Doctoral thesis

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VOLATILE COLLECTION, PERCEPTION, AND BEHAVIOUR – THREE ASPECTS OF INSECT CHEMICAL ECOLOGICAL STUDIES

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INTRODUCTION

Research Background

The study of chemical ecology has grown in importance due to its critical role in understanding insect behaviour and its implications for sustainable agriculture and plant protection. As globalisation and climate change accelerate, the challenges posed by invasive pest species have become more pronounced, necessitating innovative, eco-friendly strategies to manage their impact on ecosystems and crops. The escalating use of pesticides poses risks to both human health and biodiversity, intensifying the need for alternative solutions that integrate chemical ecology principles.

Insects rely heavily on chemical signals for vital behaviours such as locating hosts, finding mates, and avoiding predators. These interactions are mediated by semiochemicals, including pheromones and allelochemicals. Pheromones are primarily used for intraspecific communication, facilitating mate attraction and aggregation behaviour, whereas allelochemicals, such as allomones and kairomones, influence interspecific interactions. Among these, plant-emitted volatiles are of particular importance in mediating insect-host interactions, often acting as repellents or attractants (Hansson and Wicher, 2016). Recent advances in volatile collection techniques, such as dynamic headspace sampling and solid-phase microextraction (SPME), have enhanced the identification of plant-emitted compounds relevant to insect behaviour (Hansson and Wicher, 2016; Tholl et al., 2021). These compounds are identified with chromatography-mass spectrometry (GC-MS). Simultaneously, electrophysiological methods, including gas chromatography-electroantennographic detection (GC-EAD), have provided insights into the olfactory systems of pests, enabling the identification of volatiles with the potential to affect behaviour.

The hemipteran pest *Metcalfa pruinosa* and the drosophilid *Drosophila suzukii* are exemplary cases of invasive species causing significant agricultural damage. *M. pruinosa* is a highly polyphagous vector pest that not only carries pathogens but also facilitates the spread of black mould through its honeydew secretion (Seo et al., 2019; Mergenthaler et al., 2020). *D. suzukii* is able to oviposit in ripening fruit, causing direct damage to soft fruits such as cherries and berries (Asplen et al., 2015; Knapp et al., 2021).

The role of microbial communities, such as yeasts, has gained increasing attention in insect ecology. Yeasts associated with fruits and insects can produce volatile organic compounds (VOCs) that attract pests like *D. suzukii* (Becher et al., 2012). These yeasts, such as *Hanseniaspora uvarum*, emit compounds like ethyl acetate and isoamyl acetate, which are potent attractants (Revadi et al., 2013; Piñero et al., 2019). The integration of yeast-based lures into pest management strategies offers an environmentally sustainable alternative to chemical insecticides.

Objectives

This thesis is divided into three studies, each focusing on significant aspects of chemical ecology relevant to pest management:

Comparison of various techniques for volatile collection from headspace: The first study compares combinations of various adsorbents and sampling times for collecting volatiles from a plant's headspace, aiming to identify the optimal method. This is crucial because the compounds gathered can vary significantly based on the collection technique, impacting subsequent analyses of plant-insect interactions.

Development of an electrophysiological measurement method for a hemipteran species: Beside developing a reliable method for conducting electrophysiological measurements on the hemipteran species *Metcalfa pruinosa*, the second study addresses the understudied olfactory systems of Auchenorrhyncha species, with the goal of identifying the volatile compounds that *M. pruinosa* perceives, which is essential for understanding its behaviour in colonizing new territories and locating suitable habitats.

Development of novel, yeast-based, field-effective attractants for D. suzukii: The third study focuses on developing novel, yeast-based attractants for *Drosophila suzukii,* leveraging the association between this pest and specific yeast species like *Hanseniaspora uvarum*. Given the limited data on the attractiveness of live yeasts and yeast-infested fruit in field conditions, this study tests various yeast species and their emitted volatiles to identify effective and selective attractants while ensuring minimal impact on non-target species.

Overall, my studies contribute to various stages of chemical ecology by addressing specific challenges related to invasive insect species and their interactions with plants.

