



Trichome mimics: sprayable plant-based adhesives for crop protection against thrips

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Chapter 2

Sticky plants and plant-based glues: Potential for pest control

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ABSTRACT

Adhesive substances are produced by many vascular plants to protect themselves against herbivores and environmental conditions. Some plant species also trap arthropods for their own nutrition and to engage in mutualistic relationships with carrion scavenging predators. While the role of stickiness in direct and indirect plant defense is well established, our understanding of the mechanisms and factors that determine the successful capture of arthropods by sticky plants and how we can utilize this knowledge about plant-based adhesives to increase the sustainability of our agricultural practices is still limited. Here, we reviewed the literature on arthropod-trapping sticky plants and the use of plant-based adhesives in agriculture. In summary, there are many factors involved in the successful capture of arthropods by sticky plants, including: plant health status, the morphological characteristics of the adhesive secreting organs, the physiochemical properties of their glues, the use of visual cues and volatiles to lure or repel arthropods, the influence of environmental factors, and adaptations of arthropods in their behavior, morphology, and chemistry to avoid being captured. Considering agricultural potential, ameliorating crops with sticky features can become a novel way of crop protection and an alternative for pesticides. Plant-based glues are becoming more popular in many applications in agriculture e.g., as glues for sticky traps, as sprayable adhesives for physical plant protection, and as carriers of botanicals and pesticides. However, several technological and resource related challenges must be overcome before plant stickiness and plant-based glues can be fully utilized for crop protection.

1. Introduction

For millions of years, plants have existed in various environments and coexisted with arthropods and other organisms with ferocious appetites. To survive and thrive, plants utilize a wide array of strategies, including the use of sticky substances to repel, hinder and trap arthropods (Darwin 1875). One of the most common plant structures from which adhesive mucilage or resin may be secreted are glandular trichomes: epidermal plant hairs with specialized gland cells that contain and/or release various metabolites (Wagner 1991). Plants with such trichomes are often described as “sticky”, “adhesive”, “clammy”, “glandular”, “glutinous”, “gummy”, “resinous”, “viscid”, “tarry”, “tacky”, or “mucilaginous”; terminology that may also be found in their common and scientific names (Wheeler and Krimmel 2015). In this review, we consider sticky plants to be those plants that secrete adhesive mucilage or other adhesive fluids, either via glandular trichomes or other gland types, that can trap other organisms.

Plants from over 110 genera in 49 families have already been identified to possess arthropod-trapping abilities, and most often this is due to their stickiness (LoPresti et al. 2015). Famous examples of arthropod-trapping sticky plants include carnivorous and protocarnivorous species, for example: *Pinguicula* spp., *Byblis* spp., *Roridula* spp., and Darwin’s beloved *Drosera* spp. (Chase et al. 2009; Adlassnig et al. 2010). These plants possess specialized, often elongated glandular trichomes that secrete adhesive mucilage or resin-like substances that allow the plants to immobilize their prey (Fig. 2.1a-c) (Li et al. 2023). Captured arthropods drown or starve to death and are then decomposed using enzymes (e.g., proteases and phosphatases) or by other organisms like microbes, fungi, or carrion feeding arthropods (Peroutka et al. 2008). In this way, these arthropod-trapping plants can obtain essential nutrients, especially nitrogen, phosphorus, and other trace elements (Ellison 2006; Adlassnig et al. 2012), which contribute to healthy plant growth and increased fitness (Givnish et al. 2018; Klink et al. 2019). There are also many (presumably) non-carnivorous species of sticky plants, including herbs such as *Datura wrightii*, *Madia elegans*, *Geranium*

spp., crop species such as cotton (*Gossypium* spp.), tomato (*Solanum lycopersicum*) and tobacco (*Nicotiana tabacum*) (Lopresti et al. 2015; Nelson et al. 2019a), and woody plants such as *Rhododendron macrosepalum* (Sugiura and Yamazaki 2006) and horse-chestnut (*Aesculus hippocastanum*) (Voigt et al. 2020). The density of mucilage producing trichomes or general stickiness of these plants is often the greatest around the reproductive organs such as buds, flowers, and fruits (Lopresti et al. 2018b; Chautá et al. 2022). Some trees of the genus *Pisonia* are even known to occasionally trap birds in the mucilage surrounding their seedpods (Burger, 2005).

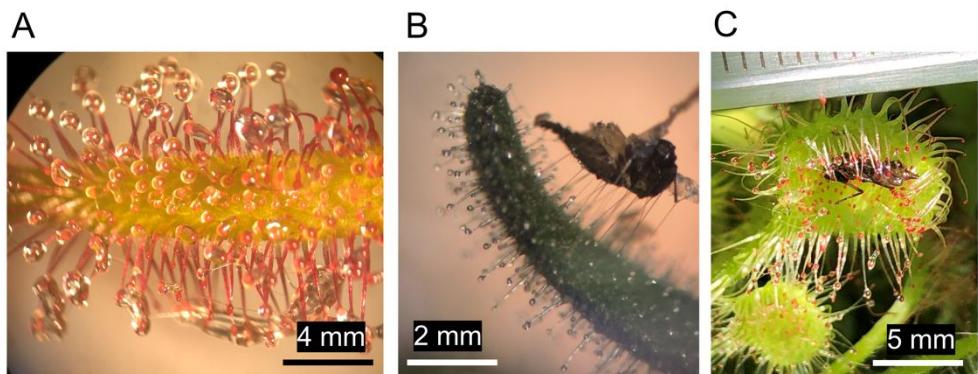


Fig. 2.1 Mucilage covered glandular trichomes of the arthropod-trapping outer part of the leaves of the carnivorous plant *Drosera capensis* (A). Carcass of a fungus gnat (Diptera) being pulled from the glandular trichomes on the sepal of a sticky *Petunia* cultivar, several stretched glue wires can be seen to adhere to the insect body (B). *Drosera rotundifolia* leaf with its trichomes bent around a captured insect (C).

