Research review

Sticky mucilages and exudates of plants: putative microenvironmental design elements with biotechnological value

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Summary

Plants produce a wide array of secretions both above and below ground. Known as mucilages or exudates, they are secreted by seeds, roots, leaves and stems and fulfil a variety of functions including adhesion, protection, nutrient acquisition and infection. Mucilages are generally polysaccharide-rich and often occur in the form of viscoelastic gels and in many cases have adhesive properties. In some cases, progress is being made in understanding the structure–function relationships of mucilages such as for the secretions that allow growing ivy to attach to substrates and the biosynthesis and secretion of the mucilage compounds of the Arabidopsis seed coat. Work is just beginning towards understanding root mucilage and the proposed adhesive polymers involved in the formation of rhizosheaths at root surfaces and for the secretions involved in host plant infection by parasitic plants. In this article, we summarise knowledge on plant exudates and mucilages within the concept of their functions in microenvironmental design, focusing in particular on their bioadhesive functions and the molecules responsible for them. We draw attention to areas of future knowledge need, including the microstructure of mucilages and their compositional and regulatory dynamics.

Introduction

Land plants have a great ability to adapt to a diverse range of environments. Being sessile and unable to evade unfavourable conditions, their survival depends critically on their ability to sense their environment and, if possible, create favourable local conditions. To meet these demands, plants have developed a range of strategies, including morphological adaptations, long-distance communication via volatiles or synthesis of protective metabolites. Plants have also evolved ways to bioengineer favourable microenvironments in their immediate surroundings by the secretion or exudation of mucilages from various surfaces. Mucilage, defined by Sasse *et al.* (2018) as a matrix of high-molecular-weight compounds, is secreted as a viscoelastic gel that is often polysaccharide-rich. The wider term exudates encompasses mucilages but can also include compounds of lower molecular weight and more soluble high-molecular-weight polysaccharide and protein components that may not contribute to gel-like structures. Depending on the plant species, exudates and mucilages can be secreted by almost any plant organ, and seemingly from all clades of the angiosperms (Brown *et al.*, 2017), and in a few cases multiple exudate types with different origins have been described for the same species or genus (e.g. seed coat, haustorial and stem exudates for parasitic dodder (*Cuscuta* spp.)) (Schaffner, 1976; Lyshede, 1984; Vaughn, 2002). Mucilages and other exudates provide an effective means to execute a variety of functions beyond the confines of their tissues and organ surfaces. Classic examples include the capacity of climbing plants to climb up vertical surfaces using sticky tendrils or roots (Endress & Thomson, 1977; Groot *et al.*, 2003; Huang *et al.*, 2016). Other types of exudates are produced by leaves or by stems and have become known as extrafloral nectars (Deynze *et al.*, 2018; Pierce, 2019). Below ground, the roots are equally adept in producing mucilages that have an impact on the properties of their immediate soil environment (Sasse *et al.*, 2018). Each type of secretion essentially consists of a unique blend of molecules that, depending on its location, serves a specific set of functions. These functions range from attracting beneficial microbiota (Haichar *et al.*, 2014) and insects (Deynze *et al.*, 2018), modifying soils for enhanced nutrient and water uptake (Galloway *et al.*, 2018) or surface anchorage for climbing (Bowling & Vaughn, 2008) to attachment to hosts before their infection (Vaughn, 2002).

