < 0.05$). df = degrees of freedom.

Treatments	Height (cm)		Length (cm)	Fresh weight (g)		Biomass (g)	
	Total	Stem	Root	Shoot	Roots	Shoot	Root
C	60.80±4.96a	15.60±0.98a	59.10±3.29a	11.10±1.20a	0.51±0.04a	0.80±0.08a	0.35±0.01ab
HS	60.70±3.84a	15.30±1.41a	64.50±3.86a	9.85±1.62a	0.75±0.05b	0.74±0.10a	0.53±0.02c

Si	62.60±4.10a	16.90±1.46a	54.70±3.14a	10.80±1.57a	0.46±0.06a	0.87±0.10a	0.33±0.04a
Si+HS	69.70±4.15a	17.10±1.21a	59.30±1.79a	14.60±1.96a	0.58±0.04ab	1.05±0.12a	0.44±0.03bc
F	0.99	0.54	1.65	1.66	6.27	1.60	11.72
gl	3.32	3.32	3.32	3.32	3.32	3.32	3.32
P	0.41	0.66	0.20	0.19	0.001	0.21	<0.001

Host Acceptance and Oviposition Preference by D. maidis

Fertilization of maize plants significantly affected host acceptance for oviposition by *D. maidis* (F = 4.16; df = 3,44; P = 0.01, Fig. 1). Females deposited fewer eggs on maize plants treated with Si and Si+HS compared to the control (Fig. 1). Oviposition by *D. maidis* on maize plants treated with HS did not differ from the control or from the Si and Si+HS treatments.

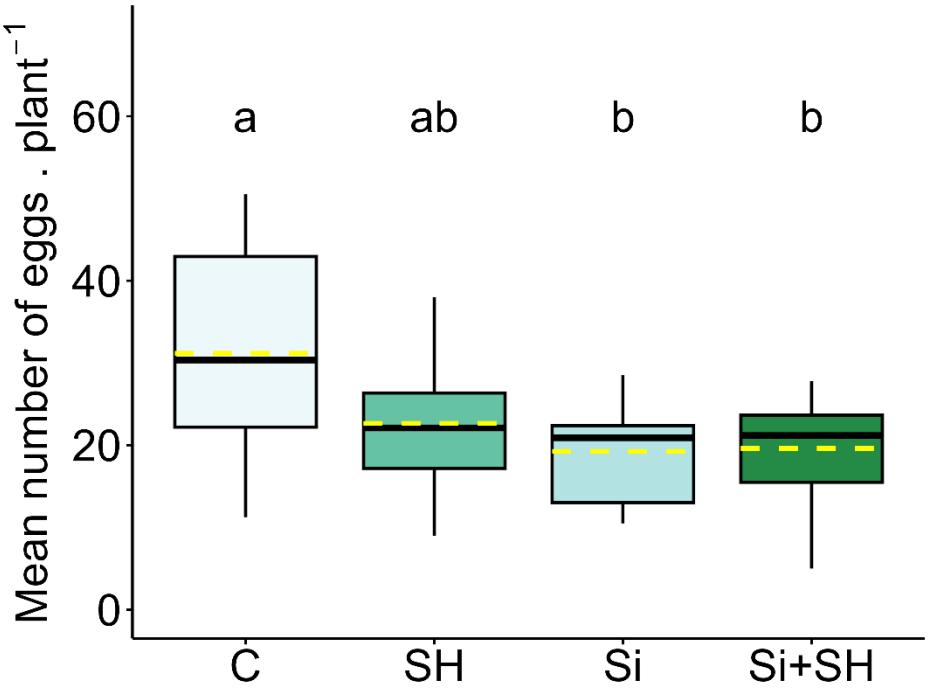

Fig. 1 Host acceptance by *Dalbulus maidis* for oviposition on maize plants (*Zea mays*) treated with the biostimulants silicon and humic substances, applied individually or in combination. Plants without biostimulant – Control (C) and plants treated with the biostimulants humic substances (HS), silicon (Si), and their combination (HS + Si). The yellow dashed line indicates the mean. Treatment means followed by different letters differ significantly according to Tukey's test (P < 0.05)

On the other hand, in the choice assay, where *D. maidis* females were free to select among the different treatments, no significant differences were observed in the proportion of eggs laid on each plant ($\chi^2 = 0.66$, df = 3,44, P = 0.88, Fig. 2).

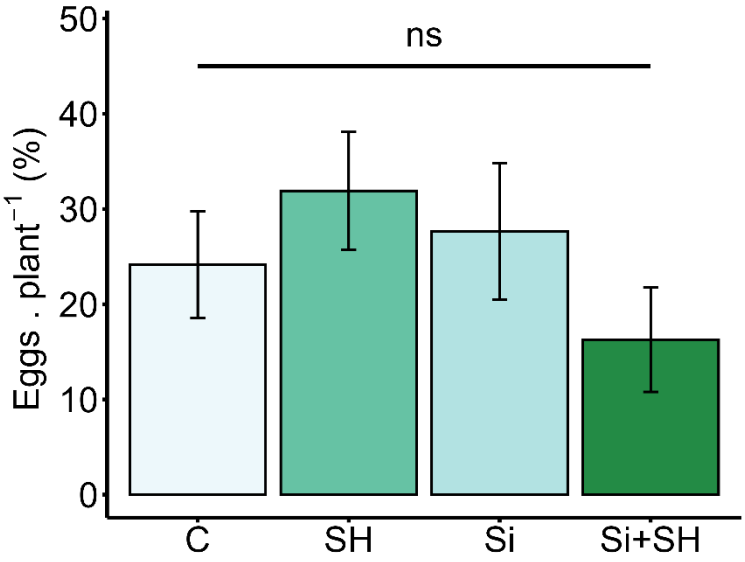

Fig. 2 Oviposition choice by the corn leafhopper, *Dalbulus maidis* (choice assay), among maize plants (*Zea mays*) treated with the biostimulants silicon and humic substances, applied individually or in combination. Plant without biostimulant – Control (C) and plants treated with the biostimulants humic substances (HS), silicon (Si), and their combination (HS + Si). ns: not significant (P > 0.05)

Biological parameters of the first and second generations of D. maidis

There was a significant difference among treatments, and the Si+HS treatment showed the shortest instar-transition time (F = 3.37; df = 3,41; P = 0.03) (Fig. 3). The duration of the first nymphal instar on maize plants treated with Si+HS was shorter compared to the control treatment. In contrast, the treatments with Si and HS applied individually did not alter the duration of the nymphal instar relative to the other treatments (Fig. 3).

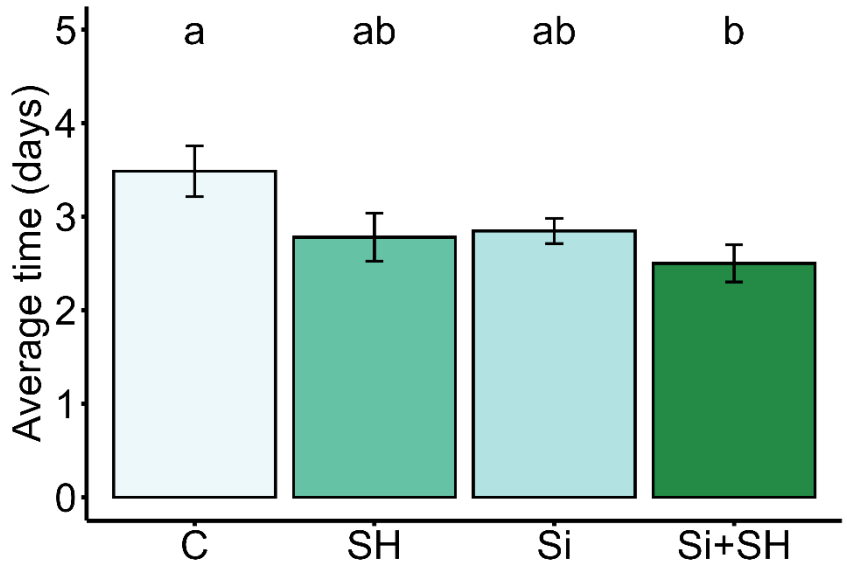

Fig 3 Mean duration (± SE) of the first nymphal instar of *Dalbulus maidis* on maize (*Zea mays*) plants treated with the biostimulants silicon (Si) and humic substances (HS), applied individually or in combination. Treatments included: plants without biostimulants – Control (C), plants treated with humic substances (HS), plants treated with silicon (Si), and plants treated with the combination of both biostimulants (Si + HS). Treatments marked with different letters differ significantly according to Tukey's test ($P < 0.05$)

Regarding the second generation of *D. maidis*, fertilization with Si and HS, either individually or in combination, did not influence fecundity (number of eggs laid in 48 h) ($\chi^2 = 3.05$; df = 3,39; $P = 0.38$) or embryonic viability ($F = 0.05$; df = 3,39; $P = 0.95$) on maize plants (Fig. 4).

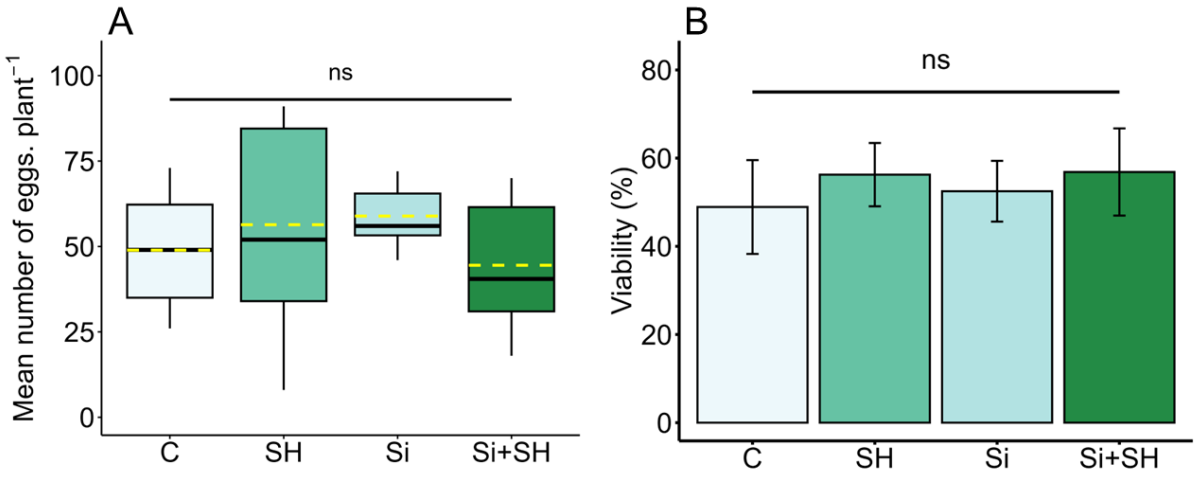

Fig. 4 Biological parameters of second-generation *Dalbulus maidis* females on maize plants (*Zea mays*) treated with the biostimulants silicon and humic substances, applied individually or in combination. **(A)** Fecundity (number of eggs plant^{-1}) and **(B)** embryonic viability (proportion of eggs from which nymphs emerged). Plants without biostimulant – Control (C), and plants treated with the biostimulants humic substances (HS), silicon (Si), and the combination of both (HS + Si). ns: not significant (P > 0.05)

Total phenolic compounds

Fertilization with Si and SH, either alone or in combination, did not result in significant differences in the levels of constitutive total phenolic compounds among treatments (F = 0.85; df = 3,31; P = 0.48) (Fig. 5A). However, following herbivory by *D. maidis*, a significant decrease in induced total phenolic compounds was observed in maize plants treated with Si compared to the control and Si+HS treatments (F = 3.06; df = 3,36; P = 0.02, Figure 5B). Additionally, maize plants treated with HS exhibited intermediate levels of induced total phenolics, which did not differ from the other treatments (Fig. 5B).

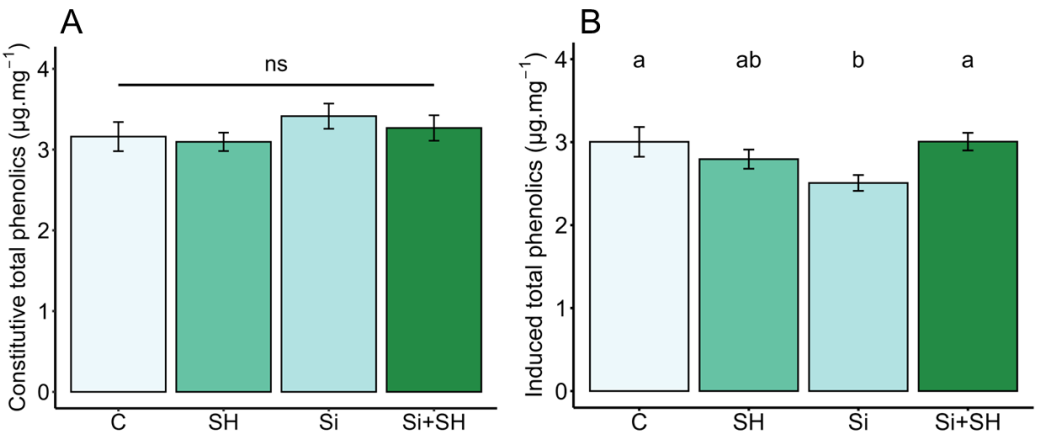

Fig. 5 Total phenolic compounds in maize plants (*Zea mays*) treated with the biostimulants silicon and humic substances, applied alone or in combination. Plants without biostimulants – Control (C), and plants treated with the biostimulants: humic substances (SH), silicon (Si), and the combination of both (HS + Si). (A) Constitutive levels (without herbivory) and (B) Levels induced by herbivory from the corn leafhopper, *Dalbulus maidis*. Treatment means followed by different letters differ statistically according to Tukey's test ($P < 0.05$). ns: not significant.

Antioxidant metabolism enzymes

The activity of antioxidant enzymes varied significantly among the treatments with biostimulants. Superoxide dismutase (SOD) activity was markedly reduced in maize plants treated with Si and in the Si+HS combination, which showed the lowest values compared with the other treatments ($F = 38.09$; $df = 3,35$; $P < 0.01$) (Fig. 6A). In contrast, catalase (CAT) activity showed a reduction only in plants from the Si+HS treatment compared with the control ($F = 3.30$; $df = 3,35$; $P = 0.03$) (Fig. 6B).