MATERIALS AND METHODS

Comparison of Multiple Techniques for Sampling Optimization

Volatile compounds were collected from *Lactuca sativa* using dynamic headspace methods. Experiments were conducted with three types of adsorbents: Porapak Q, HayeSep Q, and Carbotrap, using sampling durations of 1, 2, 4, and 6 hours. Plants were grown under controlled greenhouse conditions, with temperature maintained between 18-25 °C and relative humidity at approximately 40%.

The volatile traps contained 50 mg of adsorbent material, which was pre-cleaned as described by Molnár et al. (2015). A continuous flow of charcoal-filtered air (1 L/min) was drawn through the system using a vacuum pump (Thomas G 2/02 EB). Volatiles were desorbed from the adsorbent filters using 300 µL of n-hexane and analysed using an Agilent 6890 gas chromatograph coupled with a 5975 C MSD mass spectrometer. The GC parameters included a non-polar HP-5 UI column, a splitless injection mode, and helium as the carrier gas at a flow rate of 1 mL/min. The oven temperature program ranged from 50 °C to 300 °C. Mass spectra were recorded within the 35-500 m/z range. Compound identification was performed using the NIST 2017 Mass Spectral Library and Kovats indices.

The efficiency of the volatile collection setups was evaluated using the Sum of Ranking Differences (SRD) method, implemented in Microsoft Excel. SRD allowed for the comparison of adsorbents and sampling durations based on their ability to capture volatile compounds effectively. Each experiment included four replicates for statistical reliability.

Methodology Development in Electrophysiological Experiments

Specimens of *Metcalfa pruinosa* were collected as nymphs from Martonvásár, Hungary, and reared on *Buxus sempervirens* under controlled climate chamber conditions (26 ± 2 °C, 50 ± 10% RH, 16:8 L:D photoperiod). Both adults and nymphs were used for gas chromatography-electroantennographic detection (GC-EAD) experiments to identify antennal responses to plant volatiles.

Volatiles were collected from shoots of *Tagetes patula*, *Ailanthus altissima*, and *Aristolochia clematitis* using a dynamic headspace system equipped with a charcoal trap. GC-EAD recordings were conducted with an HP Agilent 5890 GC and Syntech IDAC-2 interface. The experimental setup included Ringer solution-filled electrodes, with the recording electrode placed near the pedicel and the reference electrode inserted into the insect's thorax.

Both female and male adults were tested using *T. patula* (N_f = 9, N_m = 8), *A. altissima* (N_f = 3, N_m = 3), and *A. clematitis* (N_f = 4, N_m = 3) extracts. The sensitivity of nymphs was evaluated using *T. patula* (N_n = 9). For statistical analyses, Fisher's exact tests and Wilcoxon rank-sum tests were applied using the rstatix package in R (v4.1.2). P-values were adjusted using the false discovery rate method. Response amplitudes were analysed using linear mixed-effects models (lme4 package), with replicate number included as a random effect.

Development of Novel, Yeast-Based, Field-Effective Attractants for *D. suzukii*

Four yeast species – *Hanseniaspora uvarum* (HU), *Metschnikowia pulcherrima* (MP), *Pichia terricola* (PT), and *Saccharomyces cerevisiae* (SC) – were cultured on MGYP plates and maintained under standard laboratory conditions. Yeasts were inoculated into autoclaved MGYP broth or apple juice (HU) and grown in a horizontal shaker at 26 °C and 150 rpm to achieve high cell densities (129 ± 15.5 cells/mL).

Field experiments were conducted in a commercial sour cherry orchard (Berkenye, Hungary) from September to October 2019. Bottle traps (500 mL) with 9 entry holes were baited with 200 mL of yeast cultures and hung in the orchard at 170 cm height. Lures were replaced every three days, and captured insects were identified under a stereomicroscope. Statistical analyses of catch data were performed using generalised linear models (MASS package) in R. Non-parametric pairwise comparisons were conducted using the multcomp package. Volatile profiles of yeast cultures were analysed using non-metric multidimensional scaling (NMDS) and PERMANOVA (vegan package). Peak areas were normalised and standardised before calculating Jaccard dissimilarity indices.

RESULTS AND DISCUSSION

Comparison of Multiple Techniques for Sampling Optimization

A total of 149 volatile compounds were identified during the TIC analysis. Several of the identified compounds are consistent with previous studies that identified compounds such as *α*- and *β*-pinene, D-limonene, and *β*-caryophyllene in lettuce volatiles (Lonchamp et al., 2009; Nomaani et al., 2013).