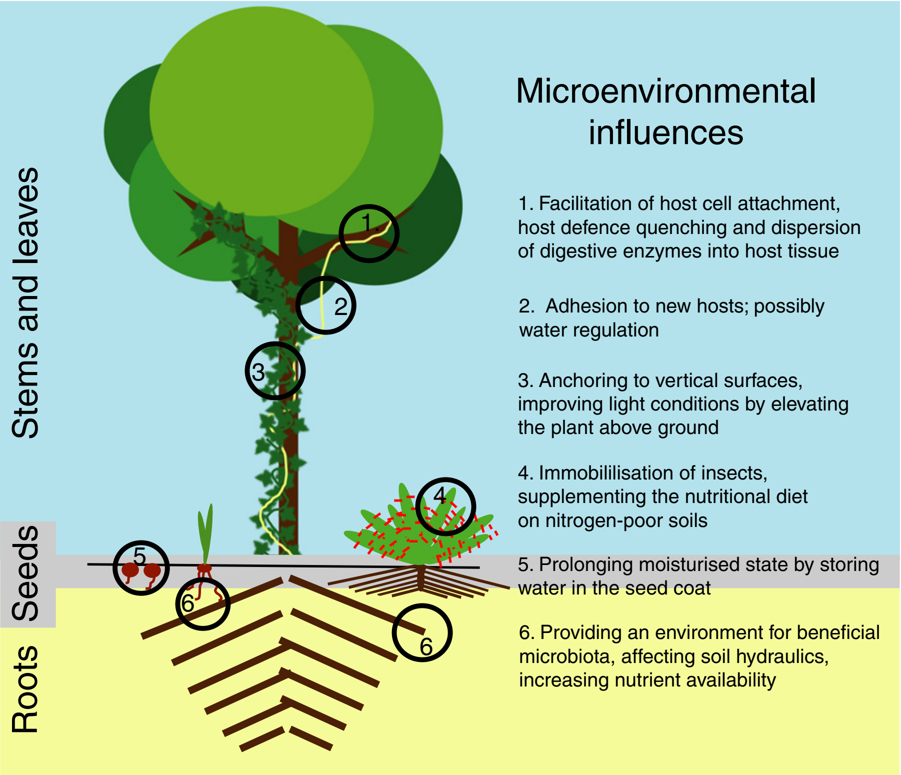
Some molecules within mucilages have bioadhesive properties, making them sought-after materials for biotechnological, biomedical or agricultural applications (Favi *et al.*, 2014; George & Suchitra, 2019). Important breakthroughs have been made in the last few years in investigations of the sticky adhesives used by English ivy and by sundew (Zhang *et al.*, 2010; Lenaghan & Zhang, 2012), and a current focus on molecular genetic investigations of seed coats (Golz *et al.*, 2018; Sechet *et al.*, 2018) and the rhizosheath (Sasse *et al.*, 2018) underpins the potential of this field. With this review we first highlight the wealth of the different sticky mucilage types that are produced by plants. We further elaborate on the current state of the art regarding the analysis of the molecules lending bioadhesive plant secretions their specific functions and point out where future efforts could be focused.

Plant exudate and mucilage diversity

Exudates and mucilages can be categorised based on their location and on their potential to influence the microenvironment of the plant in various ways (Fig. 1). Some mucilages are highly conspicuous such as the droplets on the glandular hairs produced by carnivorous plants to capture insects and supplement their diet with nitrogen (Huang *et al.*, 2015). Others are less obvious or even hidden from sight as they are produced below ground (Baetz & Martinoia, 2014). The following sections give a brief overview of their diversity.

Aerial adhesive mucilages facilitating climbing motion

Some climbing plants stick to surfaces of almost any nature with adhesive structures (Fig. 2a). A study of the attachment organs of climbing fig (*Ficus pumila*) and English ivy (*Hedera helix*) identified clusters of adventitious roots as the organ from which an adhesive mucilage that robustly secures the plant to vertical surfaces is secreted (Groot *et al.*, 2003; Melzer *et al.*, 2010). Virginia creeper (*Parhenocissus quinquefolia*), by contrast, produces adhesive discs at the end of short tendrils for climbing (Bowling & Vaughn, 2008). A detailed compositional analysis has been so far only performed for *H. helix* (Huang *et al.*, 2016) and revealed that the major components of the mucilage secreted by English ivy are pectic rhamnogalacturonan-I (RG-I) polysaccharide domains that are held together by a nanospherical arabinogalactan protein (AGP) molecule (Table 1). This multipolysaccharide architecture is supported by calcium-driven electrostatic interactions between the acidic residues of the AGP and RG-I domain (Huang *et al.*, 2016). The AGP nanoparticles are highly uniform and evenly spread over the attachment area (Lenaghan & Zhang, 2012). The firm attachment is further supported by cellulose microfibril-dependent shape changes of adventitious root hairs at the attachment interface (Melzer *et al.*, 2010), accentuating the possibility that structural and chemical features have been fine-tuned together to form an attachment organ that meets the special needs of climbing plants. Whether the polysaccharide composition of the adhesive mucilages and their nanostructures are conserved amongst climbing plants or whether each climber has its own