There are many studies, books (e.g., Adlassnig et al. 2010) and reviews (e.g., Wheeler and Krimmel, 2015; Mithöfer, 2022; Luna-Samano et al. 2024), that describe sticky plants, their general ecology, and interactions with arthropods. Therefore, this review does not aim to be exhaustive or all-encompassing but rather builds on this prior knowledge to seek a deeper understanding of what determines successful arthropod capture in sticky plants, and in what ways we can utilize these plants, their associated predatory

arthropods, and other plant-derived sticky materials for crop protection. First, we will summarize the main mechanisms and factors involved in the successful trapping of arthropods by naturally sticky plants. Then, we will highlight some of the most recent developments on how sticky plants, natural adhesiveness, sticky plant predators, and plant-derived glues can be and are already applied in agriculture for arthropod pest control, with an emphasis on the integration with existing IPM techniques.

Initially, a systematic search was done for literature on sticky plants on May 1st 2024 in Web of Science, using a specific search term: “(adhesi* OR stic* OR trap* OR catch* OR adhere* OR attach*) (mucous OR mucus OR mucilag* OR exudate* OR resin*) (plant OR plants OR tree OR trees OR sundew Or drosera OR pinguicula OR butterwort OR tarweed) (insect* OR mite* OR athropod* OR spider*)” and using a broader search term: “(adhes* OR stick*) plant”. Thereafter, the same method was used to search for studies on the use of plant-based adhesives for pest control using keywords such as “(plant-derived OR plant-based OR natural OR bio-based) (adhesive* OR glue* OR resin*) (“pest control” OR “pest management” OR “crop protection” OR “biological control””). Searches were repeated on February 25th 2025 to include the most recent literature. Other papers were found using Google Scholar and by examining references within papers.

2. Evidence for the role of stickiness in plant defense

Glandular trichomes occur in around 30% of vascular plants (Glas et al. 2012). By now, the role of glandular trichomes and general plant stickiness in direct and indirect plant defense against herbivores and protection against environmental factors such as UV radiation and dehydration is well recognized (Glas et al. 2012). Some examples: Several genera of the *Nyctaginaceae* family possess glands that produce sticky rings on their stems that form a barrier for ants and other insects (da Cunha Neto et al. 2019). Floral stickiness has been linked to reduced florivory and prevention of nectar robbing (Jaime et al. 2013; Monteiro and Macedo 2014; McCarren et al. 2021; Chautá et al. 2022). Tomato trichomes repel and trap various small

arthropods including caterpillars, aphids, whitefly, spider mites, and thrips (Simmons et al. 2003; 2004; Blanco-Sánchez et al. 2021; Narita et al. 2023; Popowski et al. 2024; Tabary et al. 2024a, 2024b). The glandular trichomes of *Madiinae* (tarweeds), *Roridula* spp. and many other sticky plants are often covered with carrion (dead arthropods) which may attract predatory arthropods including assassin bugs and spiders. Many of these predators have adapted to life on sticky plants and are able to avoid getting stuck while scavenging carrion. Their presence provides indirect defense to the plant (Anderson 2006; Romero et al. 2008; Riddick and Simmons 2014; Wheeler and Krimmel 2015; LoPresti et al. 2018a; Karban et al. 2019; Pearse et al. 2024). Some predators, such as resin bugs, even collect sticky plant materials to enhance their own prey capture abilities (Avila-Núñez et al. 2016; Jiménez-Pomárico et al. 2019). Another form of indirect defense is the entrapment of sand (psammophory) which may reduce herbivory (LoPresti and Karban 2016). Likewise, adhesive seed coatings that bind soil particles help to prevent granivory (Pan et al. 2021). Experimental removal of glandular trichomes or their adhesives generally leads to significant increases in herbivory (Alcalá et al. 2010).

3. Morphology and physiology of sticky plants

3.1 Morphological characteristics of sticky traps

The book chapter by Adlassnig et al. (2010) provides an extensive summary of the morphology and chemical nature of the traps of carnivorous sticky plants, while Adamec (1997) and Luna-Samano et al. (2024) already discuss the importance of plant nutritional and developmental status. Therefore, the following sections are kept brief, mainly incorporating new insights from studies published after 2010 and information on non-carnivorous plants.

In many sticky plants, the glands (or glandular trichomes) that produce adhesive fluids look similar and generally consist of a head containing the glandular cells with a neck cell in the center that is attached to a uni- or multi-cellular stalk (Adlassnig et al. 2010). Glandular trichomes of different lengths

may be present on different plant organs that may contain different metabolites and fulfill different functions. In most carnivorous plants with sticky traps, such as *Pinguicula* spp., *Drosera* spp. and *Byblis* spp., the longer glands secrete more viscous fluids with larger adhesive strengths that are primarily involved in prey capture and retention, while the shorter, stalkless, sessile glands secrete less adhesive fluids that contain larger amounts of digestive enzymes (Huang 2015; Li et al. 2023; Natale et al. 2024). Movement of the trichomes may also play a significant role in the prey trapping process. For example, in *Drosera*, when prey is captured using the longer trichomes with estimated adhesive strength of $2.197 \pm 0.135 \text{ N/m}^2$ (Huang et al. 2015), the trichomes bend inwards and the leaf curls around the prey to further immobilize them and to bring them in contact with shorter trichomes that secrete the digestive enzymes (Fig. 2.1c) (Darwin, 1875). In *Pinguicula* spp., the trichomes are relatively short and cover the leaf surface and flowering stalks (Lustofin et al. 2023). After capturing prey, the trichomes and leaf cells below the prey lose turgor to create a pool of digestive fluids while the leaf edges may also bend inwards (Legendre 2000). Likewise, the trichomes of *Byblis* vary in length and the longer ones may collapse upon stimulation with prey to perform a similar function (Poppinga 2022). In *Roridula* spp., the dimensions of the glandular trichomes and their physical properties play a major role in the successful capture of arthropods. Out of three general lengths, the longest trichomes are more flexible and less adhesive than the middle-length and short ones, with 17,500, 24,500 and 156,200 median N/m^2 adhesion strengths respectively. Initial contact with the long trichomes will cause them to bend so that a struggling insect can easily contact the shorter trichomes (Voigt et al. 2009).