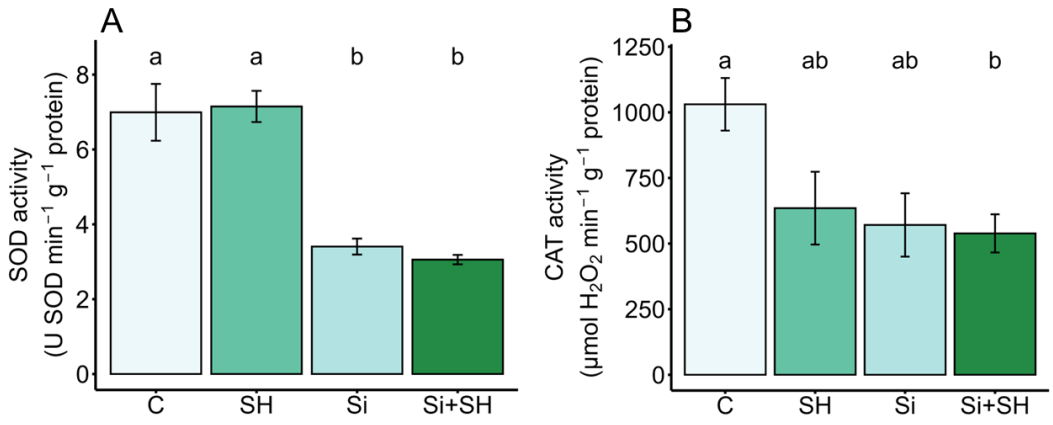

Fig. 6 Activities of antioxidant metabolism enzymes in maize plants (*Zea mays*) induced by herbivory from the corn leafhopper, *Dalbulus maidis*. Plants without biostimulants – Control (C) and plants treated with the biostimulants: humic substances (SH), silicon (Si), and the combination of both (HS + Si). **(A)** Superoxide dismutase (SOD) and **(B)** catalase (CAT). Treatment means followed by different letters differ statistically according to Tukey's test ($P < 0.05$)

DISCUSSION

Given the challenges in managing the corn leafhopper *D. maidis* in the field and the growing demand for eco-friendly strategies, we investigated whether the biostimulants silicon (Si) and humic substances (HS), applied alone or in combination, enhance maize resistance to this pest. Our study showed that neither biostimulant promoted shoot growth, and only HS increased root biomass; this effect disappeared when HS was combined with Si, suggesting that Si may interfere with HS-mediated root development. Treatments containing Si (Si and Si+HS) reduced host acceptance for oviposition, although they did not impair leafhopper performance, in terms of first instar development time, fecundity, and egg viability. In fact, Si+HS accelerated nymphal development, indicating a potential compensatory or hormetic effect on the insect. Overall, Si conferred only modest resistance by reducing host acceptance without improving plant-based constraints on insect development. This reduced acceptance did not align with total phenolic levels, which were lower in Si-treated plants compared to controls. Finally, Si, alone or combined with HS, mitigated the oxidative stress induced by *D. maidis*, as reflected by decreased SOD and CAT activities.

The most frequently reported function of plant fertilization with HS is the enhancement of root system development (Rose et al., 2014; Nardi et al., 2017). Humic substances contribute to increased growth of lateral roots, root length, and biomass production (Canellas et al., 2014). Humic substances act on the plant root system through physical, chemical, and physiological mechanisms. Initially, they stimulate ATPase activity, intensifying the electrochemical gradient and favoring both nutrient uptake and cell expansion—processes that enable the formation of lateral roots. Part of this effect is associated with the presence of small bioactive molecules, such as auxins, trapped within the structure of SH, which modulate signaling pathways involved in root growth. In addition, HS fertilization through the soil induces changes in redox homeostasis and the balance of reactive oxygen species, elements essential for cell division, differentiation, and elongation (Canellas et al., 2014; García et al., 2019). Our results are consistent with previously published studies, demonstrating a more pronounced effect of humic substances (HS) on root development, reflected in the increased fresh weight and root biomass in the treatments that received SH.

The information available in the literature regarding the effects of HS on the aerial parts of plants is still limited (Olaetxea et al., 2018). Moreover, the method of application and the dosage of these substances are determining factors for obtaining consistent responses, since the chemical mechanisms associated with shoot growth differ from those involved in root development, with cross-communication between plant tissues being an essential component of this process (Rose et al., 2014). Thus, it is possible that the application strategy and dosage used in this study contributed to the absence of significant differences in the parameters evaluated in the aerial part of the plants.

Although Si fertilization is widely recognized for promoting the growth of several crops—such as rice, strawberry, and corn—under different environmental conditions (Delavar et al., 2017; Hajiboland et al., 2017; Nascimento et al., 2018; Ramírez-Olvera et al., 2019), our results did not follow this trend. The application of Si did not enhance root development or shoot growth and, additionally, the Si+HS combination negatively interfered with the isolated effect of HS on root development. These findings contrast with reports available in the literature on the effects of HS fertilization combined with Si, which describe enhanced responses promoted by these biostimulants. In wheat plants, Jodaugienė et al. (2023) observed positive effects on both root and shoot parameters using a lower fertilizer dose than the one applied in the present study. Conversely, in corn plants, Hassan et al. (2019) reported increases in shoot

development when more than one fertilization event was applied, resulting in total doses higher than those used here.

Silicon fertilization can enhance direct defenses through the deposition of silicon in the leaf cuticle, which affects herbivore feeding, growth, and survival (Singh et al., 2020). In sap-sucking insects, these structural changes hinder or even inhibit phloem sap feeding (Yang et al., 2017a). In addition, Si modulates plant chemical defenses, which are regulated by several anti-herbivory phytohormones (Hall et al., 2019). Humic substances can stimulate plant defenses against insects by promoting increased synthesis of phenolic compounds, including phenolics derived from the phenylpropanoid and flavonoid pathways (Schiavon, 2010). In addition, they modulate signaling pathways mediated by phytohormones such as abscisic acid, gibberellins, and auxins (Canellas et al., 2020).

In the no-choice host acceptance bioassays, a resistance pattern consistent with the previously cited literature was observed: maize plants treated with silicon, both in the isolated treatment (Si) and in the Si+HS combination, showed fewer eggs compared with the control. However, the simultaneous application of both biostimulants did not result in an additional effect, indicating that the observed response can be attributed to Si. Similar results are reported in the literature, such as the reduction in feeding and oviposition of *Nilaparvata lugens* (Stål, 1854) (Hemiptera: Delphacidae) on rice (Yang et al., 2017b), the decrease in oviposition of *Bemisia tabaci* (Gennadius, 1889) (Insecta: Hemiptera: Aleyrodidae) on cotton (Abbasi, Sufyan & Arif, 2020), and of *Mythimna (Pseudaletia) separata* (Walker, 1865) on wheat (Gulzar, 2025).

On the other hand, in the choice assay no oviposition preference was observed, indicating that the insects did not discriminate between treated and control plants. Similar findings have been reported in different biological systems, such as the absence of preference by *Leucoptera coffeella* (Guérin-Méneville, 1842) (Lepidoptera: Lyonetiidae) for coffee plants treated with HS (de Souza et al., 2025), as well as in studies involving Si for *Bemisia tabaci* (Gennadius, 1889) (Insecta: Hemiptera: Aleyrodidae) on soybean (Ferreira, Moraes & Antunes, 2011) and in host plant selection by the aster leafhopper *Macrosteles quadrilineatus* (Forbes, 1885) (Hemiptera: Cicadellidae) (Romero et al., 2022). These results reinforce that, under certain conditions, the applied compounds or treatments may not exert a significant influence on host selection by insects.

However, no negative effects of the Si or Si+HS treatments were observed on the insect's biological parameters, including development, fecundity, and embryonic viability. Notably, the Si+HS treatment accelerated instar transition, positively influencing the development of *D. maidis*. These findings contrast with reports in the literature indicating that fertilization with Si and HS typically exerts negative effects on insect development and fecundity (Santos et al., 2025; de Souza et al., 2025). A similar pattern has been described for the fruit fly *Drosophila melanogaster* (Meigen, 1830) (Diptera: Drosophilidae), in which individuals maintained for multiple generations on nutritionally inadequate diets exhibited higher egg-to-adult viability and faster development when reared on low-quality diets (Munjong et al., 2009). These results have been interpreted as reflecting adaptations to nutritional stress, possibly associated with physiological changes that are not yet fully understood (Munjong et al., 2009). In the study by Munjong and colleagues, insects had been maintained in laboratory culture for an extended period over multiple generations—a condition similar to that of the population used in the present study. Thus, it is plausible that the adaptive potential developed across generations was retained, allowing improved performance even under suboptimal nutritional conditions. Furthermore, because *D. maidis* is a specialist herbivore, the coevolution between the corn leafhopper and maize plants may have favored the acquisition of additional adaptive mechanisms in response to variations in host quality. Therefore, only a subtle increase in plant resistance was observed in Si-treated plants, which reduced host acceptance without accelerating insect development, unlike the combined Si+HS treatment.

Plants synthesize a wide variety of secondary metabolites with defensive functions, among which phenolic compounds stand out as one of the largest and most diverse groups of plant bioactive substances (Tsimogiannis & Oreopoulou, 2019). Following pest infestation, these defense mechanisms are induced, resulting in quantitative and qualitative changes in phenolic compounds. These modifications, in turn, can directly influence insect behavior and biology (Kulbat, 2016; Dar et al., 2017). The availability of information regarding the relationship between humic substances (HS) and the stimulation of phenolic compounds is still limited, although reports demonstrating this effect already exist (Conselvan et al., 2017; Gholami et al., 2018), including in maize plants (Schiavon et al., 2010). HS are known to stimulate the activity of the enzyme phenylalanine ammonia-lyase (PAL), considered the initial step in the biosynthetic pathway of phenolic compounds. However, in our study we did not observe this response pattern: constitutive phenolic compounds were not affected by the

application of the treatments, and, additionally, the increased resistance conferred by Si did not coincide with the levels of total phenolic compounds, which were reduced in this treatment compared to the control.

The literature presents diverse findings regarding the quantification of total phenolic compounds in plants treated with silicon (Si). Several studies indicate that Si application can increase phenolic synthesis in different crops as a defense mechanism against insects, including wheat and rice (Reynolds et al., 2016; Luyckx et al., 2017; Yang et al., 2017a; Dorneles et al., 2018). In contrast, other studies report reductions in total phenolic content in Si-fertilized plants (Cooke & Leishman, 2012; Schaller et al., 2012; Hajiboland et al., 2017). This decrease is particularly evident in Si-accumulating species, in which a compensatory relationship occurs between chemical defenses based on phenolic compounds and tissue silicification, suggesting that Si-induced defense may be more efficient (Cooke & Leishman, 2012). When Si-treated plants invest more resources in biomechanical defenses, they become less dependent on induced chemical defenses (Hall et al., 2019). Furthermore, a differential distribution of phenolic compounds across plant tissues has been observed: photosynthetically active tissues tend to exhibit higher Si concentrations and lower phenolic levels, whereas the opposite pattern is found in the stem (Schaller et al., 2012). Considering that the material collected for chemical analysis was leaf tissue, our results support the aforementioned study regarding the differential distribution of phenolic compounds among distinct plant structures.

However, our results contrasted with the initial hypotheses and with part of the evidence available in the literature. A significant reduction in SOD activity was observed in maize plants treated with Si and Si+HS compared with the other treatments, whereas CAT activity decreased only in the Si+HS treatment relative to the control. These findings demonstrate a protective effect of Si, applied either alone or in combination with HS, against the oxidative stress caused by *D. maidis*. Although there are no reports of reduced activity of these enzymes in response to HS application, a similar decrease has been documented in wheat treated with Si and infected by the fungus *Pyricularia oryzae* (Cavara) (teleomorph: *Magnaporthe grisea*), indicating the activation of alternative defense pathways (Debona et al., 2014).

The results of this study, together with previously available evidence in the literature, demonstrate that the biostimulants Si and HS can exert distinct effects on plant development and insect behavior, depending on both the dosage used and the method of application. It was observed that HS, when applied alone, promoted an increase in root growth, whereas its

combination with Si negatively interfered with this effect. A slight increase in the resistance of plants treated with Si was also detected, reflected in the reduced host acceptance by *D. maidis*, although without any impact on insect development. However, this increased resistance did not correlate with the levels of total phenolic compounds, which were reduced in this treatment compared with the control. Additionally, a protective effect of Si, either alone or in association with SH, was identified against the oxidative stress caused by *D. maidis*, as evidenced by the reduced activities of the oxidative enzymes SOD and CAT.

These results reinforce the need for future studies that investigate additional aspects of defense induction in this plant–insect system, as well as a deeper understanding of the chemical interactions between the two biostimulants and of possible physiological adaptations of *D. maidis* over multiple generations. It also becomes relevant to evaluate the performance of these biostimulants under field conditions and to explore new combinations of substances capable of enhancing alternative practices for integrated pest management.

REFERENCES

Abbasi, A., Sufyan, M., Arif, M. J., et al. (2020). Effect of silicon on tritrophic interaction of cotton (*Gossypium hirsutum*), *Bemisia tabaci*, and the predator *Chrysoperla carnea*. *Arthropod-Plant Interactions, 14*, 717–725. DOI: https://doi.org/10.1007/s11829-020-09786-1

Alhousari, F., & Greger, M. (2018). Silicon and mechanisms of plant resistance to insect pests. *Plants, 7*(2), 33.

Barbosa, M. F., Sales, R. M. M., Galarza, F. A. D., Kruger, C. Q., Fávaro, L. C. L., & Quirino, B. F. (2025). Biological resources driving productivity: Bioinputs for sustainable plant agriculture in Brazil. *Sustainable Microbiology, 2*(3), qvaf011. DOI: https://doi.org/10.1093/sumbio/qvaf011

Bhatt, D., & Sharma, G. (2018). Role of silicon in counteracting abiotic and biotic plant stresses. *International Journal of Chemical Studies, 6*(2), 1434–1442.

Bhupenchandra, I., Chongtham, S. K., Devi, E. L., R, R., Choudhary, A. K., Salam, M. D., ... & Khaba, C. I. (2022). Role of biostimulants in mitigating the effects of climate change on crop performance. *Frontiers in Plant Science*, *13*, 967665. DOI: doi.org/10.3389/fpls.2022.967665

Bradford, M. M. (1976). A rapid and sensitive method for the quantification of microgram quantities of protein utilizing the principle of protein–dye binding. *Analytical Biochemistry, 72*, 248–254. DOI: https://doi.org/10.1006/abio.1976.9999

Brown, P., & Saa, S. (2015). Biostimulants in agriculture. *Frontiers in Plant Science, 6*, 671.