Microenvironmental influences

1. Facilitation of host cell attachment, host defence quenching and dispersion of digestive enzymes into host tissue
2. Adhesion to new hosts; possibly water regulation
3. Anchoring to vertical surfaces, improving light conditions by elevating the plant above ground
4. Immobililisation of insects, supplementing the nutritional diet on nitrogen-poor soils
5. Prolonging moisturised state by storing water in the seed coat
6. Providing an environment for beneficial microbiota, affecting soil hydraulics, increasing nutrient availability

Fig. 1 Overview of plant mucilage types. Schematic representation of the location of plant mucilage production (indicated by circles) and the corresponding specific tasks of the sticky secretions. Above-ground organs are shown against a blue background, soil surface is shown on a grey background and the soil body with the root systems is shown in yellow. The ways in which they can shape the microenvironment of the plant are listed to the right.

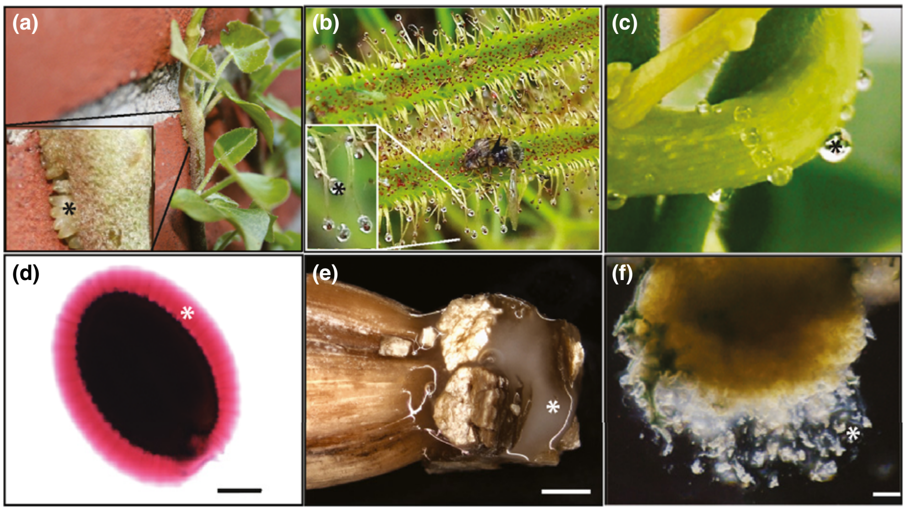


Fig. 2 Examples of sticky mucilages secreted by plants. (a) Tendrils of climbers from ivy adhere to a brick wall. (b) Hairy glands have captured an insect (arrowhead) on the leaves of the carnivorous *Drosera binata*. (c) Extrafloral nectar drops cover the stem of *Cuscuta reflexa*. (d) *Arabidopsis thaliana* seeds produce a gelatinous seed coat, as visualised by staining with ruthenium red. Bar, 0.2 mm. (e) *Hordeum vulgare* L. primary rootlet from a germinating grain produces rhizal secretions. Pieces of vermiculite on which the grains were germinated are firmly sticking to the mucilage. Bar, 0.5 mm. (f) Haustoria of parasitic plants (here cross-section from *C. reflexa* haustorium grown on a synthetic foam to visualise the mucilage) secrete a gelatinous matrix containing cell-wall-dissolving enzymes. Bar, 0.1 mm. Asterisks mark the secreting organs (a), secreted droplets (b, c) or mucilage sheaths (d–f).

'signature cement' is an intriguing question that should be addressed in the future.