3.2 glue chemistry

The type of glue and its physical properties are a major factor in the ability of plants to capture arthropods. The glandular exudates of plants commonly contain a variety of phenols, (mono-, sesqui-, di-, tri-, etc.) terpenes, alkaloids, (poly)saccharides, lipids, fatty-acids, and other compounds (Glas et al. 2012; Muravnik 2020). Of these compounds, terpenes, essential oils,

and sugar esters are well known to have adhesive properties which can help to immobilize arthropods (Wagner 1991). While the chemical compositions of sticky plant exudates are diverse, there are also similarities between different plant groups.

For plants belonging to the *Solanaceae*, acylsugars and terpenes are thought to play a major role in the stickiness of their trichome exudates. In *Lycopersicon* (tomato) species, different non-glandular and glandular trichome types occur. The type IV trichomes (especially of wild varieties) contain high amounts of acylsugars and smaller amounts of terpenes, while type VI trichomes contain mostly terpenes and methyl-ketones (Tabary et al. 2024a). The sticky exudates of these two types of trichomes function as deterrents and traps for small arthropods (Goffreda et al. 1989; Simmons et al. 2004; Lucini et al. 2015). Similar acylsugar-rich trichomes help to protect potato (e.g. *Solanum berthaultii*) plants against various arthropods including aphids, leafhoppers, beetles, and mites (Tingey 1991). Different from carnivorous sticky plants, instead of being continuously sticky, arthropods first need to contact the trichomes of tomato and potato to make the glands rupture and release their contents, which then rapidly oxidize to immobilize the nearby arthropods (Duke 1994). In tobacco (*Nicotiana* sp.), the longer trichome types secrete a similar, clear, resinous material containing diterpenes (e.g. cembranoids), acylsugars, and other compounds (Meyberg et al. 1991; Uzelac et al. 2021; Feng et al. 2022). For *Datura wrightii*, phenotypes with glandular trichomes containing acylsugars trap small arthropods and show increased resistance to several herbivores (Hare and Elle 2002; Hare 2005; Goldberg et al. 2021) but are also more susceptible to other herbivores such as *Tupiocoris notatus* (Hare and Smith 2005). Likewise, the trichomes of *Petunia axillaris* (Nadakuduti et al. 2017) and *Salpiglossis sinuata* (Moghe et al. 2017) contain high amounts of acylsugars and these plants may be covered with dead insects.

For carnivorous plants with sticky trichomes, at least two different types of glues have evolved. Carnivorous plants of the order *Lamiales* (*Pinguicula*

and *Byblis*) and *Nephentales* (*Drosera*, *Drosophyllum*, *Triphyophyllum*) produce viscous fluids mostly made up of a watery solution of polysaccharides (Hatcher et al. 2020). In *Byblis* spp. (and presumably also *Pinguicula* spp.) pectin is a main constituent of the mucilage (Giuliani and Maleci Bini 2008; Li et al. 2023). In *Drosera* spp., the mucilage consists of around 4% polysaccharides, a large volume of water, and some other compounds, including *myo*-inositol and inorganic cations (e.g. Ca^{2+} , Mg^{2+} , K^+ , Na^+) (Rost and Schauer 1977; Loewus and Murthy, 2000; Kokubun, 2017; Vanda et al. 2021). The physical properties of the mucilage and the presence of nanostructures and nanoparticles play a large role in the ability of the fluid to stretch and adhere to arthropods (Erni et al. 2011; Huang et al. 2015; Li et al. 2019; 2020). The viscous pitcher fluids of carnivorous *Nepenthes* spp. and glues and seed coatings of other sticky plants that show similar mechanical properties to the fluid of *Drosera* spp., are likely comparable in terms of chemical composition (Bonhomme et al. 2011; Kang et al. 2021; Kreitschitz et al. 2021), although for many plant species this has not been confirmed yet. Polysaccharides such as pectin also occur in the trichome secretions of other non-carnivorous sticky plant species including *Leonotis leonurus*, *Salvia* spp., *Fagonia* spp. and *Cucurbita pepo* var. *styriaca* (Ascensão et al. 1997; Serrato-Valenti 1997; Corsi and Bottega 1999; Fahn, 2000; Kolb and Müller, 2004). Lipids and other compounds may also be present alongside polysaccharides, as is the case for *Inula viscosa* (Werker and Fahn 1981). For *Ibicella lutea* and *Proboscidea louisianae* (Lamiaceae), the oily materials secreted from their sticky trichomes, contain mainly glycosylated fatty acids, glycerides, and dammarane triterpenes (Asai et al. 2010).

The other type of glue, which is produced by the trichomes of the protocarnivorous plants *Roridula dentata* and *Roridula gorgonias*, is a highly viscous, lipophilic resin. This adhesive substance is mainly composed of acylglycerides and triterpenoids, with small quantities of flavonoids and other unknown triterpenols (Simoneit et al. 2008; Wollenweber 2007). The glue does not contain enzymes, proteins or saccharides. In *R. dentata* glue extracts,

the main triterpenoids are dihydroxyolean-12-ene and dihydroxyurs-12-ene, while in *R. gorgonias*, taxeradiol is the major component (Simoneit et al. 2008). Contrary to the polysaccharide-based mucilage of *Drosera* spp. which are soluble in water and may disappear during rain or when relative humidity is low, the glues of *Roridula* spp. are more water-resistant and function under a wide range of humidities (Voigt and Gorb 2010a; Voigt et al. 2015). In a way, the visco-elastic secretions from the glandular trichomes of *Roridula* spp. are comparable to pressure sensitive adhesives (Voigt et al. 2009).