Canellas, L. P., & Olivares, F. L. (2014). Physiological responses to humic substances as plant growth promoter. *Chemical and Biological Technologies in Agriculture, 1*(1), 1–11. DOI: https://doi.org/10.1186/2196-5641-1-3

Canellas, L. P., Canellas, N. O. A., Irineu, L. E. S. da S., et al. (2020). Plant chemical priming by humic acids. *Chemical and Biological Technologies in Agriculture, 7*(1), 12. DOI: https://doi.org/10.1186/s40538-020-00178-4

Conselvan, G. B., Pizzeghello, D., Francioso, O., et al. (2017). Biostimulant activity of humic substances extracted from leonardites. *Plant and Soil, 420*, 119–134. DOI: https://doi.org/10.1007/s11104-017-3373-z

Cooke, J., & Leishman, M. R. (2012). Tradeoffs between foliar silicon and carbon-based defences: Evidence from vegetation communities of contrasting soil types. *Oikos, 121*(12), 2052–2060. DOI: https://doi.org/10.1111/j.1600-0706.2012.20057.x

Coskun, D., et al. (2019). The role of silicon in higher plants under salinity and drought stress. *Frontiers in Plant Science, 10*, 1359. DOI: https://doi.org/10.3389/fpls.2019.01359

Cristofano, F., El-Nakhel, C., & Rouphael, Y. (2021). Biostimulant substances for sustainable agriculture: Origin, operating mechanisms and effects on cucurbits, leafy greens, and nightshade vegetables. *Biomolecules, 11*(8), 1103.

Dar, S. A., Rather, B. A., Wani, A. R., & Ganie, M. A. (2017). Resistance against insect pests by plant phenolics and their derivative compounds. *Chemical Science Review and Letters, 6*(22), 1073–1081.

De Oliveira, C. M., et al. (2024). Influence of latitude and elevation on polymorphism among populations of the corn leafhopper, *Dalbulus maidis* (Hemiptera: Cicadellidae), in Brazil. *Environmental Entomology, 33*(5), 1192–1199.

De Souza, L. A., Andrade, F. M., Penido, E. S., et al. (2025). Formulação à base de substâncias húmicas em mudas de café: crescimento vegetal aprimorado e resistência ao minador-do-café. *International Journal of Tropical Insect Science*. DOI: https://doi.org/10.1007/s42690-025-01618-0

Debona, D., Rodrigues, F. A., & Datnoff, L. E. (2017). Silicon's role in abiotic and biotic plant stresses. *Annual Review of Phytopathology, 55*, 85–107. DOI: https://doi.org/10.1146/annurev-phyto-080417-050056

Debona, D., Rodrigues, F. A., Rios, J. A., Nascimento, K. J. T., & Silva, L. C. (2014). The effect of silicon on antioxidant metabolism of wheat leaves infected by *Pyricularia oryzae*. *Plant Pathology, 63*(3), 581–589.

Delavar, K., Ghanati, F., Zare-Maivan, H., & Behmanesh, M. (2017). Effects of silicon on the growth of maize seedlings under normal, aluminum, and salinity stress conditions. *Journal of Plant Nutrition, 40*(10), 1475–1484. DOI: https://doi.org/10.1080/01904167.2016.1269344

Dorneles, K. R., Pazdiora, P. C., Hoffmann, J. F., Chaves, F. C., Monte, L. G., Rodrigues, F. A., & Dallagnol, L. J. (2018). Wheat leaf resistance to *Pyrenophora tritici-repentis* induced by silicon activation of phenylpropanoid metabolism. *Plant Pathology, 67*(8), 1713–1724.

Du Jardin, P. (2015). Plant biostimulants: Definition, concept, main categories and regulation. *Scientia Horticulturae, 196*, 3–14.

Epstein E. (1994) The anomaly of silicon in plant biology. *Proceedings National of Academy Science*, 91(1):11-7. Doi: 10.1073/pnas.91.1.11

Erenstein, O., Jaleta, M., Sonder, K., & others. (2022). Global maize production, consumption and trade: Trends and R&D implications. *Food Security, 14*, 1295–1319. DOI: https://doi.org/10.1007/s12571-022-01288-7

FAO. Food and Agriculture Organization. https://www.fao.org/faostat/en/#rankings/countries_by_commodity

Ferreira, R. S., Moraes, J. C., & Antunes, C. S. (2011). Silicon influence on resistance induction against *Bemisia tabaci* Biotype B (Genn.) (Hemiptera: Aleyrodidae) and on vegetative development in two soybean cultivars. *Neotropical Entomology, 40*, 495–500. DOI: https://doi.org/10.1590/S1519-566X2011000400014

Gámez, R. (1973). Transmission of rayado fino virus of maize (*Zea mays*) by *Dalbulus maidis*. *Annals of Applied Biology, 73*(3), 285–292. DOI: https://doi.org/10.1111/j.1744-7348.1973.tb00935.x

García, A. C., van Tol de Castro, T. A., Santos, L. A., Tavares, O. C. H., Castro, R. N., Berbara, R. L. L., & García-Mina, J. M. (2019). Structure–property–function relationship of humic substances in modulating the root growth of plants: A review. *Journal of Environmental Quality, 48*(6), 1622–1632.

Gholami, H., Saharkhiz, M. J., Fard, F. R., Ghani, A., & Nadaf, F. (2018). Humic acid and vermicompost increased bioactive components, antioxidant activity and herb yield of chicory (*Cichorium intybus* L.). *Biocatalysis and Agricultural Biotechnology, 14*, 286–292. DOI: https://doi.org/10.1016/j.bcab.2018.03.021

Gianopolitis, C. N., & Ries, S. K. (1977). Superoxide dismutases: I. Occurrence in higher plants. *Plant Physiology, 59*(2), 309–314. DOI: https://doi.org/10.1104/pp.59.2.315

Gopal, D., Prasad, T. N. V. K. V., Pradeep, T., Reddy, C. B. R., NirmalKumar, A. R., Naseeruddin, R., & Naidu, M. V. S. (2024). Effects of nanoparticulate delivery of silicon on the growth and yield of rice (Oryza sativa L.). *Silicon*, *16*(1), 253-263. DOI: doi.org/10.1007/s12633-023-02673-3

Gulzar, I., Ahmad, T., Shameen, F., et al. (2025). Silicon enhanced wheat: Effects on development, oviposition preferences and mandibular wear in Oriental armyworm, *Mythimna separata*. *Phytoparasitica, 53*, 25. DOI: https://doi.org/10.1007/s12600-025-01245-y

Hajiboland, R., Bahrami-Rad, S., & Poschenrieder, C. (2017). Silicon modifies both a local response and a systemic response to mechanical stress in tobacco leaves. *Biologia Plantarum, 61*, 187–191. DOI: https://doi.org/10.1007/s10535-016-0633-3

Hajiboland, R., Moradtalab, N., Eshaghi, Z., & Feizy, J. (2017). Effect of silicon supplementation on growth and metabolism of strawberry plants at three developmental stages. *New Zealand Journal of Crop and Horticultural Science, 46*(2), 144–161. DOI: https://doi.org/10.1080/01140671.2017.1373680

Hall, C. R., Waterman, J. M., Vandegeer, R. K., Hartley, S. E., & Johnson, S. N. (2019). The role of silicon in antiherbivore phytohormonal signalling. *Frontiers in Plant Science*, *10*, 1132. DOI: doi.org/10.3389/fpls.2019.01132

Hassan, H. H., Huthily, K. H., & Mohsen, K. H. (2019). Effect of humic acid and silicon on some growth characteristics of maize (*Zea mays* L.). *Basrah Journal of Agricultural Sciences*, *32*(2), 23-32. DOI: doi.org/10.37077/25200860.2019.190

Havir, E. A., & McHale, N. A. (1987). Biochemical and developmental characterization of multiple forms of catalase in tobacco leaves. *Plant Physiology, 84*(2), 450–455. DOI: https://doi.org/10.1104/pp.84.2.450

Hawerroth, C., Araujo, L., Bermúdez-Cardona, M. B., Silveira, P. R., Wordell Filho, J. A., & Rodrigues, F. A. (2019). Silicon-mediated maize resistance to macrospora leaf spot. *Tropical Plant Pathology*, *44*, 2, 192-196. DOI: https://doi.org/10.1007/s40858-018-0247-8

Hayes, M. H. B., & Clapp, C. E. (2001). Humic substances: Considerations of compositions, aspects of structure, and environmental influences. *Soil Science, 166*(11), 723–737.

IBGE - Instituto Brasileiro de Geografia e Estatística. Produção Agrícola - Lavoura Temporária. Disponível em: < https://cidades.ibge.gov.br/brasil/pesquisa/14/10193>.

Idrees, K., Aziz, A., Naeem, M., Azhar, M. F., Farooq, S., & Hussain, M. (2024). Combined application of zinc and silicon improved growth, gas exchange traits, and productivity of maize (*Zea mays* L.) under water stress. *Silicon*, *16*(2), 831-841. DOI: doi.org/10.1007/s12633-023-02732-9

Jodaugienė, D., Čepulienė, R., Mažuolytė-Miškinė, E., & Vagusevičienė, I. (2023). The effect of humic acids and silicon on spring wheat productivity. In *Rural Development: Proceedings of the International Scientific Conference* (pp. 15-20). DOI: doi.org/10.15544/RD.2023.010

Kulbat, K. (2016). The role of phenolic compounds in plant resistance. *Biotechnology and Food Science, 80*(2), 97–108. DOI: https://doi.org/10.34658/bfs.2016.80.2.97-108

Lattanzio, V., Lattanzio, V. M., & Cardinali, A. (2006). Role of phenolics in the resistance mechanisms of plants against fungal pathogens and insects. In *Phytochemistry: Advances in Research* (pp. 23–67).

Lopes, R. B., Faria, M., & Oliveira, C. M. (2025). Susceptibility of *Dalbulus maidis* to insect-pathogenic fungi: Unveiling the protective role of brochosomes and self-cleaning behavior. *Journal of Pest Science, 98*, 759–768. DOI: https://doi.org/10.1007/s10340-024-01823-9

Luyckx, M., Hausman, J. F., Lutts, S., & Guerriero, G. (2017). Silicon and plants: Current knowledge and technological perspectives. *Frontiers in Plant Science, 8*, 411.

Ma, J. F., & Yamaji, N. (2015). Silicon uptake and accumulation in higher plants. *Trends in Plant Science, 20*(7), 435–442. DOI: https://doi.org/10.1016/j.tplants.2015.04.007

Machado, E. P., Souza, E. V., Dias, G. S., Sacilotto, M. G., & Omoto, C. (2024). Is insecticide resistance a factor contributing to the increasing problems with *Dalbulus maidis* (Hemiptera: Cicadellidae) in Brazil?. *Pest Management Science*, *80*(10), 5120-5130. DOI: **doi.org/10.1002/ps.8237**

Maffia, A., Oliva, M., Marra, F., Mallamaci, C., Nardi, S., & Muscolo, A. (2025). Humic substances: Bridging ecology and agriculture for a greener future. *Agronomy, 15*(2), 410. DOI: https://doi.org/10.3390/agronomy15020410

MAPA – Ministério da Agricultura, Pecuária e Abastecimento. (2021). *Instrução Normativa nº 53, de 23 de outubro de 2021: Dispõe sobre o registro, classificação e uso de bioestimulantes de plantas*. Diário Oficial da União.

Munjong Kolss, M., Vijendravarma, R. K., Schwaller, G., & Kawecki, T. J. (2009). Life-history consequences of adaptation to larval nutritional stress in *Drosophila*. *Evolution, 63*(9), 2389–2401. DOI: https://doi.org/10.1111/j.1558-5646.2009.00718.x

Nardi, S., Ertani, A., & Francioso, O. (2017). Soil–root cross-talking: The role of humic substances. *Journal of Plant Nutrition and Soil Science, 180*(1), 5–13. DOI: https://doi.org/10.1002/jpln.201600348

Nascimento, A. M., Assis, F. A., Moraes, J. C., & Souza, B. H. S. (2018). Silicon application promotes rice growth and negatively affects development of *Spodoptera frugiperda* (J. E. Smith). *Journal of Applied Entomology, 142*(1–2), 241–249. DOI: https://doi.org/10.1111/jen.12461

Nault, L. R. (1980). Maize bushy stunt and corn stunt: A comparison of disease symptoms, pathogen host ranges, and vectors. *Phytopathology, 70*(7), 659–662. DOI: https://doi.org/10.1094/Phyto-70-659

Olaetxea, M., De Hita, D., Garcia, C. A., Fuentes, M., Baigorri, R., Mora, V., ... & Garcia-Mina, J. M. (2018). Hypothetical framework integrating the main mechanisms involved in the promoting action of rhizospheric humic substances on plant root and shoot growth. *Applied Soil Ecology, 123*, 521–537.

Oliveira, C. M. D., & Frizzas, M. R. (2022). Eight decades of *Dalbulus maidis* (DeLong & Wolcott) (Hemiptera, Cicadellidae) in Brazil: What we know and what we need to know. *Neotropical Entomology, 51*(1), 1–17. DOI: https://doi.org/10.1007/s13744-021-00932-9

Oliveira, C. M. de, & Lopes, J. R. S. (2004). Técnicas para criação da cigarrinha-do-milho e inoculação de molicutes e vírus em plantas. In *Doenças em milho: molicutes, virus, vetores, mancha por Phaeosphaeria*. Brasilia: Embrapa Informação Tecnológica.

Oliveira, C. M., Frizzas, M. R., & de Oliveira, E. (2020). Overwintering plants for *Dalbulus maidis* (DeLong and Wolcott) (Hemiptera: Cicadellidae) adults during the maize off-season in central Brazil. *International Journal of Tropical Insect Science, 40*, 1105–1111. DOI: https://doi.org/10.1007/s42690-020-00165-0

Oliveira, C. M., Lopes, J. R. S., & Nault, L. R. (2013). Survival strategies of *Dalbulus maidis* during maize off-season in Brazil. *Entomologia Experimentalis et Applicata, 147*(2), 141–153. DOI: https://doi.org/10.1111/eea.12059

Oliveira, C. M., Lopes, J. R. S., Dias, C. T. S., & Nault, L. R. (2004). Influence of latitude and elevation on polymorphism among populations of the corn leafhopper, *Dalbulus maidis* (DeLong and Wolcott) (Hemiptera: Cicadellidae), in Brazil. Environmental Entomology, 33, 1192–1199. DOI: https://doi.org/10.1603/0046-225X-33.5.1192

Oliveira, L. M., et al. (2023). Silicon-mediated resistance in plants: Recent advances and future perspectives. *Plants, 12*(4), 789. DOI: https://doi.org/10.3390/plants12040789

Pereira, P., Morales-Silva, T., Coelho, R. S., Pec, M., Azevedo, K. E. X., Prado, A., ... & Peñaflor, M. F. G. V. (2025). Silicon fertilization in maize increases attractiveness of nocturnal herbivore-induced plant volatiles to Spodoptera frugiperda natural enemies. *Pest Management Science*. DOI: **doi.org/10.1002/ps.8768**

Pereira, R. V., et al. (2021). The effects of biostimulants on induced plant defense. *Frontiers in Agronomy, 3*, 630596.