Extrafloral nectars secreted by stems, leaves or aerial roots to provide protection and nutrition

Many land plant species secrete mucilage through their stems as extrafloral nectar (Deynze *et al.*, 2018; Pierce, 2019). Despite their name, extrafloral nectars are not involved in attracting pollinators but rather entice invertebrates such as ants or wasps to protect the plants from herbivorous predators (Gaume & Forterre, 2007; Llhan *et al.*, 2007) or to supplement their diet with nitrogen by trapping insects or cultivating microbial symbionts (Adlassnig *et al.*, 2010; Deynze *et al.*, 2018). Sundew (genus *Drosera*) (Fig. 2b) or butterworts (genus *Pinguicula*) possess trichomes with terminal glands, which produce the mucilage in small droplets on their upper leaf surface (Adlassnig *et al.*, 2010) while pitcher plants secrete larger volumes of their mucilage in special leaves formed like a cone (Gaume & Forterre, 2007). So far, only the mucilage of *Drosera* has been subjected to an analysis of its polysaccharide composition and was shown to contain predominantly high-molecular-weight substances that resemble pectins (Tables 1, 2) (Huang *et al.*, 2015). The architecture of the mucilage appears to have a higher order nanostructure that changes depending on the presence or absence of tensile forces (Huang *et al.*, 2015). A hypothetical polygonal polysaccharide-based nanonetwork was proposed based on atomic force microscopy images. These nanostructures can be transformed into a parallelogram shape upon application of a tensile force, which would explain the high tensile strength reached by the sundew mucilage (Huang *et al.*, 2015). *Myo*-inositol (MI) was identified in the lower molecular weight fraction as the predominant nonpolysaccharide organic component (Kokubun, 2017). MI seems to be unique for sundew and could not be detected in other plant mucilages that served as control (Kokubun, 2017).

The parasitic giant dodder (*Cuscuta reflexa*), which infects shoots of other land plants, was also found to possess a stem exudate in the form of droplets whose sticky nature helps it to facilitate contact with host surfaces (Fig. 2c) (Schaffner, 1976). It has been hypothesised that the dodder secretes excess sugars with it in order to secure the flow of less abundant organic or inorganic compounds and maintain an osmotic balance (Schaffner, 1976). The composition of this exudate has not yet been examined.

Haustorial mucilage aids in the infection process by parasitic plants

In addition to the extrafloral 'nectar', *Cuscuta* also produces additional types of secretions that are crucial for succeeding with its infection (Vaughn, 2002). Being shoot-parasitic, *Cuscuta* species wrap around the stems of other plants (their hosts) and withdraw their nutrients by forming physical and physiological nutrient bridges, called haustoria. To penetrate the plant cell wall barrier, the parasite must firmly attach to their hosts and push the haustorium into the host tissue using a combination of mechanical force and chemical tissue maceration (Vaughn, 2002). To provide a counterforce for the penetration process, the upper haustorium (sometimes also termed appressorium) exudes a viscous mucilage from club-shaped epidermal cells that form at the interface with the host (Vaughn, 2002). Immunological analyses revealed that this mucilage is mainly composed of pectins, extensins and AGPs (Table 1). In addition, another mucilage was observed surrounding the developing endophytic part of the *C. reflexa* haustorium (Fig. 2f). This mucilage is predominantly visible during early infection stages and is difficult to analyse without interference from host activities, explaining why it has not yet been characterised.

Table 1 Polysaccharides present in representative plant exudates and mucilages.