The glandular trichomes on the leaves, shoots, buds, and flowers of *Robinia viscosa* var. *hartwigii* trees secrete sticky fluids consisting of a mixture of metabolites including lipids, polysaccharides, flavonoids, proteins and alkaloids (Konarska and Łotocka 2020). In a similar way, young shoots of the legume tree *Schizolobium parahyba* are covered in adhesive secretions (made by epidermal cells) that contain terpenes and lipids (mixtures of essential oils and oleoresins) (Paiva et al. 2022). Other trees such as the silver birch (*Betula pendula*), black poplar (*Populus nigra*), black alder (*Alnus glutinosa*), Scots pine (*Pinus sylvestris*) and horse-chestnut (*Aesculus hippocastanum*) have buds covered with small trichomes that secrete sticky resins made up of complex mixtures which include various amounts of terpenoids, fatty acids, phenylpropanoids and flavonoids (Isidorov et al. 2016). For horse-chestnut, a glandular secretion with adhesive strength of up to 204,300 N/m², depending on temperature and humidity, is present most of the year. This adhesive substance can be thought of as an aliphatic hydrocarbon resin which contains 43.4% triterpenoids, 13% flavonoids and a distinctive 20.1% Aliphatic 3-hydroxyacids with long chains in the range of C14-C22 (Isidorov et al. 2016; Voigt et al. 2020). While occasionally trapping small arthropods, bud secretions like these are mainly for protection of the buds against dehydration and other environmental factors. The composition of horse-chestnut mucilage resembles that of the resin of *R. gorgonias* and adhesive seed coating of the radiator plant *Peperomia polystachya*, which are also mixtures of resins based on aliphatic esters and carboxylic acids (Frenzke et al. 2016; Voigt et al. 2020). The resin of

tarflower (*Befaria racemosa*), with adhesive strength comparable to commercial flypaper glue (40,000 to 50,000 N/m²) (Eisner and Aneshansley 1983; Voigt et al. 2009), is likely similar. However, detailed chemical studies are still lacking, as is the situation for the composition of the adhesive seed coverage of *Pisonia* tree fruits, the exudates of tarweed (*Madia elegans*), the sticky flowers of *Bejaria resinosa* (Chautá et al. 2022) and *Erica* spp. (likely carbohydrate based) (Vlok and Schutte-Vlok, 2003), and glandular secretions of many other sticky plants.

4. Visual cues and volatiles for arthropod attraction or repellence

Arthropods use visual and chemical cues to navigate their environment, locate food sources, and avoid danger (Wenninger et al. 2009) The visual appearance of the leaves, flowers, trichomes, and other parts of sticky plants and the volatile compounds they release therefore can act as powerful signals to influence arthropod behavior (Luna Samano et al. 2024). Carnivorous plants such as *Drosera* spp. and *Pinguicula* spp. make use of different volatile blends to attract prey towards their adhesive leaves and pollinators towards their flowers (Jürgens et al. 2009; Ojeda et al. 2021; Cuevas et al. 2023). Meanwhile, pitcher plants use flower-like scents and extrafloral nectar to lure insects towards their pitfall traps (Mithöfer 2022). In contrast, the glandular trichomes and exudates of plants that use stickiness primarily for their own defense commonly contain or release volatiles that repel a wide range of arthropods, while being attractive towards some (often sticky plant specialized) herbivorous and predatory arthropods (van Dam and Hare, 1998; Murungi et al. 2016).

In addition to differences in volatile composition between flowers and traps, the color of green leaves seems more attractive to prey than red leaves and UV patterns of flowers and their spatial separation from traps have been suggested to reduce pollinator capture in sticky plants (El-Sayed et al. 2016; Luna-Samano 2024). Next to this, the visual and volatile cues from carrion present on sticky plants may attract scavenging arthropods (Nelson et al. 2020) Whether the presence of carrion on plant surfaces also deters prey is

still unclear (Lev-Yadun 2014). Likewise, it is still unknown if herbivorous arthropods are able to sense the presence of carrion scavenging predatory arthropods and if herbivores then avoid sticky plants where these predators occur (Dicke and Grostal 2001). To what extent the shiny appearance of mucilage droplets and the red pigments found in the trichomes, and other parts of plants play a role in defense against herbivores, prey and predator attraction, or as a visual cue that prevents pollinators from becoming trapped is still not entirely clear (Jürgens et al. 2015; Mithöfer 2022).

5. Environmental factors affecting capture success

Temperature variations, wind speed, relative humidity, rainfall, light intensity, and the presence of dust or other particles may all affect the physical and chemical properties of the adhesive traps of sticky plants, and hence their effectiveness, as well as the presence and behavior of arthropods that become trapped in them (Zamora 1995; Obrycki and Tauber 1984; Nihoul 1993). In general, plants with sticky trichomes occur in places where the environmental conditions allow for their adhesives to work, either because these conditions were suitable from the start such as in high humidity or moist areas, or because it was possible to adapt the formulations of the sticky fluids, such as is needed in dry environments. Especially for glues that are watery solutions of polysaccharides or that contain other less rigid substances, certain minimum temperatures and levels of humidity are often required for the traps to work as seen in *Pinguicula* spp. and *Drosera* spp. where sticky droplets may change in viscosity based on temperature, may evaporate under low humidity, or may temporarily be washed away by rain (Rost and Schauer 1977; Crowder et al. 1990; Legendre 2000). The traps of *Roridula* spp. are more robust. Their resin changes only slightly under temperature ranges of 20-25 °C (viscosity and adhesive strength do change at more extreme temperatures) and remains sticky in dry environments and under water for long time periods, even when plants are dead (Voigt and Gorb 2010a; Voigt et al. 2015). For many sticky plants, information on how abiotic factors affect the chemical composition, adhesive strength, and longevity of their adhesive exudates under natural and laboratory conditions is still lacking.