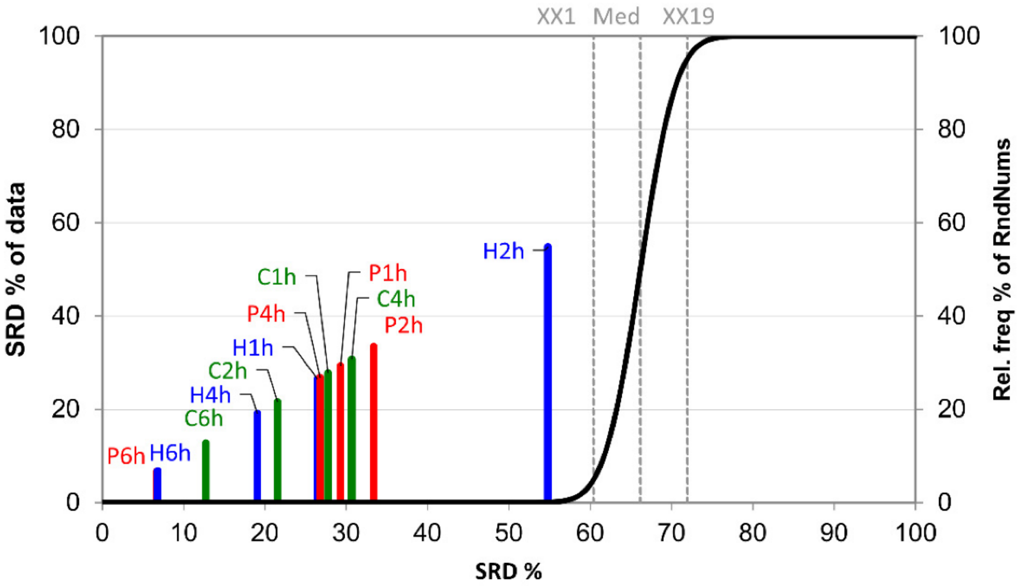

Figure 1 *The scaled SRD values of the sampling procedure based on integrated peak area by sum of ranking differences. The maximum values of the compounds were used as the reference (benchmark) column. Scaled SRD values are plotted on the x-axis; the right y-axis shows the relative frequencies. Probability levels of 5% (XX1), median (Med), and 95% (XX19) are also given. Diagrams were produced by compound intensity values on a total ion chromatogram (N = 149). In the abbreviations, the letter denotes the type of adsorbent used (P for Porapak Q, H for Hayesep Q, and C for Carbotrap), while the number indicates the sampling duration (1, 2, 4, or 6 hours).*

To ensure the most effective sampling setup, SRD analysis was performed, using compound intensity maxima as the reference column. Among the tested setups, the 6-hour sampling duration captured the most volatiles. Specifically, Porapak Q (P6h) and HayeSep Q (H6h) ranked highest in capturing both highly volatile and semi-volatile compounds, followed by Carbotrap (C6h). Shorter durations (1-4 hours) also showed acceptable performance. For example, HayeSep Q at 4 hours (H4h) was particularly effective in balancing time efficiency and compound recovery (Figure 1).

Our findings provide a systematic evaluation of sampling methods and durations for maximizing volatile capture. However, in chemical ecology, minor compounds can play disproportionately significant roles in ecological interactions. For example, pheromones, even in trace amounts, can elicit strong behavioural responses (Arn et al., 1983). Similarly, certain groups of volatiles may be more critical depending on the ecological context (Stensmyr et al., 2012). The

SRD method must be applied with the research objectives in mind. Methods capturing fewer total volatiles may outperform others if they selectively target behaviourally active compounds. Tailoring SRD analysis to specific ecological questions ensures its applicability and aligns it with the unique demands of chemical ecology.

Methodology Development in Electrophysiological Experiments

In our experiments, fourth and fifth nymphal stages of *M. pruinosa* detected 20 volatile compounds across various chemical classes. To date, only a few studies have successfully conducted GC-EAD experiments on nymphal stages of Auchenorrhyncha (Yoon et al., 2011; Moon et al., 2011). Our findings highlight the remarkable olfactory sensitivity of nymphs, which may aid host plant location and feeding.