Type	Species	Polysaccharides									Collection method[a]	Reference[b]
		AGP	Arabinan	Callose	Cellulose	Extensin	Pectin	Heteromannan	Xylan	Xyloglucan		
Aerial adhesive – climbing	English ivy (*Hedera helix*)	●					●				WW	1
	Virginia creeper (*Parthenocissus quinquefolia*)	●					●				N	2
Aerial adhesive – insect capture	Sundew (*Drosera* spp.)						○				DS	3
Haustorial	Broomrape (*Orobanche crenata*)						●				DS	4
	Giant dodder (*Cuscuta reflexa*)	●		●	●	●	●				DS	5
Rhizal adhesive	Barley (*Hordeum vulgare*)	●				●	●		●	●	H	6
	Cowpea (*Vigna unguiculata*)	●	●				●				LC, ME	7
	Cress (*Lepidium sativum*)	●	●				●				LC, ME	8
	Indian rhododendron (*Melastoma malabathricum*)	●									LC	9
	Lupin (*Lupinus angustifolius*)	●	●				●				ME	10
	Maize (*Zea mays*)	●	●				●		●	●	LC, ME, TT, H	6, 11–14
	Pea (*Pisum sativum*)	●				●	●			●	ME, H	6, 15, 16
	Rapeseed (*Brassica napus*)	●							●	●	H	6, 16
	Thale cress (*Arabidopsis thailana*)	●				●	●			●	ME	6, 17
	Tomato (*Solanum lycopersicum*)	●				●	●			●	H	6
	Wheat (*Triticum aestivum*)	●				●			●	●	LC, H	6, 7
Seed coat	Dodder (*Cuscuta pedicellata*, *C. campestris*)						●				DS	18
	Mistletoe (*Phorademdrum californicum*)		●				●	●	●	●	WW	19
	Flax (*Linum* sp.)		●		●		●		●	●	WW	20
	Thale cress (*Arabidopsis thailana*)	●	●		●		●	●	●		WW, ME	21–24

Closed circles represent constituents that were identified by direct means (e.g. by immunological means), while the open circle indicates that components have been characterised indirectly by a comparative approach (X-ray photoelectron spectroscopy).

[a] Collection methods: DS,dissolved in solvent; WW, water washing; N, nitrocellulose sheets; H, hydroponics (root only submersion into medium); LC, liquid medium extract (full plant submersion into medium); ME, medium extract; TT, test tube manual collection.

[b] 1, Huang *et al*. (2016); 2, Bowling & Vaughn (2008); 3, Huang *et al*. (2015); 4, Perez-de-Luque *et al*. (2006); 5, Vaughn (2002); 6, Galloway *et al*. (2018); 7, Moody *et al*. (1988); 8, Ray *et al*. (1988); 9, Watanabe *et al*. (2008); 10, Read & Gregory (1997); 11, Bacic *et al*. (1986); 12, Guinel & McCully (1986); 13, McCully & Sealey (1996); 14, Osborn *et al*. (1999); 15, Knee *et al*. (2001); 16, Cannesan *et al*. (2012); 17, Durant *et al*. (2009); 18, Lyshede (1984); 19, Gedalovich *et al*. (1988); 20, Miart *et al*. (2019); 21, Macquet *et al*. (2007), 22, Haughn & Western (2012); 23, Voiniciuc *et al*. (2015); 24, Tsai *et al*. (2017).

Table 2 Carbohydrates present in plant mucilages.

Type	Species	Sugars											Reference[a]
		Arabinose	Fucose	Galactose	Galacturonic acid	Glucose	Glucuronic acid	Mannose	Rhamnose	Sucrose	Uronic acid	Xylose	
Aerial adhesive	Sundew (*Drosera* spp.)	●		●		●		●				●	1
Extrafloral nectar	Giant dodder (*Cuscuta reflexa*)									●			2
	Jute mallow (*Corchorus olitorius*)			●	●	●	●		●		●		3
	Maize (*Zea mays*)	●	●	●			●					●	4
Seed coat	Pignut (*Hyptis suaveolens*)		●	●		●	●	●				●	5
	Mistletoe (*Phoradendrum californicum*, *Acreythobium americanum*, *Phthirusa pyrifolia*)	●									●	●	6

[a] 1, Huang *et al*. (2015); 2, Schaffner (1976); 3, Llhan *et al*. (2007); 4, Deynze *et al*. (2018); 5, Gowda (1984); 6, Gedalovich-Shedletzky *et al*. (1989).