6. Morphological and behavioral adaptations of arthropods to prevent adhesion

The morphology and behavior of herbivores, pollinators, and predatory arthropods in relation to trap morphology and adhesive strength are important factors that determine whether these arthropods become stuck or not in the adhesive secretions of sticky plants. The type of arthropods captured by sticky plants are usually a subset of the arthropods that are available in the environment (Gibson ,1991). In general, healthy plants with sticky traps that are not damaged, plants with larger or more complex trapping structures and stronger adhesives, and the traps of multiple plants combined capture more and larger arthropods (Zamora 1995; Gibson and Waller 2009). For example, *Drosera* spp. and *Pinguicula* spp. capture mainly small insects in their polysaccharide glues including flies, springtails, beetles, thrips and leafhoppers. Larger and stronger insects like ants, moths and small damselflies are only captured occasionally (Zamora 1999; Ellison and Gotelli 2009; personal field observations). In contrast, the resinous secretion from the trichomes of *Roridula* captures various arthropods of considerable size, particularly flying ones (Voigt and Gorb 2008) and pitcher plants capture a lot of ants and not many flying insects (Zamora 1999). As mentioned before, pollinators may also be among trapped arthropods, but temporal, spatial, or chemical separation of traps from flowers and adaptations of pollinators to recognize traps help pollinators to avoid becoming trapped, hence lessening the “pollinator prey conflict” that sticky plants otherwise face (El-Sayed et al. 2016; Tagawa 2020).

Instead of becoming trapped, some carrion scavenging arthropods and herbivores avoid being captured and use sticky plants as a habitat and food source. Often this is possible due to behavioral or morphological adaptations. *Pameridae roridulae* true bugs (*Miridae*) possess waxy cuticula, strong limbs and a sturdy body which allows them to plow through the adhesives of their host plant *Roridula* (Voigt and Gorb 2008). Crab spiders living on *Roridula* have also been suggested to use greasy materials to avoid adhering to the

trichomes (Marloth 1903). Likewise, several mealybug species have waxy exteriors which help to prevent them from becoming trapped, for instance while feeding on the sticky flowers and buds of *Erica* sp. (Krimmel and Wheeler 2015) In contrast, *Dicyphus errans*, another mirid bug that occurs on *Roridula*, avoids contact of its slender body with the trichomes by using its long legs to grab on to trichome stalks and walking over them (Voigt and Gorb 2010b). Other mirid bugs that live on sticky plants have similar adaptations (Fig. 2.2) (Wheeler and Krimmel 2015; LoPresti and Toll 2017).



Fig. 2.2 Many Mirid bugs, such as the herbivore *Metatropis rufescens* depicted here, use their long legs to walk over glandular trichome covered plant surfaces.

Another way in which arthropods can avoid being captured is by detachment of limbs, hairs, scales and by having other protective coatings (Betz and Kölsch 2004; Krueger et al. 2023). For example, some leafhopper and whitefly species have renewable powder coats that help to prevent adhesion (Gibson and Turner 1977; Rakitov and Gorb 2013). Finally, some arthropods are simply small enough to simply crawl among the trichomes of sticky plants or may avoid becoming stuck by removing trichomes or their adhesives. Tiny

mites and crane fly larvae (*Tipulidae*) move effortlessly along the leaf surface underneath the sticky trichomes of *Pinguicula* plants without issue, while some *Drosera* spp. are home to the trichome devouring larvae of the sundew plume moth (*Buckleria paludum*) and carrion scavenging larvae of the sundew flower fly (*Toxomerus basalis*) (Eisner and Shepherd 1965; Antor and Garcia 1995; Zamora and Gómez 1996; Osaki and Tagawa 2020; Fleischmann et al. 2022).

7. Agricultural applications

7.1 Breeding for stickiness

Several crop species and their wild counterparts have sticky features including forage crops like alfalfa, gourds such as pumpkin, hops, cotton, tobacco, tomato, potato, cannabis and horticultural household plants like petunia, geranium, and mints (Wheeler and Krimmel 2015; López-Gallego et al. 2019; Nelson et al. 2019a). Since glandular trichomes and plant stickiness are involved in several aspects of direct and indirect plant defense against herbivores and environmental factors, breeding to enhance these plant characteristics could be a worthwhile approach to prevent crop losses and improve overall yield (Tingey 1991; Nelson et al. 2019a). However, due to the complexity of the interactions between arthropods and plant glandularity, the outcome of large scale trichome alterations may be difficult to predict (Wheeler and Krimmel 2015). Furthermore, since many different genes may play a role in trichomes as a defense, engineering trichomes for specific functions may be challenging. Currently, only simple modifications are possible, such as selection for increased content of specific substances via knockout or over-expression of target genes in key pathways. As research continues and more details regarding the genes and pathways involved in trichome defenses are uncovered, more options should open-up for targeted trichome engineering (Glas et al. 2012). Of course, one could also consider getting rid of trichomes. Usually this is easier to achieve (e.g., via knock-out of key trichome development genes). In tomato cultivars without trichomes, predatory mites were shown to suppress spider mite and tomato russet mite

populations faster and better (Legarrea et al. 2022). This illustrates that with respect to trichome engineering there may be multiple viable strategies to achieve reliable pest control of some target pests in some crop systems.

7.2 Sticky plants as a trap crop

Sticky plants passively trap certain sizes of arthropods that occur in their environment and provide predators with carrion. Pest insects such as thrips are commonly caught (Fig. 2.3a) As such, using sticky crops or sticky companion plants could be useful for trapping small arthropod pests to protect neighboring plants and for maintaining predator populations in agricultural areas (Sánchez et al. 2003; Tagawa and Watanabe 2021), although predatory arthropods may also be negatively influenced by stickiness (Fig. 2.3b).