Piccolo, A. (2002). The supramolecular structure of humic substances: A novel understanding of humus chemistry and implications in soil science. In *Advances in Agronomy* (Vol. 75, pp. 57–134). Academic Press. https://doi.org/10.1016/S0065-2113(02)75003-7

Poole, N., Donovan, J., & Erenstein, O. (2021). Agri-nutrition research: Revisiting the contribution of maize and wheat to human nutrition and health. *Food Policy, 100*, 101976. DOI: https://www.sciencedirect.com/science/article/pii/S0306919220301809

Ramírez-Olvera, S. M., Trejo-Téllez, L. I., Pérez-Sato, J. A., & Gómez-Merino, F. C. (2019). Silicon stimulates initial growth and chlorophyll a/b ratio in rice seedlings and alters the concentrations of Ca, B, and Zn in plant tissues. *Journal of Plant Nutrition, 42*(16), 1928–1940. DOI: https://doi.org/10.1080/01904167.2019.1648678

Reynolds, O. L., Padula, M. P., Zeng, R., & Gurr, G. M. (2016). Silicon: Potential to promote direct and indirect effects on plant defence against arthropod pests in agriculture. *Frontiers in Plant Science, 7*, 744.

Romero, B., Olivier, C., Wist, T., & Prager, S. M. (2022). Do options matter? Settling behavior, stylet sheath counts, and oviposition of aster leafhoppers (Hemiptera: Cicadellidae) in two-choice bioassays. *Environmental Entomology, 51*(2), 460–470. DOI: https://doi.org/10.1093/ee/nvab148

Rose, M. T., Patti, A. F., Little, K. R., Brown, A. L., Jackson, W. R., & Cavagnaro, T. R. (2014). A meta-analysis and review of plant-growth response to humic substances: Practical implications for agriculture. *Advances in Agronomy, 124*, 37–89.

Sabato, E. de O., Landau, E. C., & Oliveira, C. M. (2014). *Recomendações para o manejo de doenças do milho disseminadas por insetos-vetores* (Circular Técnica, 205). EMBRAPA/CNPMS.

Salim, B. B. M., Abou El-Yazied, A., Salama, Y. A. M., Raza, A., & Osman, H. S. (2021). Impact of silicon foliar application in enhancing antioxidants, growth, flowering and yield of squash plants under deficit irrigation condition. *Annals of Agricultural Sciences*, *66*(2), 176-183. DOI: doi.org/10.1016/j.aoas.2021.12.003

Santos, D. G. dos, Dias, L. L. C., Avellar, G. S. de, Simeone, M. L. F., Oliveira, I. R. de, Menezes, C. B. de, … Mendes, S. M. (2025). Effect of silicon on *Melanaphis sorghi* (Hemiptera: Aphididae) infesting grain sorghum (*Sorghum bicolor*). *International Journal of Pest Management*, 1–10. DOI: https://doi.org/10.1080/09670874.2025.2453838

Savant, N. K., Snyder, G. H., & Datnoff, L. E. (1999). Silicon management and sustainable rice production. *Advances in Agronomy, 58*, 151–199. DOI: https://doi.org/10.1016/S0065-2113(08)60255-2

Savvas, D., & Ntatsi, G. (2015). Atividade bioestimulante do silício na horticultura. *Scientia Horticulturae, 196*, 66–81. DOI: https://doi.org/10.1016/j.scienta.2015.09.010

Schaller J., Brackhage, C., Dudel, E. G. (2012). Silicon availability changes structural carbon ratio and phenol content of grasses. *Environmental and Experimental Botany, 77*, 283–287. DOI: https://doi.org/10.1016/j.envexpbot.2011.12.009

Schiavon, M., Ertani, A., Nardi, S., & Varani, G. (2010). High molecular size humic substances enhance phenylpropanoid metabolism in maize (*Zea mays* L.). *Journal of Chemical Ecology, 36*, 662–669. DOI: https://doi.org/10.1007/s10886-010-9790-6

Singh, A., Kumar, A., Hartley, S., & Singh, I. K. (2020). Silicon: its ameliorative effect on plant defense against herbivory. *Journal of Experimental Botany*, *71*(21), 6730-6743. DOI: doi.org/10.1093/jxb/eraa300

Spanos, G. A.; Wrolstad, R. E. (1990). Influence of processing and storage on the phenolic composition of Thompson seedless grape juice. *Journal of Agricultural and Food Chemistry*, 38 7, 1565-1571.

Syman, K., Turpanova, R., Nazarova, G. A., et al. (2024). Role of oxidative stress enzymes in abiotic and biotic stress. *Caspian Journal of Environmental Sciences, 22*(2), 521–528.

Tsimogiannis, D., & Oreopoulou, V. (2019). Classification of phenolic compounds in plants. In *Polyphenols in plants* (pp. 263–284). Academic Press. DOI: https://doi.org/10.1016/B978-0-12-813768-0.00026-8

Van Nieuwenhove, G. A., Frías, E. A., & Virla, E. G. (2016). Effects of temperature on the development, performance and fitness of the corn leafhopper *Dalbulus maidis* (DeLong) (Hemiptera: Cicadellidae): Implications on its distribution under climate change. *Agricultural and Forest Entomology, 18*(1), 1–10.

Veljković, V. B., Biberdžić, M. O., Banković-Ilić, I. B., Djalović, I. G., Tasić, M. B., Nježić, Z. B., & Stamenković, O. S. (2018). Biodiesel production from corn oil: A review. *Renewable and Sustainable Energy Reviews, 91*, 531–548. DOI: https://www.sciencedirect.com/science/article/abs/pii/S136403211830234X

Vilela, M., et al. (2014). Induced resistance to *Diatraea saccharalis* (Lepidoptera: Crambidae) via silicon application in sugarcane. *Revista Colombiana de Entomología, 40*, 44–48.

Wadas, W., & Kondraciuk, T. (2025). The Role of Foliar-Applied Silicon in Improving the Growth and Productivity of Early Potatoes. *Agriculture*, *15*(5), 556. DOI: **doi.org/10.3390/agriculture15050556**

Wang, Y., Mostafa, S., Zeng, W., & Jin, B. (2021). Function and Mechanism of Jasmonic Acid in Plant Responses to Abiotic and Biotic Stresses. *International Journal of Molecular Sciences*, *22*(16), 8568. DOI: **doi.org/10.3390/ijms22168568**

Waquil, J. M., Fernandes, O. A., Nascimento, A. R., & Silva, R. A. (1999). Aspectos da biologia da cigarrinha-do-milho, *Dalbulus maidis* (DeLong & Wolcott) (Hemiptera: Cicadellidae). *Anais da Sociedade Entomológica do Brasil, 28*, 413–420. DOI: https://doi.org/10.1590/S0301-80591999000300005

Whitcomb, R. F., et al. (1986). *Spiroplasma kunkelii* sp. nov.: Characterization of the etiological agent of corn stunt disease. *International Journal of Systematic and Evolutionary Microbiology, 36*(2), 170–178. https://doi.org/10.1099/00207713-36-2-170

Xie, X., He, Z., Chen, N., Tang, Z., Wang, Q., & Cai, Y. (2019). The roles of environmental factors in regulation of oxidative stress in plant. *BioMed Research International, 2019*, 9732325.

Yakhin, O. I., Lubyanov, A. A., Yakhin, I. A., & Brown, P. H. (2017). Biostimulants in plant science: A global perspective. *Frontiers in Plant Science, 7*, 2049.

Yang, L., Han, Y., Li, P., et al. (2017a). Silicon amendment is involved in the induction of plant defense responses to a phloem feeder. *Scientific Reports, 7*, 4232. DOI: https://doi.org/10.1038/s41598-017-04571-2

Yang, L., Han, Y., Li, P., Wen, L., & Hou, M. (2017b). Silicon amendment to rice plants impairs sucking behaviors and population growth in the phloem feeder *Nilaparvata lugens* (Hemiptera: Delphacidae). *Scientific Reports, 7*, 1101. DOI: https://doi.org/10.1038/s41598-017-01060-4

Ye, M., et al. (2013). Priming of jasmonate-mediated antiherbivore defense responses in rice by silicon. *Proceedings of the National Academy of Sciences, 110*, 631–639.

Supplementary material

Table S1 Analysis of the composition of red latosol – horizon C

Chemical Analysis (Macronutrients & Acidity)			Exchange Complex & Micronutrients)			Physical Analysis (Texture)		
Parameter	**Value**	**Unit**	**Parameter**	**Value**	**Unit**	**Parameter**	**Value**	**Classification**
pH (KCl)	5.6	-	SB	2.18	cmol_c/dm³	Clay	58	-
K	35.98	mg/dm³	t	2.22	cmol_c/dm³	Silt	30	-
P	1.08	mg/dm³	T	4.40	cmol_c/dm³	Sand	12	-
Ca	1.93	cmol_c/dm³	V	49.60	%	Textural Class	-	Soil Type 3
Mg	0.16	cmol_c/dm³	m	1.80	%	-	-	-
Al	0.04	cmol_c/dm³	OM	1.29	dag/kg	-	-	-
H+Al	2.22	cmol_c/dm³	P-rem	7.49	mg/L	-	-	-
-	-	-	S	168.30	mg/dm³	-	-	-
-	-	-	B	0.01	mg/dm³	-	-	-
-	-	-	Cu	4.08	mg/dm³	-	-	-
-	-	-	Fe	62.95	mg/dm³	-	-	-
-	-	-	Mn	19.16	mg/dm³	-	-	-
-	-	-	Zn	1.58	mg/dm³	-	-	-

Table S2 Chemical composition of the SH- based commercial formulation Solohumics® (Class A; Solohumics Indústria e Comércio de Fertilizantes LTDA, Viana, Brazil)

Parameter	Value
Electrical Condutivity(mS/cm)	3.66
pH	7.9
Density (g/kg)	1.04
Total Nitrogen (%w/w)	1.40
Water Soluble Potassium (%w/w)	1.50
Organic Carbon (%w/w)	45.4
Organic Matter (% w/w)	78.09
Humic Acid (% w/w)	26.99
Fulvic Acid (% w/w)	6.92
C/NRatio	32.14

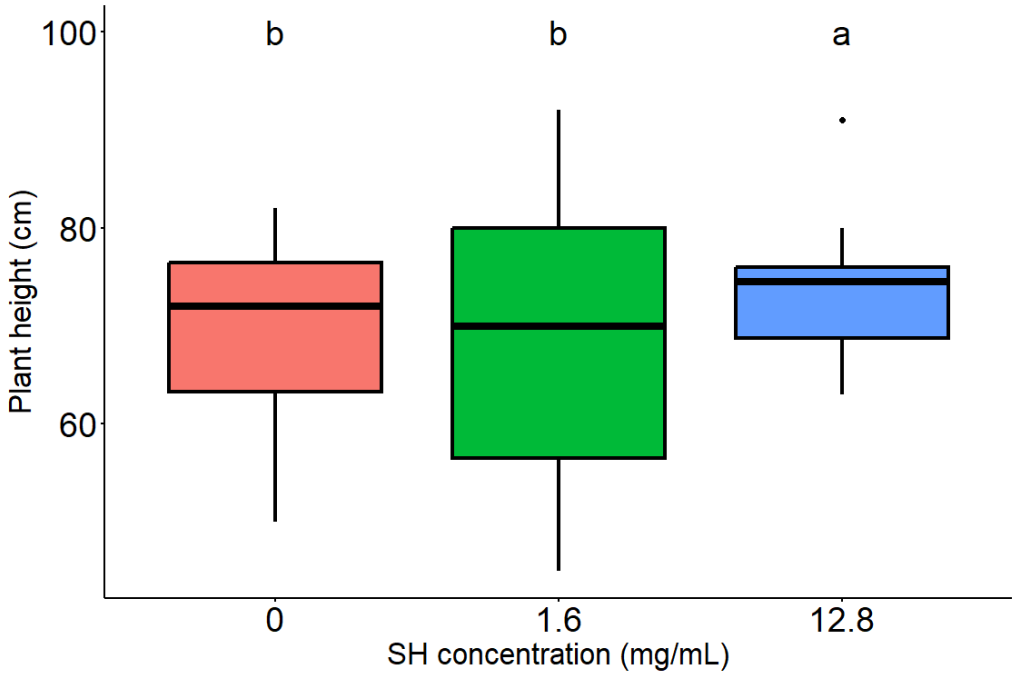

Fig. S1 Plant height (± standard error, N = 12) in maize plants treated with HS at concentrations of 1.6 mg and 12.8 mg, and in untreated plants. Biomass was significantly higher in plants treated with 12.8 mg of HS ($F = 3.3456$; d.f. = 2,33; $P = 0.04753$). A GLM was used. Different letters indicate significant differences

Artigo 2- Dose-dependent effect of plant volatiles on the oviposition preference of the corn leafhopper *Dalbulus maidis*

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Short-running title: Synthetic plant volatiles on *D. maidis*

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Abstract – Maize (*Zea mays* L.) is a major annual crop cultivated worldwide. In the Americas, the corn leafhopper *Dalbulus maidis* (DeLong) (Hemiptera: Cicadellidae) is a key pest of this crop, causing direct damage to plants through phloem feeding and indirect damage by transmitting phytopathogens. Despite extensive efforts, effective management and control of this pest remain challenging. In this study, we assessed the effects of volatile organic compounds (VOCs)—myrcene, linalool, and methyl salicylate (MeSA), which are emitted by maize either constitutively or in response to herbivory plants—and methyl jasmonate (MeJA), a compound detectable in the volatile emissions of some maize genotypes. Dual-choice assays consisted of releasing female leafhoppers into cages containing a pair of maize plants: one associated with a dispenser loaded with the tested VOC at one of the three concentrations (2, 20, or 200 ng μL^{-1}) and the other with a dispenser containing only the solvent (paraffin oil). Myrcene at 20 ng μL^{-1} significantly reduced oviposition, whereas MeSA at 2 ng μL^{-1}, myrcene at 200 ng μL^{-1}, and linalool at 200 ng μL^{-1} significantly increased the number of eggs laid on maize plants. MeJA, at any concentration, had no effect on oviposition preference of *D. maidis*. These results demonstrate a dose-dependent behavioral response of *D. maidis* to specific VOCs, with myrcene acting as a repellent at moderate dose and MeSA, myrcene (high dose), and linalool functioning as attractants. Such responses underscore the potential of these synthetic compounds for integration into semiochemical-based strategies aimed at manipulating *D. maidis* oviposition, either by deterring or attracting females, depending on the dose and compound used.