Besides *Cuscuta*, the root parasite *Orobanche crenata* was also found to produce a pectin-rich mucilage at the interface between itself and its hosts (Perez-de-Luque *et al.*, 2006). *O. crenata* forms similar host attachments as *C. reflexa* but with the difference that it connects to the host root system below ground. Interestingly, the mucilage that the parasite secretes and that may help the parasite to infect susceptible hosts appeared to fill host xylem vessels in resistant hosts and ultimately led to the death of the parasite (Perez-de-Luque *et al.*, 2006). Future investigations need to focus on comprehensive analyses of the haustorial mucilage composition in these two and other species, and also link possible differences in composition to differences in infection strategies, host specificity and host responses. In this context, and with the tensile strength of the infection organ in mind, a nanostructural analysis of the mucilages involved in parasitic plant infection would be very interesting.

Desiccation prevention and surface adhesion properties of seed coat mucilage

The production of a coat of gelatinous material derived from cell wall polysaccharides is fairly widely found in seeds of land plants (Fig. 2d). A prominent example of seed coat mucilage is the viscin produced by hemiparasitic mistletoe species. This mucilage protects the seeds during their passage through the guts of birds and ensures that the seed is firmly attached to the branches of its host trees when excreted by the birds. The viscin mucilage of *Phoradendron californicum* has been subject to extensive biochemical characterisation and was found to consist predominantly of highly branched xylans, arabinans, pectic rhamnogalacturonans and xyloglucans (Gedalovich *et al.*, 1988). A comparative study involving *P. californicum* and two other Viscaceae species indicated that compositional differences, mainly in the type of neutral sugars, exist between the species and that these may be specific enough to serve as taxonomic markers (Gedalovich-Shedletzky *et al.*, 1989).

In the model land plant *Arabidopsis thaliana*, specialised mucilage secretory cells (MSCs) in the outer integument produce large amounts of mucilaginous hydrophilic polysaccharides in rings around a central columella that is compositionally similar to a secondary cell wall (Haughn & Western, 2012). The mucilaginous rings in each cell dehydrate during seed maturation but rapidly expand when in contact with water during imbibition of the mature seed, accompanied by rupturing and rapid degradation of the outermost cell walls (Golz *et al.*, 2018). The released mucilage envelope can be divided into an inner and an outer layer (Haughn & Western, 2012), and this organization provides coherence and stability (Voiniciuc *et al.*, 2015). The outer layer is a poor adhesive due to its higher content of unbranched pectic RG-I that stretches out into the soil (Tsai *et al.*, 2017), whereas the inner layer has strong adhesive properties and contains pectins in a matrix of cellulose scaffolds that span this layer and connect it to the seed coat (Macquet *et al.*, 2007; Voiniciuc *et al.*, 2015). Linkage analyses and the investigation of mutants impaired in several cell-wall-associated proteins pointed towards a significant contribution of proteins, including AGPs of type I, in the seed coats (Haughn & Western, 2012) (Table 1). The analysis of flax mucilage revealed that many of these components are located in distinct domains or layers (Miart *et al.*, 2019), suggesting a highly sophisticated and complex regulatory network in charge of seed coat production. High-throughput screens for phenotypic differences in the mucilaginous seed coats of *Arabidopsis* mutants have helped to identify specific genes that secure proper seed coat production (Golz *et al.*, 2018, and references herein). In particular, these studies have highlighted the contribution of transcription factors to MSC differentiation and have led to a proposed hierarchical network involving three distinct tiers or levels of regulation (Golz *et al.*, 2018).

Seed coats are a potential source for carbon and therefore tentatively a source for nourishing the developing seed, although some studies suggest that this resource is not utilised (Huang *et al.*, 2004). Rather, the seed coat mucilage seems to enhance water availability to the seed and make it less vulnerable to short-term dry spells (Huang *et al.*, 2004). It provides a barrier to the environment and keeps the seed moist due to its water-holding capacity. It is further implicated in the mediation of germination under waterlogged conditions (Haughn & Western, 2012), in soil seed bank maintenance and in seed dispersal (Yang *et al.*, 2012; Voiniciuc *et al.*, 2015; Tsai *et al.*, 2017). The specific set of functions can vary between species. It is plausible that seed coat mucilage could also be involved in the recruitment of beneficial soil microbiota (as hypothesised for root bioadhesives), which is a crucial foothold for plant growth, although experimental evidence for this has yet to be generated.