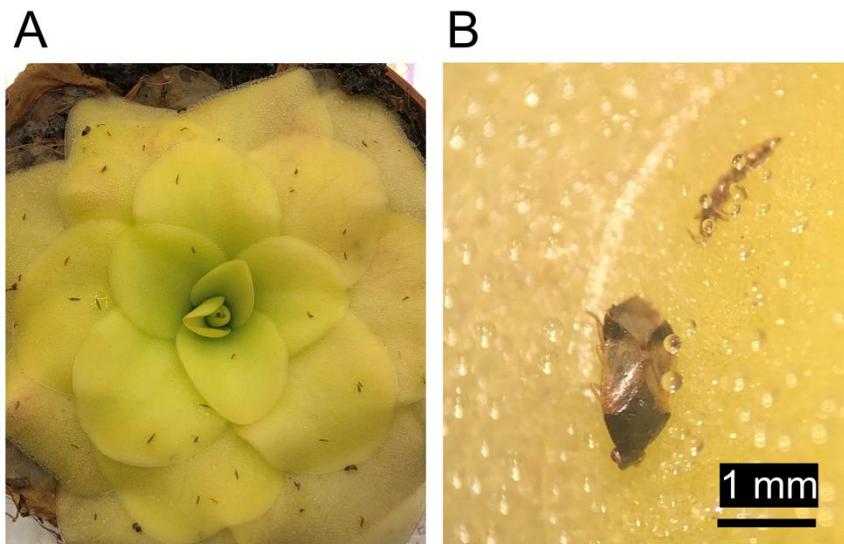


Fig. 2.3 Leaf rosette of *Pinguicula* cultivar 'Tina' (*P. agnata* × *P. zecheri*) with western flower thrips and a predator of thrips, *Orius laevigatus* stuck to the glandular trichomes on the leaves (A), and a close-up of one leaf with many small mucilage covered glandular trichomes and a trapped *Orius laevigatus* individual and a trapped western flower thrips individual (B).

In one study, a pumpkin cultivar with adhesive trichomes (*Lagenaria siceraria*), was used as a trap crop for whitefly (*Bemisia tabaci*) and this reduced populations of this pest in greenhouse grown tomato (López-Gallego 2019). In another greenhouse trial, a special laboratory strain of tobacco (*Nicotiana benthamiana*) was used as a trap crop and found to be as efficient as sticky traps in killing whitefly and thrips while having minimal effects on predatory arthropods (Han et al. 2024). Furthermore, this tobacco grew well under several greenhouse conditions and was preferred by whitefly and thrips over other main crops such as tomato and cucumber. Soon after, the resistance of this tobacco strain was linked to acylsugars, creating an opportunity for breeding (Wang et al. 2024). In orchards, *N. benthamiana* may also be useful as a dead-end trap crop for sap-sucking arthropods like the citrus psyllid *Diaphorina citri* (Zheng et al. 2023). The potential of sticky plants for arthropod trapping is further illustrated by observations made in a teak plantation in India where an undergrowth of malvaceous weeds with sticky trichomes was found to trap and cause high mortality of teak defoliator moth larvae (Loganathan et al. 1999). Growing sticky legumes in pastures could also be beneficial to entrap cattle ticks (Sutherst et al. 1982). Wheeler and Krimmel (2015) furthermore suggested the use of sticky plants in hedgerows to support mirid bugs, other sticky plant specialist predators, and bees and other insects that utilize resin for nestbuilding. The use of carnivorous plants as companion plants for arthropod trapping seems a rather unexplored area. People living in South-Africa hang the branches of *Roridula dentata* and *R. gorgonias* in their house to trap flies (Marloth 1903), but otherwise carnivorous plants are rarely used for pest control. More research is needed before we can conclude whether carnivorous sticky plants can be used as trap crops in agriculture.

7.3 Compatibility of plant stickiness with predatory arthropods and pollinators

Predatory arthropods and pollinators are commonly used in agriculture to suppress pest populations. From an applied perspective, plant stickiness may have positive and negative effects on predatory arthropods and pollinators.

Plants covered in carrion and pollen due to their stickiness may attract and maintain higher predator populations (Krimmel and Pearse 2013; Nelson et al. 2019a). In addition, the presence of glandular trichomes may reduce intraguild predation (predators eating each other), a phenomenon that can otherwise considerably reduce the effectiveness of predatory arthropods to suppress pests (Griffin and Yeargan 2002; Barriault et al. 2019). Some generalist predators also perform better on sticky plants than on plants without trichomes (Krimmel and Pearse 2014). However, this seems to be the exception rather than the rule since several studies have shown that the mobility and effectiveness of many commonly used predatory arthropods (e.g., ladybeetles, lacewing and hoverfly larvae, parasitoids, and predatory mites) are significantly hindered by the glandular trichomes of several plant species (Romeis et al. 1999; Gassmann et al. 2005; Riddick and Simmons 2014; Wheeler and Krimmel, 2015; Legarrea et al. 2022; Carretero et al. 2022). Next to this, the presence of carrion may also increase cannibalism among predators on some sticky plants (LoPresti et al. 2018a).

Meanwhile, specialist arthropod predators of sticky plants seem to have less trouble with navigating on plants with glandular trichomes and therefore seem more suitable for use alongside sticky crops (Krimmel and Pearse, 2013). In fact, some of these specialist predators are already employed as biocontrol agents or occur freely in agricultural areas, e.g., the stiltbug *Jalysus wickhami* in tobacco (Nelson et al. 2019a, 2019b) and several species of stilt bugs and mirid bugs, including *Tupiocoris cucurbitaceus*, in cultivated tomato (López et al. 2019; Montiel Cáceres et al. 2023). Other sticky plant predators remain to be utilized for crop protection, perhaps seeing use after breeding for desired traits (Pérez-Hedo et al. 2021) or may be unsuitable due to these predators also causing feeding damage to crops (Castañé et al. 2011) or eating each other (Moreno-Ripoll et al. 2012; Vila et al. 2012).

Next to the identity of the specific predators and plants involved, the success of predatory arthropods to establish on sticky plants furthermore depends on other factors than stickiness alone (Krimmel and Pearse 2014). Under

greenhouse conditions, the negative effects of glandular trichomes on predatory arthropods may be greater than in field situations where environmental factors such as temperature fluctuations, dust, wind, and rainfall may reduce the stickiness of the adhesive trichomes (Obrycki and Tauber 1984). Some predators may also learn to adapt to sticky plants when reared on them (Drukker et al. 1997). Altogether, there seems to be potential for utilizing predatory arthropods, especially specialists, alongside sticky crops, but management practices may have to be adapted before the use of these predators can be successful on sticky crops. (For more information on Mirid predators and their potential for agriculture see Wheeler and Krimmel 2015).