Keywords: semiochemicals, olfactory response, *Zea mays*, linalool, myrcene, methyl salicylate

INTRODUCTION

Maize (*Zea mays* L.) is a widely cultivated annual monocot and one of the world's most important crops. The Americas are the leading production region, with the United States and Brazil among the top producers. Brazil ranks third in global maize production and is among the largest producers and exporters, producing 115.7 million tons in 2023/2024 season (USDA, 2025; CONAB, 2025). The crop holds high economic and social relevance, serving diverse purposes, including human consumption, animal feed, ethanol production, and applications in high-tech industries (Ranum, Peña-Rosas & Garcia-Casal et al., 2014; Contini et al., 2019).

In Brazil, the corn leafhopper *Dalbulus maidis* (DeLong) (Hemiptera: Cicadellidae) is a key pest affecting maize crops (Oliveira & Frizzas, 2022). Native to the Americas, its distribution extends from the southern United States to South America (Carloni, Carpane, Paradell, Laguna & Pecci, 2013; Jones, Esparza-Diaz, Wayadande & Badillo-Vargas, 2021; Oliveira & Frizzas, 2022; Rodríguez-del-Bosque et al., 2024), with northward expansion in North America likely driven by global warming, which favors its development and performance (Van Nieuwenhove, Frías & Virla, 2016; Santana, Kumar, Da Silva, Pereira, & Picanço, 2019; Faris et al., 2024). *D. maidis* is a phloem-feeding insect typically found in the maize whorl, with seasonal and temperature-dependent fluctuations in abundance (Davis, 1966; Todd, Madden & Nault, 1991). Its life cycle lasts about 25–30 days, with females laying 400–600 eggs, within the epidermis and central vein of maize leaves (Waquil et al., 1999; Sabato, Landau & Oliveira, 2014).

Direct damage from feeding can reduce plant vigor and yield, but the most severe losses result from transmission of phytopathogens, including *Spiroplasma kunkelii* (maize bushy stunt) and maize bushy stunt phytoplasma (red leaf stunt), both Mollicutes causing chlorosis, leaf reddening, stunting, excessive tillering, and malformed ears (Whitcomb et al., 1986; Nault, 1980). The species also transmits maize rayado fino virus (MRFV), which causes chlorotic streaking and growth delays (Gámez, 1973). In Brazil, high incidences of these diseases have caused widespread and persistent outbreaks across multiple cropping cycles, particularly in the Northeast, Central-West, and South (Oliveira & Frizzas, 2022).

The high efficiency of *D. maidis* in transmitting phytopathogens, combined with its high dispersal ability, survival on refuge plants during the off-season, and insecticide resistance, makes *D. maidis* a persistent management challenge (Oliveira, Lopes & Nault, 2013; Oliveira, Frizzas & de Oliveira, 2020; Cota et al., 2021; Machado, Souza, Dias, Sacilotto & Omoto, 2024). Control of *D. maidis* relies mainly on seed treatment and foliar insecticides applied from

emergence to the V8 stage, when maize has developed eight fully expanded leaves (Oliveira & Frizzas, 2022), with 97 registered products in Brazil, including neonicotinoids, organophosphate, pyrethroids, and tetranortriterpenoid (AGROFIT, 2025). Despite the broad availability of synthetic insecticides, *D. maidis* management still faces major challenges, often resulting in the recurrent use of chemical control involving multiple phytosanitary products. Recently, reduced susceptibility of *D. maidis* to pyrethroid and neonicotinoid insecticides has been reported, helping to explain the difficulty in controlling its populations in Brazil (Machado, Souza, Dias, Sacilotto, Omoto, 2024). Complementary tactics include biological control, cultural practices, and partially resistant cultivars (Cota et al., 2021; Pozebon et al., 2022). However, biological control can be hampered by the protein–lipid brochosome layer and the leafhopper's self-cleaning behavior, which together reduce conidia adhesion to the cuticle (Lopes, Faria, Oliveira, 2025).

Semiochemicals offer a promising alternative to enhance pest monitoring and control (Gross & Franco, 2022; Serdo, 2024). Volatile organic compounds (VOCs) emitted by plants can attractant or repel insect herbivores, enabling behavioral manipulation (Szendrei & Rodriguez-Saona, 2010; Piesik et al., 2013). While *D. maidis* relies heavily on visual cues, plant olfactory stimuli may enhance host location or elicit behavioral responses in the absence of visual signals (La Grange, Schröder, Glinwood, Ignell & Krüger, 2017; Coll-Aráoz et al., 2019). Beyond feeding cues, oviposition preferences are critical for understanding host selection and developing behavioral control strategies (Ramos, Esteves, Cortés & Lopes, 2020; Melchert, Manzano, Virla & Luft-Albarracin, 2023; de Oliveira et al., 2024). Attractive VOCs can improve the effectiveness of traps used in pest monitoring (Zhang et al., 2022), while combinations of repellents and attractants VOCs can be integrated into push-pull systems (Pickett, Woodcock, Midega & Khan, 2014; La Grange et al., 2017; El-Ghany, 2019).

In this study, we investigated whether synthetic versions of the VOCs myrcene, linalool, methyl salicylate (MeSA), and methyl jasmonate (MeJA) affect *D. maidis* oviposition preference. Myrcene and linalool are monoterpenes emitted constitutively by several maize genotypes (Degen, Dillmann, Marion-Poll & Turlings, 2004; Oluwafemi, Birkett, Caulfield & Pickett, 2012) and are often induced at higher levels following herbivory (Yan & Wang, 2006; Skoczek et al., 2017; Silva, Canale, Magalhães, Lopes & Bento, 2025). MeSA a volatile methyl ester form of salicylic acid, being commonly synthetized and released by maize in response to insect herbivory (Oluwafemi, Birkett, Caulfield & Pickett, 2012; Gondor et al., 2022), including herbivory by the corn leafhopper (Hill et al., 2024; Sanches et al., 2025), and has been

previously reported as a repellent to other leafhopper species (Oluwafemi, Bruce, Pickett, Ton & Birkett, 2011). MeJA, a volatile derived of jasmonic acid, has been detected in the volatile emissions of only certain maize genotypes in response to *D. maidis* herbivory (Hill et al., 2024). Based on this information, we hypothesized that associating maize plants with the release of the monoterpenes myrcene and linalool would increase their attractiveness for *D. maidis* oviposition, whereas the release of MeSA and MeJA—compounds typically linked with herbivory-induced defenses—would reduce plant attractiveness.

MATERIALS AND METHODS

Plants and Insects

Maize seeds (hybrid DKB390) were grown in a greenhouse located in Lavras, Minas Gerais, Brazil (21°13'35.1"S, 44°58'30.6"W), without light or temperature control, from July to December 2024. Sowing was performed in plastic pots (400 mL capacity) containing a commercial substrate composed of pine bark and peat (SV Substrato Vegetal, Vida Verde Indústria e Comércio de Insumos Orgânicos Ltda, Mogi Mirim, Brazil). Prior to planting, all seeds were treated with a fungicide based on Carboxin and Thiram (Vitavax Ultra, UPL do Brasil, Ituverava, Brazil). Two seeds were sown per pot, and five days after emergence, thinning was carried out, leaving only one seedling per pot. Plants were maintained in the greenhouse, fertilized once with NPK 4-14-8 (5 g per pot) seven days after germination, and irrigated as needed. In all experiments, 15- to 20-day-old plants at the V4 stage were used.

The laboratory colony of the corn leafhopper *D. maidis* was established using hundreds of adults collected from maize fields in Lavras, Minas Gerais, Brazil (21°12'51.1"S, 45°03'18.1"W). Field-collected adults were kept for 48 h in cages containing healthy maize plants for oviposition. To eliminate potentially infected individuals from the rearing, the laboratory colony was initiated exclusively from eggs, which were excised from leaves five days after deposition (the period necessary to visualize the eggs within the plant tissue) and placed in Petri dishes lined with moistened filter paper (Ramos et al. 2020). Newly hatched *D. maidis* nymphs were transferred to healthy maize plants. The colony was maintained under controlled laboratory conditions (25 ± 2 °C, 70 ± 10% RH, and a 14 h photophase) in voile cages (23 × 45 × 93 cm). Plants were replaced as needed, however, leaves containing eggs were preserved, and the nymphs were subsequently transferred to new plants. After adult emergence, males and females were kept together in the same cage for seven days to allow mating.

Preparation of Dispensers

The plant-derived volatile organic compounds (VOCs) evaluated in this study were commercially obtained as synthetic standards: myrcene (99%), linalool (95%), methyl salicylate (MeSA, 99%), and methyl jasmonate (MeJA, 95%) (Sigma-Aldrich, St. Louis, USA). Solutions at concentrations of 2 ng μL^{-1}, 20 ng μL^{-1}, and 200 ng μL^{-1} were prepared by diluting each compound in paraffin oil (Sigma-Aldrich, St. Louis, USA). Dispenser consisted of dental cotton rolls (4 cm height x 1 cm diameter) inserted into the upper end of a wooden stick (30 cm height), which was wrapped in plastic film to prevent solution absorption. A 200 µL aliquot of each VOC solution was applied to the cotton roll. Control dispensers received 200 µL of pure paraffin oil.

Oviposition Preference and Data Analyses

The dual-choice bioassays were conducted in a greenhouse with no light or temperature control, located in Lavras, Minas Gerais, Brazil (21°13'35.1"S, 44°58'30.6"W), between July and December 2024. Each assay evaluated the oviposition preference of *D. maidis* for maize plants associated with a control dispenser (paraffin oil) versus plants associated with a dispenser containing one of the VOCs at one of three concentrations (2, 20, or 200 ng μL^{-1}). These concentrations were selected based on preliminary trials. Four hours prior to the assays, one plant was paired with a dispenser containing paraffin oil (control), while the other was paired with a dispenser containing one of the synthetic compounds, both placed inside a voile-covered cage (55 × 55 × 52 cm) (Figure 1 and S1). This period allowed the volatile concentration around the plants to stabilize, ensuring a consistent exposure level when insects were introduced.

Six 7-day-old mated females were released into each bioassay cage and allowed to oviposit for 48 hours. After this period, the females were removed, and the plants remained in the greenhouse for five days. This interval was chosen because the eggs turn whitish and develop red ocelli after this time, which facilitates their visualization and counting (Oliveira et al., 2024). The leaves were subsequently detached from the plants. Each leaf was then examined under a binocular stereomicroscope (7×–45× magnification), and the total number of eggs was counted. Each cage was considered one replicate, with 12 replicates per treatment conducted simultaneously. Cages in which females laid fewer than 10 eggs were excluded from the analyses, as such low oviposition may not represent a true preference. The number of eggs laid on each plant was analyzed using Generalized Linear Models (GLMs) with a binomial error

distribution, in which the number of eggs laid on a given plant was considered a “success” and the number of eggs laid on the alternative plant (total – eggs) was considered a “failure”. Models were fitted using the function glm() from the base R stats package. When overdispersion was detected, a quasibinomial distribution was applied. Graphs were prepared based on the proportion of eggs laid on each treatment relative to the total. All analyses were conducted in R version 4.4.1 (R Core Team, 2024).

Release Rate of Volatile Compounds from the Dispensers

To estimate the release rates of the volatile compounds, collections of synthetic VOCs emitted by the dispensers at each concentration were performed using a “push–pull” volatile collection system. Three dispensers per compound were prepared for each of the three tested concentrations and immediately placed inside polyester bags connected to the aeration system, with an incoming air flow rate of 800 mL min^{-1} per chamber. Air was drawn from each chamber at a flow rate of 125 mL min^{-1} per chamber using a vacuum pump connected to volatile collection filters containing 30 mg of HayeSep-Q® adsorbent polymer (Hayes Separation Inc., Bandera, TX, USA). Collections lasted 1 hour. Adsorbed volatiles were eluted with 100 µL of hexane (95%, Sigma-Aldrich, St. Louis, USA), transferred to sealed glass vials and stored at –20 °C until analysis. Analyses were performed using a gas chromatograph coupled to a flame ionization detector (GC-FID), with helium as the carrier gas at a linear velocity of 31.9 cm s^{-1}. A 1 µL aliquot of each sample was injected into a non-polar HP-5 capillary column (25 m length, 0.25 mm internal diameter, and 0.1 µm film thickness). After injection, the column temperature was held at 40°C for 5 min, then increased at a rate of 5 °C min^{-1} to 150 °C, followed by 20 °C min^{-1} to 250 °C, and held for 10 min. Detector signals were recorded and processed using the GC-FID software. For compound identification, standards were analyzed on a GC–MS under the same chromatographic conditions as for the GC-FID analyses, and mass spectra were compared with the NIST08 library. Quantification was estimated based on external calibration curves constructed from five concentrations of each compound.