Root exudates bioengineer rhizospheres for sustained resource uptake

While disputed, most data agree that plants invest a considerable amount of their resources into releasing exudates from roots (Fig. 2e), and estimates that between 10% and 40% of photosynthate 'currency' is spent on root exudates have been put forward (Newman, 1985; McNear, 2013). Root exudates, including a great complexity of both low- and high-molecular-weight components, influence zones of soil at root surfaces known as rhizospheres (Baetz & Martinoia, 2014). The release of polysaccharide-rich mucilage from root tips is well established and this may lubricate roots to ease penetration through deeper layers of soil and may also be involved in forming a protective barrier (Bacic *et al.*, 1986; Read & Gregory, 1997). It is proposed that bioadhesive mucilage components of exudates are important factors, along with root hairs, in the formation of cylinders of soil around roots known as rhizosheaths. Rhizosheaths could enable plants to sustain and increase nutrient and water uptake from the soil (Traore *et al.*, 2000; Brown *et al.*, 2017; Pang *et al.*, 2017; Galloway *et al.*, 2018). Rhizosheath bioengineering by some grass species during periods of drought has been observed, where the grasses increased the thickness of their rhizosheaths (Hartnett *et al.*, 2012). This increase in structural integrity was thought to be caused by a combination of mechanistic force exerted by root hairs as well as increased mucilage production. Xyloglucan, an otherwise abundant cell wall component, has been demonstrated to be released by plants and is a soil-binding factor that could enhance water infiltration and aeration (Galloway *et al.*, 2018). Adhesiveness is likely to be only one functional aspect of root high-molecular-weight exudates in the bioengineering of soil. There will be highly complex interactions between the structurally diverse molecules released from plant roots and the soils and soil microbiomes, which themselves are also highly heterogenous. The capacity for putative bioengineering to alter the physical microenvironments will be considerable. It appears that this will involve differing impacts on soil aggregation through varied viscosities and surface properties, on drying/wetting cycles and the potential for hydrophobicity of mucilage after drying and binding properties in general, including the sequestering of heavy metals (Ray *et al.*, 1988; Watt *et al.*, 1994; Dennis *et al.*, 2010; Naveed *et al.*, 2017; Kroener *et al.*, 2018). Similarities between some of these aspects of root mucilage properties and impacts and those of other plant secretions will be a fruitful area for future research in conjunction with detailed structural characterisations.

Regarding the mechanisms involved in root mucilage secretion, the leading hypothesis is that mucilage could be secreted from continually lysing epidermal cells on the root body (Read & Gregory, 1997). However, other reports indicate that higher amounts of mucilage could be secreted than what would be predicted from lysing cells (Guinel & McCully, 1986). Approaches using hydroponics, where roots are not subjected to penetrative forces, have also detected continual secretion (Galloway *et al.*, 2018). An important future goal will be to untangle the polysaccharide secretions from root tips and the possible secretion from root hairs that promote rhizosheath formation. Difficulties in collecting pure enough samples for immuno- and physicochemical analyses have been one limiting factor. The isolation of root-derived high-molecular-weight polymers from hydroponic media has provided a more reliable and scalable sampling method (Akhtar *et al.*, 2018) but uses an artificial environment removed from soil. Nevertheless, it is a valuable approach to understanding the formation of rhizosheaths that will hopefully in the future be supported by molecular genetic approaches.