As mentioned before, pollinators may also become trapped in sticky plants. However, sticky plants and pollinators likely have evolved adaptations, such as pollinators having an elongated proboscis, to reduce the risk of this happening (McCarren et al. 2021; Chautá et al. 2022). Commercially used pollinators such as honeybees and bumblebees are unlikely to be detrimentally impacted by plant stickiness as they are of considerable size, have co-evolved with plant stickiness as a defense, and some are used to handle plant resins for their own benefit (Shanahan and Spivak 2021). Small-sized pollinators such as wild bees, wasps, thrips and minute flies and beetles likely have a higher risk of being trapped while hoverflies, moths and butterflies are less likely to be captured (Zamora 1999).

7.4 Plant-based adhesives as sticky traps

Adhesives play a significant role in agriculture, particularly in the context of arthropod trapping and monitoring in integrated pest management strategies. In agricultural settings, sticky traps placed at different heights have been shown to be an effective method for the capture of insects like aphids, leafhoppers, and leaf beetles (Straw et al. 2011) with different trap designs show varying levels of efficacy in capturing specific arthropod species (Whitfield et al. 2019). The glues used for these commercial sticky traps are still often petroleum based (Hansupalak et al. 2023). However, research on

plant-based and other natural adhesives has recently intensified and new advantages of their application are being discovered, such as increased adhesive strength and water-resistant properties over conventional adhesives (Maassen et al. 2016; Heinrich 2019).

In search of sustainable alternatives for pest control, trapping arthropods in biological glues seems a promising alternative. In fact, plant derived materials such as vegetable oils, polysaccharide rich gums or natural rubbers, and resins are already in use and are being increasingly investigated for arthropod trapping. Tanglefoot, made of (pine) resin, castor oil (and optional: bees wax, linseed oil) has been used since the 1800s for flypaper and is still commonly slathered on tree stems to stop crawling arthropods (Lambert and Franklin 1967). Recent attempts to use glues made from natural rubber, soybean oil and surfactants and another made from natural rubber and palm oil have turned out somewhat less effective for arthropod trapping than commercially available glues. This was mainly due to the glue layer dripping down over time, which illustrates the importance of viscosity in the effectiveness of vertical sticky traps (Hansupalak et al. 2023; Wiroonpochit et al. 2024). There are no reports yet of sticky traps made with acylsugars, starch, cellulose or other trichome-inspired polysaccharide glues, most likely since these glues have low overall adhesive strengths and are sensitive to humidity and fungi, which are common challenges for polysaccharide-based glues (Heinrich 2019; Ma et al. 2023).

7.5 Plant-based sprayable adhesives for arthropod trapping on plant surfaces

Recently, developments have been made in another trapping approach: sprayable adhesives made from natural materials to provide plants with sticky defenses. With a mode of action similar to the exudates of tomato trichomes, Agri-colle (or Agricolle) is a non-toxic, sprayable glue made from propylene glycol alginate with a physical mode of action. Upon application on infested plants, small arthropods such as aphids, whitefly, psyllids, and spider mites quickly find themselves stuck and suffocating as the substance dries out

(Calagri International 2025). While this approach can be viable in glasshouse grown crops such as tomato and cucumber (Pilkington et al. 2013), achieving sufficient effectiveness in other systems, such as pear orchards, seems more challenging (Balkhoven 2009). In addition to Agri-colle, the same producers have developed Agri-50, a formulation based on potassium phosphate and xanthan gum, but this product is not yet available on the market (Calagri International 2025).

Another development in the realm of bio-inspired sprayable adhesives is the use of alginate-based solutions that contain sticky particles or droplets made from oxidized and crosslinked vegetable oils (e.g. rice oil or mixtures of sunflower-, olive-, and lindseed oil) to physically trap small arthropods on plant surfaces. When filter papers and detached leaves were sprayed with these plant oil-based adhesives in laboratory assays, high catch rates of western flower thrips (*Frankliniella occidentalis*) were obtained (Fig. 2.4a, on the next page) and thrips damage and reproduction were reduced (Bierman et al. 2024; van Zwieten et al. 2024). In later trials with caged chrysanthemum plants, the trapping effectiveness was lower. However, thrips damage and population growth were still significantly reduced on adhesive sprayed plants (Bierman et al. 2025). These results could be due to direct effects on thrips of the plant oils and the alginate and surfactant of the carrier solution, and due to indirect effects on thrips via plant metabolomic changes that occurred after spraying (Bierman et al. 2025). In continuation of this work, more fluid oil formulations (Fig. 2.4b) are currently being tested in combination with predatory arthropods. As continuous efforts are being made to make new bio-inspired adhesives, more eco-friendly pest trapping options will likely soon appear.

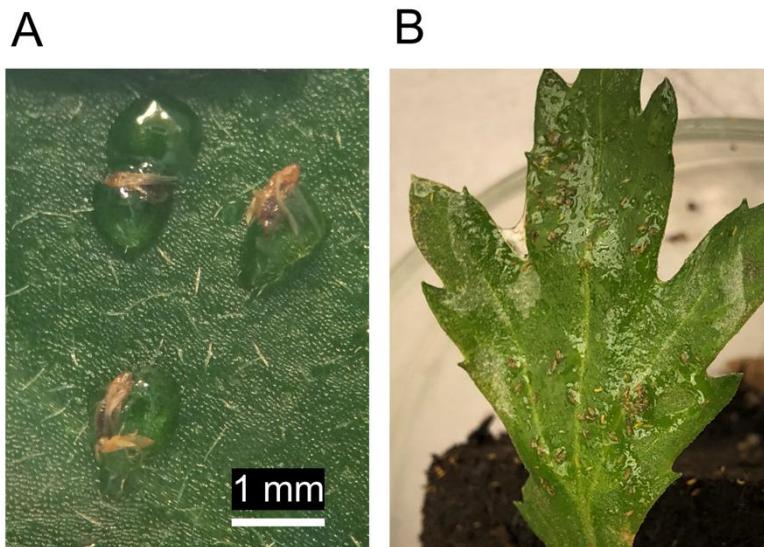


Fig. 2.4 Western flower thrips (*Frankliniella occidentalis*) female adults caught in sprayable adhesive droplets made from epoxidized rice germ oil on a *Chrysanthemum* leaf surface (A). More fluid rice germ oil-based sprayable adhesive formulation with many thrips captured on a *Chrysanthemum* leaf (B).