Out of 77 volatile compounds tested, 29 elicited electrophysiological responses on adult *M. pruinosa* antennae. These compounds represented diverse chemical classes, including ketones, aldehydes, terpenoids, and esters. While *M. pruinosa* exhibited no strong preference for specific chemical groups, key compounds such as DMNT, methyl salicylate, and piperitone despite their low concentrations in the headspace of *T. patula*, elicited the strongest responses (Figure 2), potentially playing roles in host plant selection. No significant differences in response amplitudes or the number of active compounds were observed between males and females or adults and nymphs. This suggests that *M. pruinosa* relies on similar volatile cues for host plant selection across sexes and developmental stages.

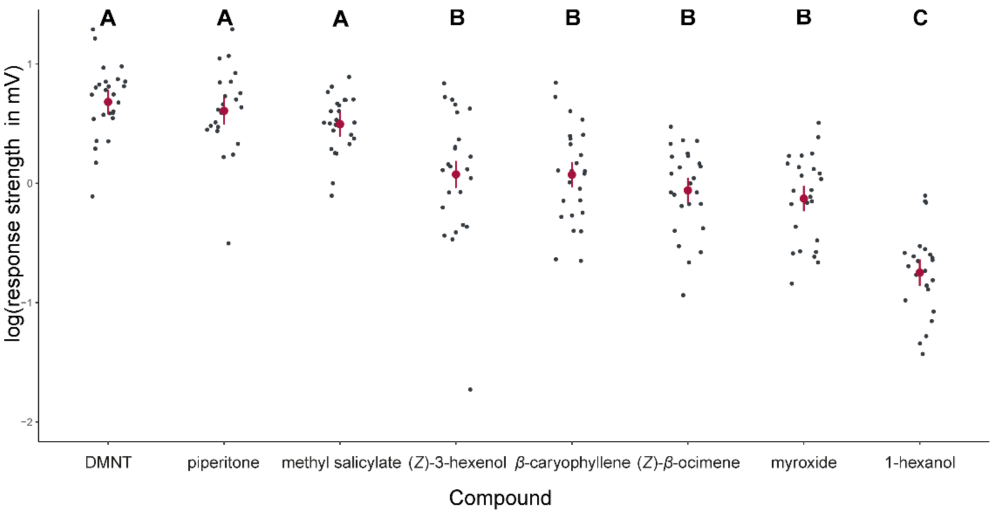

Figure 2 *Response amplitudes to the analysed compounds present in the headspace of* T. patula*. Error bars represent estimated means and 84% confidence intervals (CI) calculated from linear mixed-effects models. Nonoverlapping CIs indicate significant differences between groups after correction for FDR. Letters above the error bars represent pairwise comparisons; groups not sharing any letter differ significantly ($p < 0.05$).*

The broad olfactory sensitivity of *M. pruinosa* likely reflects its polyphagous nature and wide host range. According to the "sequential cues hypothesis" (Silva and Clarke, 2020), polyphagous insects use common volatiles like (*Z*)-3-hexenol to locate host patches and refine selection using species-specific signals such as DMNT. Migrating adults and nymphs may utilize similar volatile cues for habitat selection, though further behavioural studies are needed to confirm these roles.

Development of Novel, Yeast-Based, Field-Effective Attractants for D. suzukii

Hanseniospora uvarum (HU) lures exhibited high relative abundances of ethyl acetate, ethyl propionate, and butyl formate, a trend consistent before and after field placement. *Pichia terricola* (PT) lures emitted unique volatiles, such as ethyl octanoate and ethyl hexanoate, which dominated their profiles before and after field incubation. When HU and PT were combined (MIX), the volatile profile resembled that of PT, suggesting competitive growth dominance by PT in the mixture. *Saccharomyces cerevisiae* (SC) emitted higher proportions of 3-methyl butanol and styrene, while HU grown in apple juice (AHU) produced a more diverse profile with elevated levels of isoamyl acetate and phenethyl acetate after field incubation. These differences in volatile profiles significantly influenced lure performance.