Molecules in the mucilage conferring bioadhesive properties

Due to the range of molecules present in mucilages and due to their varying accessibility, a variety of methods have been used to isolate them (Table 1). Despite the fact that the composition of each type of mucilage has yet to be fully deciphered, some mono- and polysaccharides as well as glycoproteins that are typically also key architectural components within the plant cell wall appear to be very common in the plant mucilages (Tables 1, 2) (Voiniciuc *et al.*, 2018). AGPs and pectins (RG-I) are the key components in most mucilages, appearing in aerial, haustorial, rhizal and seed coat mucilages (Table 1). The adhesive properties of both groups of molecules are well documented, particularly with their use as emulsifiers in industry (Nakauma *et al.*, 2008). Xyloglucan along with β-1,3-glucans have recently been shown to have soil-binding properties (Akhtar *et al.*, 2018; Galloway *et al.*, 2018) and are target polymers for our understanding of rhizosheath formation. Nanostructure analysis of climbing plant and insectivourous plant mucilages has revealed highly ordered structures that contribute to extreme tensile strengths. An application of the techniques used to visualise these structures to other types of mucilages promises to be a revealing undertaking, and can uncover whether there are tentative common structures related to adhesion or other common functions, despite the differences in the mucilage compositions.

Molecular mechanisms of the secretion of mucilage

The molecular mechanisms of mucilage secretion have been mainly investigated using the *Arabidopsis* seed coat as a model, where special secretory cells are used to produce and exude the mucilage components (Sechet *et al.*, 2018). Polysaccharides are formed either through monosaccharide cytosolic synthesis or within the Golgi apparatus by glycosyl-transferase enzymes (Voiniciuc *et al.*, 2018). The exception are glycoproteins, in which the protein domain is formed within the rough endoplasmic reticulum and is attached to the polysaccharide domain within the Golgi apparatus (Voiniciuc *et al.*, 2018). How these two domains localise together remains unknown. The key proteins involved in the production of cellulose, pectin and hemicellulose moieties of mucilage include Cellulose Synthase-like (CSL) A2, Galaturonosyl Transferase-like (GATL) 5, Galaturonosyl Transferase (GAUT) 11 and Rhamnose Biosynthesis (RHM) 2 (Arsovski *et al.*, 2010; Tsai *et al.*, 2017). The products of these enzymes are packaged into vesicles and are exported to the plasma membrane where they join the apoplast pathway for secretion (Tsai *et al.*, 2017). Following the secretion of mucilage, Pectin Methylesterase Inhibitor (PMEI) 6, beta-Xylosidase (BXL) 1 and beta-Galactosidase (BGAL) 6 play a role in assembling mucilage to stabilise its final form (Arsovski *et al.*, 2010), although how they do this remains unclear. Before mucilage biosynthesis, the epidermal cell walls of the seed coat undergo major changes to accommodate such levels of secretion. For other mucilages, the principal pathways of production and shuttling to the apoplastic compartment are probably the same as for the seed coats although in some cases (e.g. in root mucilage) sloughing and lysing of cells contribute to mucilage production (Cannesan *et al.*, 2012).

Conclusion and future perspectives

Exudates and mucilages enable plants to exert influences on their immediate surroundings, creating microenvironments that can be favourable for their growth. Some molecules present in these mucilages possess naturally adhesive properties that have potential biotechnological and biomedical value in the form of glues or wound covers – although the precise bioadhesive molecules present in the secretions have rarely been identified. These adhesives could also be used to prevent or even reverse the process of soil erosion, thus potentially increasing our ability to produce sufficient food for growing populations. Their application as blueprints for natural-based soil conditioners could boost the abundance of soil aggregates and water retention, thus preventing its degradation. However, to date, most of the insight into the molecular regulation, biochemical composition and structure–function relationships of mucilages has been based on a few key model species. In the case of the most prominent model, the thale cress *A. thaliana*, it does not have an ecological or economical value *per se* and can at best serve as a guide to look for similar genes, molecules and networks. This requires good genomic knowledge on other species with more prominent or potentially more valuable mucilages. A very promising approach that has yielded major breakthroughs in recent years is the use of techniques enabling visualisation of nanostructures (Huang *et al.*, 2015, 2016). Such techniques will potentially allow novel insights into generation of mucilages and exudates, particularly when combined with molecular approaches.

Together, the benefits from translational approaches using plant mucilages and exudates as a basis for biotechnological applications give ample incentive to learn more about the common and the unique molecules that are part of the different plant mucilages and to understand their synthesis, properties and functions.

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