7.6 Plant-based materials as adjuvants and (nano)carriers of pest repellent chemicals

In addition to their use as a physical trap, plant-based and other natural materials may also be utilized as adjuvants and (nano)carriers to improve the stability, longevity, efficacy and plant surface adherence of botanicals and regular pesticides (Zainab et al. 2024). For example, Iqbal et al. (2022) used a mixture of lemongrass (*Cymbopogon citratus*) oil and *Prosopis juliflora* extracts as an adjuvant to enhance the effectiveness of neem oil application against whitefly on detached eggplant leaves. Likewise, Fang et al. (2023) used *Camellia* oil-based emulsions as nanocarriers to enhance the effectiveness of the pesticide emamectin benzoate against *Spodoptera litura* larvae on detached *Nicotiana tabacum* leaves. Although not necessarily a strong adhesive, the polysaccharide alginate has been used as an adjuvant to

reduce pesticide drifts during spraying. When used in the field, this approach led to reduced effects of the used pesticides on pollinators while maintaining efficacy against target pests (Kannan et al. 2024). Similarly, bait sprays made by encapsulation of fluid baits in alginate hydrogel beads or those made from water-based mixtures containing other saccharides, proteins or plant oils can be used to deliver pesticides, botanicals or other control measures (e.g. entomopathogenic fungi and nematodes) more efficiently to various pests, such as mosquitoes, fruit flies, moths and ants (Mason et al. 1998; Böckmann et al. 2014; Tay et al. 2020; Kumar et al. 2021; Sarma et al. 2023).

Another interesting example is “specialized pheromone and lure application technology” (SPLAT), a cream-like, tacky substance for the controlled release of volatiles. SPLAT formulations, typically made from mixtures of mainly water, wax, and vegetable oils, are successfully used for various agricultural and forestry applications, including mating disruption, mass trapping, attract and kill and repellency of fruit flies and several species of beetles and moths (Teixeira et al. 2010; Mafra-Neto et al. 2013, 2014). In addition to their use as agricultural sprays, natural adhesives may also be used as carriers of pest repellent chemicals to protect stored foods. For example, starch-based adhesives loaded with cinnamon oil were found useful to protect cardboard food packaging against *Plodia interpunctella* larvae (Kim et al. 2020).

8. Conclusion and perspectives

In conclusion, stickiness plays a major ecological role in providing plants with direct and indirect defenses as well as nutrition. The successful capture of arthropods in the glandular trichomes of sticky plants is determined by a combination of biotic and abiotic factors. Plant development and nutritional status, the morphology of the adhesive glands (e.g., their surface area, density and three-dimensional structures and mobility), the physiochemical properties of their adhesives, the potential attraction of arthropods through volatile substances and colors, environmental conditions, the specificity of adhesive traps and exudates against arthropods of varying sizes, and the

adaptions of arthropods to avoid becoming trapped all are crucial in determining the outcome of the interactions between arthropods and sticky plants. Furthermore, the intricate relationships between sticky plants, the arthropods they trap, and those that associate with sticky plants as herbivores, predators or pollinators adds to the complexity of these natural systems.

Regarding the potential of natural stickiness to enhance the sustainability of current agricultural practices, using sticky plants as trap crops, breeding for enhanced or removed sticky defenses, employment of sticky plant predators, and using plant-derived glues for sticky traps, as sprayable adhesives for physical crop protection, and as bio-based carriers for pesticides and botanicals all seem promising options for integration with existing or novel pest management strategies. By harnessing the adhesive properties found in nature and those of bio-based materials, farmers may ultimately very effectively control arthropod pests while minimizing the use of harmful chemicals, plastics, or other materials with negative aspects, thus leading to more sustainable agricultural practices. However, some major limitations and challenges will first have to be overcome before sticky plants, plant stickiness, sticky plant predators, and bio-based sticky materials can be applied on a large scale in agriculture.

First, the use of sticky plants, their arthropod predators, and plant-based adhesives is currently only partly compatible with current practices and agricultural equipment. In addition, the production of bio-based adhesives and efforts to cultivate and breed sticky crops and their predators are often still small scale. Since the development of new management practices, equipment and facilities for larger scale production take time and money and labor, this may hinder the fast adoption of these new methods by growers and farmers. Second, the use of natural methods does not always produce consistent results, which may lead to reluctance among growers to use such methods. Proper quality control and education may solve these issues, but these usually take time to be implemented. Third, a familiar issue with the use of non-crop plants and bio-based materials is that their production may

compete with other societal needs for which space, fertile land and other resources are required. The feasibility for the adoption of stickiness-related methods in agriculture is therefore dependent on whether the use of these methods conflicts with or is compatible with our prior needs as a society and whether consumers also accept these new methods. Finally, we still are lacking knowledge on the side effects of introducing new plant and predator species into our agricultural systems and on how the use of plant-based products affects our crops, non-target arthropods, soil organisms and the rest of our environment. To prevent previous mistakes and future disasters, it is necessary that we inform ourselves well before changing our global agricultural practices.

More research into the ecology, morphology and physical and chemical nature of mucilage producing plants, their secreted adhesives, and how arthropods interact with them may provide us with a better understanding of how sticky plants trap arthropods and may pave the way to future opportunities for the use of sticky plants, their predators, and the development of plant-derived glues for pest control. As more discoveries around sticky plants are being made, new formulations of bio-based glues are created continuously, and our understanding of their unique properties increases, it is likely only a matter of time before plant stickiness and natural glues will be integrated into conventional practices and replace synthetic glues for arthropod trapping.

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Author contributions

All authors took part in conceptualization and realization of the work. TVB, TMB and YHC wrote the first draft. TVB created the images.

Conflict of interest

The authors of this review have performed research on the application of plant-based adhesives in agriculture in collaboration with Wageningen University and Research, the Netherlands, which has filed a patent with the European Patent Office for the method to fabricate solutions with adhesive plant-derived oil droplets, application no. 22202752.6; EP4356732A1.