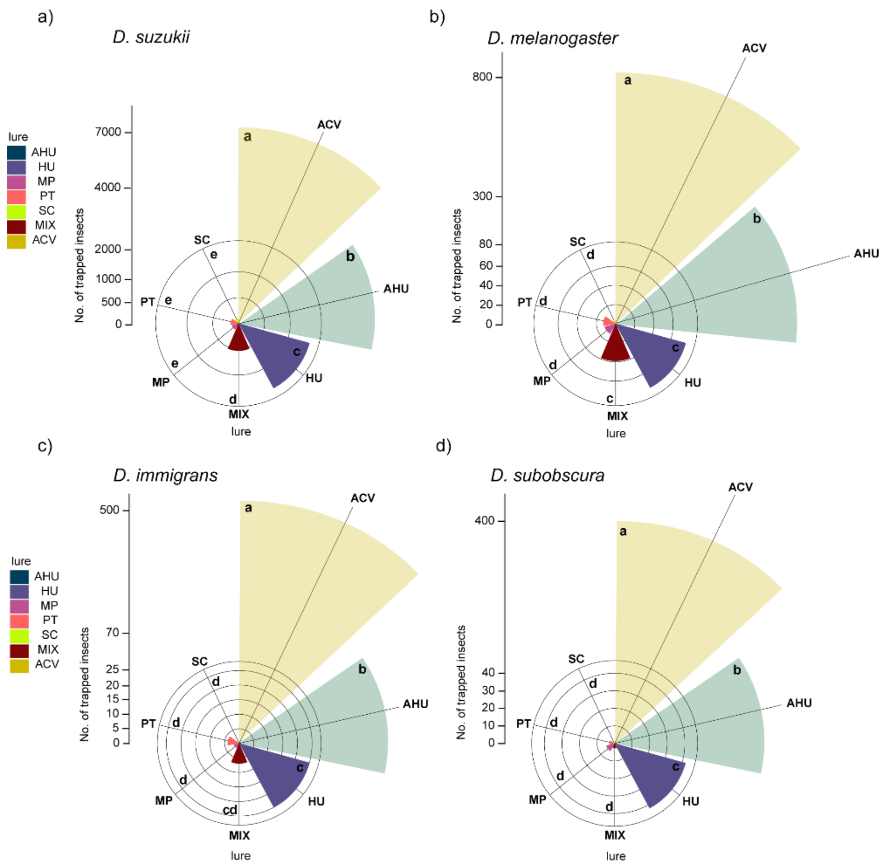

Figure 3 *The sum of target species (*D. suzukii*) and the identified non-target drosophilid specimens (*D. melanogaster, D. immigrans *and* D. subobscura*) caught during the field trials with apple cider vinegar (ACV) and traps baited with different yeast species: AHU, apple juice with* Hanseniaspora uvarum*; HU,* H. uvarum*; MIX, mixture of* Pichia terricola *and* H. uvarum*; MP,*

Metschnikowia pulcherrima*; PT,* P. terricola*; SC,* Saccharomyces cerevisiae. *Traps with different superscript letters are significantly different based on generalized linear models and pairwise comparison of groups ($p < 0.05$).*

In field trials, among the yeast-based lures, AHU lures captured the highest number of *D. suzukii* individuals. HU and AHU lures were especially effective for capturing females and winter morphs, with AHU demonstrating superior specificity for *D. suzukii*. This result aligns with earlier field studies where *H. uvarum* baits were more attractive to *D. suzukii* adults than *P. terricola* and *H. opuntiae* baits (Bueno et al., 2020) and more specific than *M. pulcherrima* and *S. cerevisiae* (Jones et al., 2021).

ACV attracted the highest overall number of drosophilids, but its specificity was lower due to higher number of non-target catches such as *D. melanogaster* and *D. immigrans* (Figure 3). In contrast, yeast-based lures, particularly HU and AHU, minimized non-target captures, providing a more environmentally friendly option for pest management. The preference of *D. suzukii* for HU and AHU lures aligns with previous studies highlighting the role of yeast volatiles in attracting mated females (Becher et al., 2012). Volatiles such as isoamyl acetate and ethyl acetate, emitted in high concentrations by HU and AHU, are known attractants for *D. suzukii* (Revadi et al., 2013). However, non-target attraction to HU lures by other drosophilids like *D. melanogaster* suggests a shared ecological association with yeast.

In future studies, reporting non-target species should be a priority, as it is vital for assessing environmental impacts and conserving biodiversity. Such data provide insights into ecological consequences, supporting sustainable and responsible solutions.