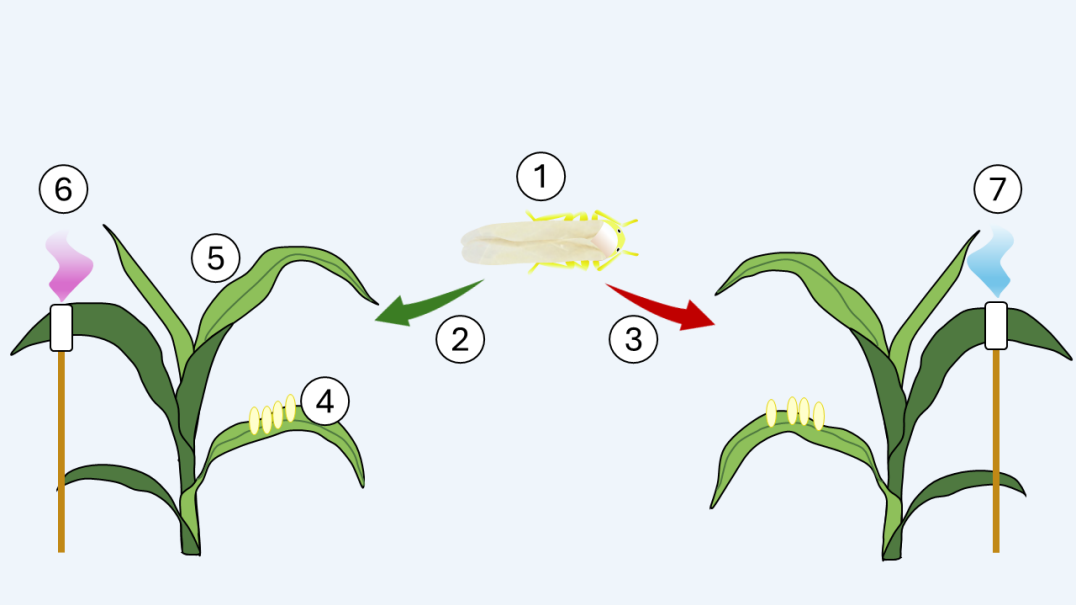

Figure 1. Schematic representation of the oviposition preference bioassay of *Dalbulus maidis*. (1) Adult female of *D. maidis*; (2) green arrow indicating attraction; (3) red arrow indicating repellence; (4) oviposition by the female on the maize plant; (5) maize plants 15–20 days old (V4 stage); (6) dispenser containing synthetic compounds (methyl salicylate – MeSA, methyl jasmonate – MeJA, myrcene, or linalool) at concentrations of 2, 20, or 200 ng·µL^{-1}; (7) dispenser containing only the solvent (paraffin oil), used as control.

RESULTS

In dual-choice assays conducted in a greenhouse, we evaluated the influence of the release of the VOCs myrcene, linalool, MeSA, and MeJA—each applied at three concentrations—on the oviposition behavior of *D. maidis* females. A significant reduction in the mean number of eggs was observed on maize plants associated with the release of myrcene at 20 ng·µL^{-1} (release rate of 251.5 ± 74.2 ng h^{-1}), compared with plants exposed to control dispensers containing only paraffin oil (Table 1, Figure 2A). Conversely, a significant increase in the mean number of eggs was recorded on maize plants associated with myrcene at 200 ng·µL^{-1} (release rate of 770.9 ± 158.1 ng h^{-1}), linalool at 200 ng·µL^{-1} (release rate of 50.5 ± 14.4 ng h^{-1}), and MeSA at 2 ng·µL^{-1} (release rate of 5.0 ± 2.5 ng h^{-1}) relative to the control treatment (Table 1, Figure 2A-C). No significant differences in *D. maidis* oviposition preference were detected between plants associated with myrcene at 2 ng µL^{-1}, linalool at 2 or 20 ng µL^{-1}, or MeSA at 20 or 200 ng µL^{-1} and those exposed to the control (Table 1, Figures 2A and 2C). These results indicate a dose-dependent effect of myrcene, acting as a repellent for oviposition at 20 ng·µL^{-1} and as an attractant at 200 ng·µL^{-1}. MeJA, in turn, did not influence the oviposition behavior of *D. maidis* at any of the tested concentrations (Table 1, Figure 2D).

Table 1. Number of eggs laid by *Dalbulus maidis* on each maize plant in dual-choice assays, comparing plants associated with the solvent paraffin oil (Control) and plants associated with VOCs: Myrcene, Linalool, Methyl salicylate (MeSA), and Methyl jasmonate (MeJA), at different concentrations (2, 20, and 200 ng·µL^{-1}). The release rate of each VOC was estimated from headspace collections of the dispensers under ambient conditions, which were analyzed by GC-FID.

Concentration (ng·µL^{-1})	**Release rate (ng·µL^{-1}.h^{-1})**	**Eggs per plant (mean±SE)**		**n**	**χ^2**	**df**	***P***
		Control	**Myrcene**				
2	13.9±5.3	18.1±6.1	9.6±3.8	7	2.16	1,12	0.17
20	251.5±74.2	11.9±2.4	2.0±0.5	7	82.27	1,12	**<0.01**
200	770.9±158.1	1.7±0.9	4.3±1.3	12	9.06	1,22	**<0.01**
		Control	**Linalool**				
2	8.6±4.9	12.3±4.7	6.7±3.3	6	0.61	1,10	0.43
20	18.9±2.5	7.7±3.8	4.3±1.8	12	0.16	1,22	0.69
200	50.5±14.4	6.5±5.3	11.7±1.7	6	4.41	1,10	**0.03**
		Control	**MeSA**				
2	5.0±2.5	40.8±7.2	72.2±8.7	12	6.23	1,22	**0.02**
20	77.2±22.6	60.8±11.1	64.7±7.5	12	0.71	1,22	0.41
200	184.6±46.8	33.2±5.6	28.4±5.0	10	1.07	1,18	0.31
		Control	**MeJA**				
2	2.0±0.8	68.3±10.8	67.1±8.9	12	0.01	1,22	0.89
20	8.0±2.8	55.0±16.9	37.3±21.4	12	0.11	1,22	0.74
200	11.4±4.8	40.1±10.0	27.7±8.8	11	1.20	1,20	0.28

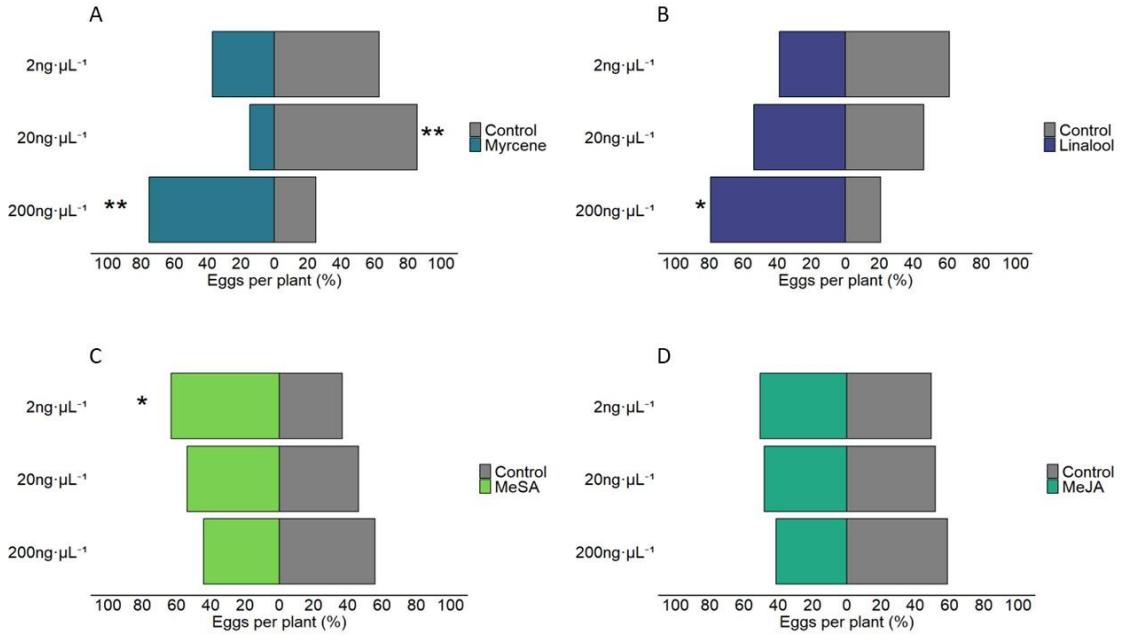

Figure 2. Mean percentage of total eggs laid by *Dalbulus maidis* on each maize plant in dual-choice assays, comparing plants associated with the solvent (paraffin oil) (Control) and plants associated with VOCs: (A) Myrcene, (B) Linalool, (C) Methyl salicylate (MeSA), and (D) Methyl jasmonate (MeJA), at three concentrations (2, 20, and 200 ng·µL^{-1}).

*$P < 0.05$, **$P < 0.01$

DISCUSSION

Due to the challenges in controlling *D. maidis*, often exacerbated by the continuous use of insecticides (Machado et al. 2024), it is crucial to explore alternative strategies for monitoring and managing this pest. In dual-choice cage experiments under semi-field conditions, where we compared egg laying by *D. maidis* on maize plants associated with VOC dispensers, we found a spectrum of oviposition responses, ranging from neutral to repellent or attractive, depending on the compound identity and concentration. Linalool increased plant attractiveness for oviposition only at the highest concentration tested. Myrcene exhibited contrasting effects, with the intermediate concentration reducing oviposition and the highest concentration stimulating it. While MeJA did not influence oviposition preference, MeSA at the lowest concentration increased egg deposition by *D. maidis*.

The influence of myrcene on the behavior of herbivorous insects has been extensively studied, revealing variable effects depending on the species. This compound can act as an attractant for several species, including leafhoppers (Coll-Aráoz et al., 2019; Dong et al., 2024; Huang et al., 2024; Liu et al., 2024), but it has also been reported to exert repellent effects on various taxa (Dardouri et al., 2019; Sun et al., 2020; Cao et al., 2022; Yan et al., 2023) or have

no detectable influence (Bleeker et al., 2009; Sullivan et al., 2021). In our study, *D. maidis* exhibited this full range of responses, with myrcene shifting from a neutral cue to a repellent and then to an attractant as the concentration increased, with average release rates ranging from 13 to 770 ng.h^{-1}. The effect of myrcene on oviposition preference also appears to be species-specific. For instance, a concentration similar to that which elicited attraction in *D. maidis* (200 ng·μL^{-1}) reduced oviposition by the moth *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) on *Mentha spicata* (L.) (Lamiales: Lamiaceae) plants (Yan et al., 2023). These findings highlight the importance of species–concentration interactions in shaping the behavioral effects of myrcene exposure and indicate that its potential as a semiochemical for integrated pest management will depend on careful optimization of formulation and application.

Linalool is a multifunctional VOC involved in mediating interactions between plants and insects from different ecological guilds and can function as either an attractant or a repellent for herbivorous insects, depending on the mode of application and the concentration used (Zhang et al., 2023). While its release has been reported to deter the oviposition of Diptera and Lepidoptera species (Reisenman, Riffell, Bernays & Hildebrand, 2010; Kim, Seo & Kim, 2020; Papanastasiou, Ioannou & Papadopoulos, 2020), linalool may also attract herbivorous insects, including leafhoppers and other Hemiptera species that are pests in maize crops (Oluwafemi et al., 2012; Coll-Aráoz et al., 2019; Jacobi et al., 2021). Our results are consistent with these studies reporting that maize-associated Hemiptera species are attracted to linalool. However, for *D. maidis*, the attractive effect of linalool on oviposition was detected only at the highest concentration tested (200 ng.μL^{-1}, release rate ~50 ng.h^{-1}). This release rate of 50 ng. h^{-1}, corresponding to dispensers loaded with 200 ng.μL^{-1} linalool, closely matches the emission of linalool by temperate maize hybrids (around 60 ng.h^{-1}), which has been associated with the greater attractiveness of maize to both *D. maidis* and *Dichelops furcatus* (F.) compared with a tropical hybrid (Hemiptera: Pentatomidae) (Coll-Aráoz et al., 2019; Jacobi et al. 2021).

The behavioral response of herbivorous insects to MeSA is highly variable. A recent meta-analysis reported that MeSA tends to repel cell-content feeders, such as mites and thrips, while attracting chewing herbivores (Rossetti, Kuzmanich, Videla, Ben-Zvi & Rodriguez-Saona, 2025). For phloem-feeding insects, the response is classified as neutral, reflecting a balance between studies reporting repellent and attractive effects (Rossetti et al., 2025). The use of MeSA as a pest management tool has been reported in the literature, with repellent effects on herbivores (Byers et al., 2021; dos Reis Brugnerotto et al., 2024), including the leafhopper of the genus *Cicadulina* (Hemiptera: Cicadellidae) that occur in maize crops (Oluwafemi et al.,

2011), as well as the inhibition of oviposition in butterflies such as *Pieris brassicae* (L.) (Lepidoptera: Pieridae) (Groux et al., 2014). However, our findings demonstrated that MeSA stimulated oviposition by *D. maidis* only at the lowest concentration tested (2 ng·μL^{-1}, release rate of 5.0 ng.h^{-1}), while higher concentrations had neutral effects. This pattern is consistent with the volatile profile of many maize genotypes, which typically do not release more than 10.0 ng.h^{-1} of this compound (Coll-Aráoz et al. 2020), even under high infestation by *D. maidis* or virus infection (Hill et al. 2024; Sanches et al. 2025; Silva et al. 2025). Therefore, MeSA at the low concentration may act as a host location cue for *D. maidis*.

While herbivore responses to MeSA have been examined across several taxa, little is known about the direct effects of MeJA on herbivore behavior (Bruce & Pickett, 2011). MeJA is a key VOC involved in plant responses to biotic stress, playing a crucial role in activating both direct and indirect defenses against herbivorous insects (Zhang, Zhang, Melotto, Yao & He, 2017). To the best of our knowledge, previous studies have focused on the use of MeJA in pest management as an elicitor of plant resistance, applied either exogenously applied or as an airborne signal to plants. In these cases, plants become more resistant through activation of the jasmonic acid pathway, often resulting in repellent effects on pest species, including phloem-feeding insects (Cao, Wang & Liu, 2014; Bayram & Tonğa, 2018; Tonğa, Şeker, Çakmak, Temiz & Bayram, 2022). Other studies have investigated direct effects of MeJA emission in attracting natural enemies of herbivores, such as parasitoids (James, 2005; James & Grasswit, 2005). Because MeJA is derived from jasmonic acid pathway, its detection by herbivores could indicate increased plant resistance and, consequently, act as a repellent cue. However, in our study, the release of MeJA did not influence host selection by *D. maidis* at any of the concentrations tested. This finding also suggests that the exposure time and airborne dose of MeJA were likely insufficient to induce resistance in maize plants associated with this compound to *D. maidis*, given that the dispensers were positioned only a few centimeters away. Furthermore, this neutral effect may be related to the fact that MeJA is not typically emitted at relevant levels by maize genotypes (Borrego and Kolomiets, 2016; Hill et al., 2024).