CONCLUSIONS AND RECOMMENDATIONS

Comparison of Multiple Techniques for Sampling Optimization

The SRD method was applied for the first time to evaluate sampling procedures, identifying 6-hour intervals as optimal. Alternatives like H4h and C2h are viable for faster sampling. Including all 149 compounds in the SRD analysis provided the greatest differentiation, but focusing on the top 20 most intense compounds yielded similar rankings, suggesting this subset may suffice for optimization. SRD's non-parametric nature allows its application across various sampling techniques, including volatile collection traps and sorptive extractions. Grouping compounds by type (e.g., aldehydes, ketones) could further refine rankings and reveal method-specific adsorption efficiency.

Pure headspace injection proved most reliable for accurate volatile analysis, minimizing losses during sampling and elution. However, low sensitivity of mass spectrometers for detecting trace volatiles remains a limitation. Future advancements in detection technology and continued exploration of alternative methods will be essential for optimizing volatile compound analysis.

Methodology Development in Electrophysiological Experiments

29 volatile compounds elicited electrophysiological responses in *M. pruinosa*, indicating sensitivity to diverse chemical cues without preference for specific classes. Both sexes and developmental stages responded similarly, suggesting reliance on common plant volatiles like (*Z*)-3-hexenol for habitat location and more specific cues like DMNT for host selection. Behavioural studies are needed to confirm the ecological roles of these volatiles.

Future research should integrate behavioural assays with electrophysiological data to clarify volatile roles in host selection. Field experiments are critical to test compounds like DMNT as attractants or repellents under natural conditions. Expanding tested compounds and employing advanced techniques such as olfactometers could enhance understanding of volatile-mediated host selection.

Development of Novel, Yeast-Based, Field-Effective Attractants for *D. suzukii*

Yeast-based lures, particularly *Hanseniaspora uvarum*-inoculated apple juice, emitted diverse volatiles that effectively attracted *D. suzukii*, especially females and winter morphs. These lures demonstrated higher specificity compared to apple cider vinegar traps most likely due to esters like isoamyl acetate in their volatile profiles. The findings highlight *H. uvarum*'s role in bait design and its close association with *D. suzukii* in natural environments.

Future studies should focus on field experiments to assess long-term lure effectiveness under varying conditions while minimizing non-target captures. Investigating different yeast strains and their blends could lead to more precise monitoring tools. Reporting non-target species should become standard practice to ensure ecological sustainability and biodiversity conservation in pest management strategies.

NEW SCIENTIFIC RESULTS

The results of this study present several novel scientific findings in the field of volatile compound analysis and sampling optimization.

First, the application of the SRD method to evaluate and optimize sampling procedures for volatile, semi-volatile, and low-volatile compounds marks a significant advancement. Notably, SRD has not been applied to such a broad range of sampling procedures before, making this a novel use of the method. An important discovery is that using a reduced number of compounds – specifically the top 20 most intensive – can still effectively determine optimal sampling procedures without sacrificing accuracy.

Second, we developed a new method for successful electrophysiological mesurements with the hemipteran species, *M. pruinosa*. For the first time, 29 volatile compounds were found to elicit electrophysiological responses in both adult and nymphal stages of *M. pruinosa*. These compounds span various chemical classes, such as terpenoids, ketones, aldehydes, alcohols, and esters, showcasing *M. pruinosa*'s broad olfactory detection capabilities. Interestingly, there were no observed qualitative or quantitative differences in olfactory sensitivity between males and females, or between adults and nymphs, suggesting that *M. pruinosa* relies on similar volatile cues throughout its life cycle, likely due to overlapping ecological roles.

Third, our findings indicate that while traditional fermentation baits like apple cider vinegar are effective in capturing a broad range of drosophilids, yeast-based lures – particularly those inoculated with *Hanseniaspora uvarum* – provide enhanced specificity for *D. suzukii*. These yeast-based lures proved valuable for monitoring and trapping *D. suzukii* across different morphs. Furthermore, our study also highlighted the presence of a wide variety of non-target drosophilids, emphasizing the need to account for both target and non-target species when designing pest monitoring tools.

These findings offer practical insights for optimizing volatile sampling and advancing pest management strategies, particularly for species such as *D. suzukii* and *M. pruinosa*.

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