Females of *D. maidis* prefer to oviposit on maize plants infested with conspecifics rather than on uninfested plants, and their offspring perform better on conspecific-infested plants (Oliveira et al. 2024). Our findings suggest that the increased levels of myrcene and linalool in *D. maidis*-infested plants (Sanches et al. 2025) may contribute to recognition of, and attraction to, conspecific-infested plants. From an applied perspective, these results indicate that VOCs such as myrcene (at release rates of 250 and 770 ng.h^{-1}), linalool (50 ng.h^{-1}), and MeSA (5

ng.h^{-1}) are promising tools for behavioral manipulation of *D. maidis*, potentially enhancing control efforts. These results expand the prospects for incorporating synthetic VOCs into semiochemical-based tactics for integrated pest management (IPM), particularly through push-pull approaches. Such tactics could combine attractive compounds—such as myrcene (200 ng μL^{-1}), linalool (200 ng μL^{-1}), and MeSA (2 ng μL^{-1})— released from the border planting lines of maize crops, with repellent compounds, such as myrcene at lower concentration (20 ng μL^{-1}), applied at the center of the field, to manipulate the behavior of *D. maidis* and concentrate its population along the borders, thereby facilitating control measures. Our findings support future research aiming to evaluate the behavioral effects of additional maize-emitted VOCs on *D. maidis*, as well as to investigate mixtures of volatile compounds that may act synergistically to influence pest behavior. Furthermore, assessing the efficacy of VOC-releasing devices under field conditions is essential.

Conflict of interest disclosure

The authors declare no conflict of interest.

Author Contribution

TCBC: conceptualization, investigation, project administration, validation, writing – original draft preparation, review & editing; EBSC: data curation, formal analysis, visualization, writing – original draft preparation, review & editing; VXNR: investigation, writing – review & editing; MFGVP: conceptualization, funding acquisition, supervision, writing – original draft preparation, review & editing.

Data availability statement

[DATASET] Peñaflor, M. F. G. V.; Cândido, T. C. B.; 2025; DATA: Dose-dependent effect of synthetic plant volatiles on the oviposition preference of corn leafhoppers (*Dalbulus maidis*);OSF; https://doi.org/10.17605/OSF.IO/6UJMH

REFERENCES

AGROFIT. Sistemas de agrotóxicos fitossanitários. https://agrofit.agricultura.gov.br/agrofit_cons/principal_agrofit_cons

Ali, J. G., & Agrawal, A. A. (2012). Specialist versus generalist insect herbivores and plant defense. *Trends in plant science*, *17*(5), 293-302. DOI: 10.1016/j.tplants.2012.02.006

Bayram, A., & Tonğa, A. (2018). Methyl jasmonate affects population densities of phytophagous and entomophagous insects in wheat. *Applied Ecology & Environmental Research*, *16*(1). DOI: 10.15666/aeer/1601_181198

Bleeker, P. M., Diergaarde, P. J., Ament, K., Guerra, J., Weidner, M., Schutz, S., ... & Schuurink, R. C. (2009). The role of specific tomato volatiles in tomato-whitefly interaction. *Plant Physiology*, *151*(2), 925-935. DOI: 10.1104/pp.109.142661

Borrego, E. J., & Kolomiets, M. V. (2016). Synthesis and Functions of Jasmonates in Maize. *Plants*, *5*(4), 41. DOI: 10.3390/plants5040041

Bruce, T. J., & Pickett, J. A. (2011). Perception of plant volatile blends by herbivorous insects–finding the right mix. *Phytochemistry*, *72*(13), 1605-1611. DOI: 10.1016/j.phytochem.2011.04.011

Byers, J. A., Maoz, Y., Cohen, B., Golani, M., Fefer, D., & Levi-Zada, A. (2021). Protecting avocado trees from ambrosia beetles by repellents and mass trapping (push–pull): experiments and simulations. *Journal of Pest Science*, *94*, 991-1002. DOI: 10.1007/s10340-020-01310-x

Cao, D., Liu, J., Zhao, Z., Yan, X., Wang, W., & Wei, J. (2022). Chemical compounds emitted from *Mentha spicata* repel *Aromia bungii* females. *Insects*, *13*(3), 244. DOI: **10.3390/insects13030244**

Cao, H. H., Wang, S. H., & Liu, T. X. (2014). Jasmonate-and salicylate-induced defenses in wheat affect host preference and probing behavior but not performance of the grain aphid, *Sitobion avenae*. *Insect science*, *21*(1), 47-55. DOI: **10.1111/1744-7917.12023**

Carloni, E., Carpane, P., Paradell, S., Laguna, I., & Pecci, M. G. (2013). Presence of *Dalbulus maidis* (Hemiptera: Cicadellidae) and of *Spiroplasma kunkelii* in the temperate region of Argentina. *Journal of Economic Entomology*, *106*(4), 1574-1581. DOI: 10.1603/EC12323

Coll-Aráoz, M. V., Jacobi, V. G., Fernandez, P. C., Albarracin, E. L., Virla, E. G., Hill, J. G., & Catalan, C. A. N. (2019). Volatiles mediate host-selection in the corn hoppers *Dalbulus maidis* (Hemiptera: Cicadellidae) and *Peregrinus maidis* (Hemiptera: Delphacidae). *Bulletin of entomological research*, *109*(5), 633-642. DOI: 10.1017/S000748531900004X

Coll-Aráoz, M. V., Hill, J. G., Luft-Albarracin, E., Virla, E. G., & Fernandez, P. C. (2020). Modern maize hybrids have lost volatile bottom-up and top-down control of *Dalbulus maidis*, a Specialist Herbivore. J Chem Ecol *46*, 906–915. DOI: 10.1007/s10886-020-01204-3

CONAB - COMPANHIA NACIONAL DE ABASTECIMENTO. Séries históricas. https://portaldeinformacoes.conab.gov.br/safra-serie-historica-graos.html.

Contini, E., Mota, M. M., Marra, R., Borghi, E., Miranda, R. D., Silva, A. D., ... & Mendes, S. M. (2019). Milho: caracterização e desafios tecnológicos. *Brasília: Embrapa. (Desafios do Agronegócio Brasileiro, 2)*.

COTA, L. V., de Oliveira, I. R., da Silva, D. D., Mendes, S. M., da Costa, R. V., de Souza, I. R. P., & da Silva, A. F. (2021). Manejo da cigarrinha e enfezamentos na cultura do milho. *EMBRAPA/Centro Nacional de Pesquisa de Milho e Sorgo*.

Dardouri, T., Gautier, H., Ben Issa, R., Costagliola, G., & Gomez, L. (2019). Repellence of *Myzus persicae* (Sulzer): evidence of two modes of action of volatiles from selected living aromatic plants. *Pest management science*, *75*(6), 1571-1584. DOI: **10.1002/ps.5271**

Davis, R. (1966). Biology of the leafhopper Dalbulus maidis at selected temperatures. DOI: **10.1093/jee/59.3.766**

Oliveira, M. C., Morales-Silva, T., Pereira, P., Pec, M., de Souza, L. A., & Peñaflor, M. F. G. (2024). Plant-mediated facilitation to conspecifics and heterospecifics by two phloem-feeding maize pests: The influence of insect identity and order of arrival. *Ecological Entomology*, *49*(5), 662-672. DOI: **10.1111/een.13338**

Degen, T., Dillmann, C., Marion-Poll, F., & Turlings, T. C. (2004). High genetic variability of herbivore-induced volatile emission within a broad range of maize inbred lines. *Plant physiology*, *135*(4), 1928-1938. DOI: 10.1104/pp.104.039891

Dong, Y., Chen, D., Zhou, S., Mao, Z., & Fan, J. (2024). Identification of Attractants from Three Host Plants and How to Improve Attractiveness of Plant Volatiles for *Monochamus saltuarius*. *Plants*, *13*(13), 1732. DOI: **10.3390/plants13131732**

dos Reis Brugnerotto, M., Ventura, M. U., de Oliveira, L. V. B., Hata, F. T., Carrilho, É. M., de Souza Machado, L. H., ... & de Resende, J. T. V. (2024). Exogenous Methyl Salicylate treatment increases tomato zingiberene levels and decreases infestation of adult whiteflies and red spider mites. *Phytoparasitica*, *52*(2), 36. DOI: 10.1007/s12600-024-01154-6

El-Ghany, N. M. A. (2019). Semiochemicals for controlling insect pests. *Journal of Plant Protection Research*, 59(1).

Faris, AM, Rodrigues Duffeck, M., Olson, JD, Espindola, AS, Muller, L., Velasco, SE, & Zambiasi, JM (2024). First Report of Dalbulus maidis (DeLong and Wolcott)(Hemiptera: Cicadellidae) in Oklahoma. *Insects*,*15* (10), 778.

Gámez, R. (1973). Transmission of rayado fino virus of maize (*Zea mays*) by Dalbulus tnaidis. *Annals of Applied Biology*, *73*(3), 285-292. DOI: **10.1111/j.1744-7348.1973.tb00935.x**

Gondor, O. K., Pál, M., Janda, T., & Szalai, G. (2022). The role of methyl salicylate in plant growth under stress conditions. *Journal of Plant Physiology*, *277*, 153809. DOI: 10.1016/j.jplph.2022.153809

Gross, J., & Franco, J. C. (2022). Novel trends on semiochemicals and semiophysicals for insect science and management. *Entomologia Generalis*, *42*(2), 163-165. DOI: 10.1127/entomologia/2022/1535

Groux, R., Hilfiker, O., Gouhier-Darimont, C., Peñaflor, M. F. G. V., Erb, M., & Reymond, P. (2014). Role of methyl salicylate on oviposition deterrence in *Arabidopsis thaliana*. *Journal of Chemical Ecology*, *40*, 754-759. DOI: 10.1007/s10886-014-0470-9

Hill, J.G., Virla, E.G., Fernandez, P.C., Luft-Albarracin, E., & Coll-Aráoz, M.V. (2024) *Dalbulus maidis* and *Peregrinus maidis*, both phloem feeding hoppers, induce different volatile profiles in

maize. Consequences for a natural enemy. *Journal of Pest Science 97*, 87–97. DOI: 10.1007/s10340-023-01612-w

Huang, W., Wei, S., Zhou, T., Fan, Z., Cao, L., Li, Z., & Guo, S. (2024). MCMV-infected maize attracts its insect vector *Frankliniella occidentalis* by inducing β-myrcene. *Frontiers in Plant Science*, *15*, 1404271. DOI: 10.3389/fpls.2024.1404271

Jacobi, V. G., Fernandez, P. C., Barriga, L. G., Almeida-Trapp, M., Mithöfer, A., & Zavala, J. A. (2021). Plant volatiles guide the new pest *Dichelops furcatus* to feed on corn seedlings. *Pest management science*, *77*(5), 2444-2453. DOI: **10.1002/ps.6273**

James, D.G. (2005) Further Field Evaluation of Synthetic Herbivore-Induced Plant Volatiles as Attractants for Beneficial Insects. *Journal of Chemical Ecology, 31*, 481–495. https://doi.org/10.1007/s10886-005-2020-y

James, D.G., Grasswitz, T.R. (2005) Synthetic Herbivore-induced Plant Volatiles Increase Field Captures of Parasitic Wasps. *Biocontrol 50*, 871–880. https://doi.org/10.1007/s10526-005-3313-3

Jang, G., Shim, J. et al. (2014). Volatile methyl jasmonate is a transmissible form of jasmonate and its biosynthesis is involved in systemic jasmonate response in wounding. *Plant biotechnology reports*, *8*, 409-419. DOI: 10.1007/s11816-014-0331-6

Jones, T. K. L., Esparza-Diaz, G., Wayadande, A., & Badillo-Vargas, I. E. (2021). Re-emergence of corn leafhopper (*Dalbulus maidis*; Hemiptera: Cicadellidae), an exotic and invasive pest of maize in South Texas. *Southwestern Entomologist*, *46*(4), 807-812. DOI: 10.3958/059.046.0401

Kim, H. K., Seo, J. W., & Kim, G. H. (2020). Various effects of volatile constituents from Magnolia kobus flowers against *Aedes albopictus* (Diptera: Culicidae). *Industrial Crops and Products*, *145*, 112109. DOI: 10.1016/j.indcrop.2020.112109

La Grange, R., Schröder, M. L., Glinwood, R., Ignell, R., & Krüger, K. (2017). Leafhopper interactions with host plants–a role for volatile cues. *IOBC-WPRS Bulletin*, *126*, 22-26.

Liu, J., Tallat, M., Wang, G., Li, G., Zhang, H., Wu, X., ... & Feng, H. (2024). The Utility of Visual and Olfactory Maize Leaf Cues in Host Finding by Adult *Spodoptera frugiperda* (Lepidoptera: Noctuidae). *Plants*, *13*(23), 3300. DOI: **10.3390/plants13233300**

Lopes, R. B., Faria, M. & Oliveira, C.M (2025). Susceptibility of *Dalbulus maidis* to insect-pathogenic fungi: unveiling the protective role of brochosomes and self-cleaning behavior. *J Pest Sci,* **98**, 759–768. DOI: https://doi.org/10.1007/s10340-024-01823-9

Machado, E. P., Souza, E. V., Dias, G. S., Sacilotto, M. G., & Omoto, C. (2024). Is insecticide resistance a factor contributing to the increasing problems with *Dalbulus maidis* (Hemiptera: Cicadellidae) in Brazil?. *Pest Management Science*, *80*(10), 5120-5130. DOI: **doi.org/10.1002/ps.8237**

Melchert, N. A., Manzano, C., Virla, E. G., & Luft-Albarracin, E. (2023). On how nitrogen fertilization affects the host election and oviposition behavior of the corn stunt spiroplasma vector, Dalbulus maidis (Hemiptera: Cicadellidae). *Arthropod-Plant Interactions*, *17*(5), 621-628. DOI: 10.1007/s11829-023-09983-8

Nault, L. R. (1980). Maize bushy stunt and corn stunt: a comparison of disease symptoms, pathogen host ranges, and vectors. *Phytopathology, 70*(7), 659-662. DOI: **10.1094/Phyto-70-659**

Oliveira, C. M. D., & Frizzas, M. R. (2022). Eight decades of *Dalbulus maidis* (DeLong & Wolcott)(Hemiptera, Cicadellidae) in Brazil: what we know and what we need to know. *Neotropical Entomology*, *51*(1), 1-17. DOI: 10.1007/s13744-021-00932-9

Oliveira, C. M., Frizzas, M. R., & de Oliveira, E. (2020). Overwintering plants for *Dalbulus maidis* (DeLong and Wolcott)(Hemiptera: Cicadellidae) adults during the maize off-season in central Brazil. *International Journal of Tropical Insect Science*, 40, 1105-1111. DOI: 10.1007/s42690-020-00165-0

Oliveira, C. M., Lopes, J. R., & Nault, L. R. (2013). Survival strategies of *Dalbulus maidis* during maize off-season in Brazil. *Entomologia Experimentalis et Applicata*, *147*(2), 141-153. DOI: **10.1111/eea.12059**

Oluwafemi, S., Birkett, M. A., Caulfield, J., & Pickett, J. A. (2012). Variability of volatile organic compounds emitted by seedlings of seven African maize varieties when infested by adult *Cicadulina storeyi* China leafhopper vectors of maize streak virus. *African Crop Science Journal*, *20*(2), 117-124.

Oluwafemi, S., Bruce, T. J., Pickett, J. A., Ton, J., & Birkett, M. A. (2011). Behavioral responses of the leafhopper, *Cicadulina storeyi* China, a major vector of maize streak virus, to volatile cues from intact and leafhopper-damaged maize. *Journal of Chemical Ecology*, *37*, 40-48. DOI: 10.1007/s10886-010-9891-2

Papanastasiou, S. A., Ioannou, C. S., & Papadopoulos, N. T. (2020). Oviposition-deterrent effect of linalool–a compound of citrus essential oils–on female Mediterranean fruit flies, *Ceratitis capitata* (Diptera: Tephritidae). *Pest Management Science*, *76*(9), 3066-3077. DOI: **10.1002/ps.5858**

Pickett, J. A., Woodcock, C. M., Midega, C. A., & Khan, Z. R. (2014). Push–pull farming systems. *Current opinion in biotechnology*, *26*, 125-132. DOI: 10.1016/j.copbio.2013.12.006

Piesik, D., Pańka, D., Jeske, M., Wenda-Piesik, A., Delaney, K. J., & Weaver, D. K. (2013). Volatile induction of infected and neighbouring uninfected plants potentially influence attraction/repellence of a cereal herbivore. *Journal of Applied Entomology*, *137*(4), 296-309. DOI: **10.1111/j.1439-0418.2012.01742.x**

Pozebon, H., Stürmer, G. R., & Arnemann, J. A. (2022). Corn stunt pathosystem and its leafhopper vector in Brazil. *Journal of Economic Entomology*, *115*(6), 1817-1833. DOI: 10.1093/jee/toac147

Ramos, A., Esteves, M. B., Cortés, M. T. B., & Lopes, J. R. S. (2020). Maize bushy stunt phytoplasma favors its spread by changing host preference of the insect vector. *Insects*, *11*(9), 600. DOI: **10.3390/insects11090600**

Ranum, P., Peña-Rosas, J. P., & Garcia-Casal, M. N. (2014). Global maize production, utilization, and consumption. *Annals of the New York academy of sciences*, *1312*(1), 105-112. DOI: **10.1111/nyas.12396**

Reisenman, C. E., Riffell, J. A., Bernays, E. A., & Hildebrand, J. G. (2010). Antagonistic effects of floral scent in an insect–plant interaction. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1692), 2371-2379. DOI: **10.1098/rspb.2010.0163**

Rodríguez-del-Bosque, L. A., Reyes, C. A., Delgado, C., Rosales, E., Vega, H. E., & Martínez, R. (2024). Unusual Abundance of *Dalbulus maidis* in Northeastern Mexico. *Southwestern Entomologist*, *49*(3), 1-4. DOI: 10.3958/059.049.0318

Rossetti, M. R., Kuzmanich, N., Videla, M., Ben-Zvi, Y., & Rodriguez-Saona, C. (2025). Meta-analysis of the effects of methyl salicylate on arthropod behavior: implications for biological control. *Entomologia Generalis*, 369-380. DOI: 10.1127/entomologia/2025/3051

Sabato, E. de O.; Landau, E. C. & Oliveira, C. M. (2014) Recomendações para o manejo de doenças do milho disseminadas por insetos-vetores. *EMBRAPA/Centro Nacional de Pesquisa de Milho e Sorgo*, 15. (EMBRAPA/CNPMS. Circular técnica, 205).

Sanches, M. D. S., Michereff, M. F. F., Borges, M., Laumann, R. A., de Oliveira, C. M., Frizzas, M. R., & Blassioli-Moraes, M. C. (2025). How Much, How Long and When: Density, Duration and Plant Stage Affect Herbivore-induced Plant Volatiles in Maize by the Corn Leafhopper. *Journal of Chemical Ecology*, *51*(3), 1-13. DOI: 10.1007/s10886-025-01600-7

Santana Jr, P. A., Kumar, L., Da Silva, R. S., Pereira, J. L., & Picanço, M. C. (2019). Assessing the impact of climate change on the worldwide distribution of *Dalbulus maidis* (DeLong) using MaxEnt. *Pest management science*, *75*(10), 2706-2715. DOI: **10.1002/ps.5379**

Serdo, D. F. (2024). Insects' perception and behavioral responses to plant semiochemicals. *PeerJ*, *12*, e17735. DOI: 10.7717/peerj.17735

Silva, L. R. S., Canale, M. C., Magalhães, D. M., Lopes, J. R. S., & Bento, J. M. S. (2025). Maize bushy stunt phytoplasma changes the emission of maize volatiles and the chemotaxis of non-infected Dalbulus maidis (Hemiptera: Cicadellidae). *Arthropod-Plant Interactions*, *19*(2), 35. DOI: 10.1007/s11829-025-10144-2

Skoczek, A., Piesik, D., Wenda-Piesik, A., Buszewski, B., Bocianowski, J., & Wawrzyniak, M. (2017). Volatile organic compounds released by maize following herbivory or insect extract application and communication between plants. *Journal of Applied Entomology*, *141*(8), 630-643. DOI: **doi.org/10.1111/jen.12367**

Sullivan, B. T., Grady, A. M., Hofstetter, R. W., Pureswaran, D. S., Brownie, C., Cluck, D., ... & Zúñiga, G. (2021). Evidence for semiochemical divergence between sibling bark beetle species: *Dendroctonus brevicomis* and *Dendroctonus barberi*. *Journal of Chemical Ecology*, *47*, 10-27. DOI: 10.1007/s10886-020-01233-y

Sun, J. S., Feng, Y., Wang, Y., Li, J., Zou, K., Liu, H., ... & Wu, Y. (2020). α-pinene, caryophyllene and β-myrcene from *Peucedanum terebinthaceum* essential oil: Insecticidal and repellent effects on three stored-product insects. *Rec Nat Prod, 14 (3), 189*. DOI: 10.25135/rnp.149.19.05.1287

Szendrei, Z., & Rodriguez-Saona, C. (2010). A meta-analysis of insect pest behavioral manipulation with plant volatiles. *Entomologia Experimentalis et Applicata*, *134*(3), 201-210. DOI: **10.1111/j.1570-7458.2009.00954.x**

Todd, J. L., Madden, L. V., & Nault, L. R. (1991). Comparative growth and spatial distribution of Dalbulus leafhopper populations (Homoptera: Cicadellidae) in relation to maize phenology. *Environmental Entomology*, *20*(2), 556-564. DOI: 10.1093/ee/20.2.556

Tonğa, A., Çakmak, S., Şeker, K., Temiz, M. G., & Bayram, A. (2020). cis-Jasmone treatments affect multiple sucking insect pests and associated predators in cotton. *Entomologia Generalis*, *40*(1). DOI: 10.1127/entomologia/2019/0771

Tonğa, A., Şeker, K., Çakmak, S., Temiz, M. G., & Bayram, A. (2022). Cotton treatment with methyl jasmonate at different growth stages reduces the population of sucking insect pests and marginally increases their associated predators. *Entomologia Experimentalis et Applicata*, *170*(3), 207-221. DOI: **10.1111/eea.13137**

United States Department of Agriculture (USDA) (2025). *Nota: ¹ 12º levantamento USDA da safra 2024/25*. https://www.usda.gov/oce/commodity/wasde/wasde0323.pdf

United States Department of Agriculture (USDA) (2025). *Nota: ¹ 12º levantamento USDA da safra 2024/25*. https://www.usda.gov/oce/commodity/wasde/wasde0323.pdf

Van Nieuwenhove, G. A., Frías, E. A., & Virla, E. G. (2016). Effects of temperature on the development, performance and fitness of the corn leafhopper Dalbulus *maidis* (DeLong)(Hemiptera: Cicadellidae): implications on its distribution under climate change. *Agricultural and Forest Entomology*, *18*(1), 1-10. DOI: **10.1111/afe.12118**

Waquil, J. M., Viana, P. A., Cruz, I., & Santos, J. P. (1999). Aspectos da biologia da cigarrinha-do-milho, *Dalbulus maidis* (DeLong & Wolcott)(Hemiptera: Cicadellidae). *Anais da Sociedade Entomológica do Brasil*, *28*, 413-420. DOI: 10.1590/S0301-80591999000300005

Whitcomb, R. F., et al. (1986). Spiroplasma kunkelii sp. nov.: characterization of the etiological agent of corn stunt disease. *International Journal of Systematic and Evolutionary Microbiology*, *36*(2), 170-178. DOI: **10.1099/00207713-36-2-170**

Yan, X. Z., Wang, Z. Y., Ma, L., Song, C. F., Zhao, J. Y., Wang, C. Z., & Hao, C. (2023). Electroantennogram and behavioural responses of *Plutella xylostella* to volatiles from the non-host plant *Mentha spicata*. *Journal of Applied Entomology*, *147*(7), 511-519. DOI: **10.1111/jen.13144**

Yan, Z. G., & Wang, C. Z. (2006). Identification of Mythmna separata-induced maize volatile synomones that attract the parasitoid Campoletis chlorideae. *Journal of Applied Entomology*, *130*(4), 213-219. DOI: **10.1111/j.1439-0418.2006.01055.x**

Zhang, L., Su, Q. F., Wang, L. S., Lv, M. W., Hou, Y. X., & Li, S. S. (2023). Linalool: A ubiquitous floral volatile mediating the communication between plants and insects. *Journal of Systematics and Evolution*, *61*(3), 538-549. DOI: **10.1111/jse.12930**

Zhang, L., Zhang, F., Melotto, M., Yao, J., & He, S. Y. (2017). Jasmonate signaling and manipulation by pathogens and insects. *Journal of experimental botany*, *68*(6), 1371-1385. DOI: 10.1093/jxb/erw478

Zhang, Z., Wang, H. B., Chen, G. F., Kong, X. B., Zhang, S. F., & Liu, F. (2022). Application of semiochemicals in insect pest monitoring. *Acta Entomologica Sinica*, 65 (3), 351-363. DOI: **10.16380/j.kcxb.2022.03.011**

Supplementary material

Figure S1. Dual-choice oviposition assay assessing the egg-laying preference of *Dalbulus maidis* adults between maize plants associated with a disperser loaded with a synthetic plant volatile solution (2, 20, or 200 ng·µL^{-1} of myrcene, linalool, methyl salicylate, or methyl jasmonate) and maize plants associated with a disperser containing only solvent (paraffin oil).

TERCEIRA PARTE

3 CONSIDERAÇÕES FINAIS

Os resultados deste estudo, aliados às evidências previamente disponíveis na literatura, demonstram que os bioestimulantes Si e SH podem exercer efeitos distintos sobre o desenvolvimento das plantas e o comportamento dos insetos, dependendo tanto da dosagem utilizada quanto da forma de aplicação. Observou-se que o SH, quando aplicado isoladamente, promoveu incremento no crescimento radicular, enquanto sua combinação com Si interferiu negativamente nesse efeito. Verificou-se também um aumento discreto na resistência de plantas tratadas com Si, refletido na redução da aceitação hospedeira por *D. maidis*, embora sem impacto sobre o desenvolvimento do inseto. Entretanto, essa maior resistência não se correlacionou com os níveis de compostos fenólicos totais, que foram reduzidos nesse tratamento em comparação ao controle. Adicionalmente, identificou-se um efeito protetor do Si, isolado ou associado ao SH, frente ao estresse oxidativo causado por *D. maidis*, evidenciado pela redução das atividades das enzimas oxidativas SOD e CAT. Esses resultados reforçam a necessidade de estudos futuros que investiguem outros aspectos da indução de defesas vegetais nesse sistema, bem como uma compreensão mais aprofundada das interações químicas entre os dois bioestimulantes e de possíveis adaptações fisiológicas de *Dalbulus maidis* ao longo de múltiplas gerações. Torna-se igualmente relevante avaliar o desempenho desses bioestimulantes em condições de campo, além de explorar novas combinações de substâncias capazes de aprimorar práticas alternativas para o manejo integrado.

O segundo artigo mostra que mirceno a 20 ng μL^{-1} reduziu significativamente a oviposição, enquanto o MeSA a 2 ng μL^{-1}, o mirceno a 200 ng μL^{-1} e o linalol a 200 ng μL^{-1} aumentaram significativamente o número de ovos depositados nas plantas de milho. O MeJA, em qualquer concentração, não teve efeito sobre a preferência de oviposição de *D. maidis*. Esses resultados demonstram uma resposta comportamental dependente da dose de *D. maidis* a VOCs específicos, com o mirceno atuando como repelente em dose moderada e o MeSA, o mirceno (em alta dose) e o linalol funcionando como atrativos. Tais respostas ressaltam o potencial desses compostos sintéticos para integração em estratégias baseadas em semioquímicos voltadas à manipulação da oviposição de *D. maidis*, seja para deter ou atrair fêmeas, dependendo da dose e do composto utilizado.

O presente trabalho oferece contribuições relevantes para o aprimoramento do manejo de pragas, especialmente no controle de *D. maidis* em plantas de milho, ao avaliar o uso de

bioinsumos — especificamente bioestimulantes e semioquímicos — como táticas alternativas de controle, reforçando o avanço de práticas agrícolas mais sustentáveis. Além disso, nossos resultados ajudam a preencher lacunas existentes na literatura relacionadas ao emprego de silício (Si) e substâncias húmicas (SH) na indução de defesas vegetais e no controle de insetos-praga. O estudo também amplia o entendimento sobre o potencial de compostos voláteis sintéticos, como mirceno, linalol, MeSA e MeJA, na modulação do comportamento de insetos, com destaque para suas interações com a cigarrinha-do-milho em plantas de milho — um sistema que tem se mostrado particularmente desafiador em condições de campo. Adicionalmente, nossos achados evidenciam lacunas ainda existentes e ressaltam a necessidade de estudos futuros para avançar no conhecimento sobre essas estratégias de manejo.