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Latex – a potential plant defense against microbes

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Laticifers – among the most common defensive reservoirs in plants – are hypothesized to benefit plant fitness by preventing microbes from entering wounds. I argue that while latex seals wounds, and can suppress microbial growth, direct evidence that these processes benefit plant fitness is scarce. I outline a roadmap for filling this knowledge gap.

Laticifers: specialized cells that may defend plants against pathogens

One of the most common defensive reservoirs in plants is a type of specialized cell, called a 'laticifer', which is present in almost 10% of all flowering plants. Laticifers are elongated, and sometimes interconnected, cells that spread throughout the plant´s body. The laticifer´s cytoplasm, called latex, is stored under pressure, and typically contains high concentrations of bioactive molecules. Upon wounding, latex oozes out and thereby confronts potential attackers with a complex emulsion of bioactive molecules. Once released, latex coagulates and thereby seals wounds. Laticifers seem of such great advantage that these cells evolved independently multiple times, suggesting important ecological functions.

Traditionally, latex has been considered as a plant defense against herbivores, and this point of view is supported by various observations and manipulations [1,2]. With growing awareness of the microbial world and its pivotal role in determining plant growth, health, and yield, questions emerged asking whether latex defends plants against pathogens and whether latex disrupts the plant´s interaction with beneficial microbes [2–4]. At least four processes may be relevant in this respect (Figure 1). First, latex could defend plants against pathogens by restricting the microbial colonization of wounds, either because latex-sealed wounds cannot be penetrated by microbes or because latex constituents reduce microbial growth [4]. Second, latex can be released into the soil through shed plant material or exuding latex, which may alter the microbial composition in the rhizosphere. For instance, roots of the Russian dandelion – which stores large quantities of natural rubber in its root laticifers – lose their outer layer during secondary growth and thereby become coated with rubber sheaths [5] (Figure 1). Rubber in the soil may serve as a carbon source for fungi [6], or alternatively, could disrupt the plant´s interactions with beneficial microbes. Third, laticifers may produce germination cues for microbes [7]. Fourth, laticifers may harbor endophytic microbes [8], although testing this hypothesis is challenging as exuding latex is easily contaminated with microbes from non-laticiferous cells. This issue may soon be overcome by using the recently developed methods in spatial meta-transcriptomics which allow characterization of microbiomes at almost single-cell level [9].

While all these mechanisms could alter the composition and abundance of microbes inside and in close proximity to plants, the first mechanism – referred to here as the 'plant defense hypothesis' – aligns best with the mode of action of laticifers, in which high concentrations of latex constituents exude through wounds [3]. The plant defense hypothesis involves two aspects:

(i) First, latex may suppress the growth of microbes. Indeed, latex often contains a species-specific set of small bioactive molecules such as terpenoids, phenolics, and alkaloids, as well as proteins including chitinases, proteases, or chitin-binding proteins that can reduce the growth of microbes [2,3,10]. Whether latex contains molecules that degrade bacterial cell walls (e.g., lysozymes) or inhibit biofilm formation by interfering with quorum sensing (quorum quenching through e.g., lactonases) is unclear.
(ii) Second, latex contains molecules that seal wounds; this may prevent microbes from entering their hosts. A molecule that is likely of particular importance in this respect is natural rubber, a large cis-1,4-polyisoprene that contributes to the stickiness of latex. Recent work provided mixed support for the wound-sealing function of natural rubber. On the one hand, *in vitro* assays showed that natural rubber can form a physical barrier to bacteria and, to a lesser extent, fungi [11]. On the other hand, roots of Russian dandelion, in which natural rubber biosynthesis was abolished through genetic engineering, did not suffer a higher colonization by pathogenic or non-pathogenic microorganisms upon wounding compared to the near-isogenic normal-rubber-content lines [4]. Thus, while latex seals wounds, it is unclear whether this restricts the entry of pathogens. Considering that wounds are major gateways for pathogens to enter their hosts, the wound-sealing function of latex should be studied in more detail.

A roadmap to test the plant defense hypothesis

To date, experimental evidence that latex benefits plant fitness by preventing microbes from entering wounds is scarce. I propose the following roadmap to fill this knowledge gap (Figure 2):

(1) Testing selected latex constituents *in vitro.* The most widely used approach to infer whether latex is defensive against microbes is to test whether latex constituents inhibit the growth or dispersion of microbes *in vitro.* The *in vitro* approach has often, but not

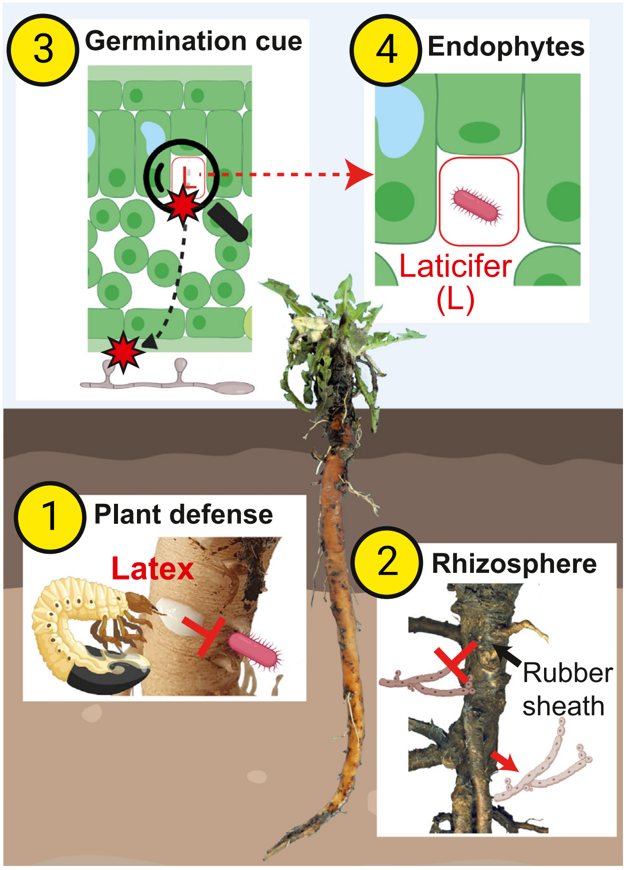

Figure 1. Laticifers may suppress or promote the plant´s interaction with microbes through at least four mechanisms. (1) Exuding latex may defend plants against pathogenic microbes by sealing wounds and inhibiting microbial growth. (2) If latex is released into the soil upon wounding, or through shed plant material, it may alter the plant microbiome in the rhizosphere. The picture shows Russian dandelion roots that have lost their outer layer during secondary growth and thereby became coated with coagulated rubber (rubber sheath, black material). (3) Laticifers may release germination cues for microbes. (4) Laticifers may harbor endophytes. Abbreviation: L, laticifer. The figure was created with BioRender.com. Picture credit: Katja Thiele and Meret Huber.

always, revealed antimicrobial activity of latex and its constituents [2,3]. The *in vitro* approach could be refined by screening not only for antibiotic and antifungal activities but also for quorum quenching, and by testing whether latex constituents have a stronger impact on plant pathogens than on commensals or symbionts. The concentrations used for *in vitro* experiments should reflect those present in the latex, which is known for many plant species. While experiments *in vitro* are ideal first steps to infer the defensive function of latex, the results should be corroborated by experiments *in planta* – not least because some latex constituents may be active only against certain microbes or upon enzymatic or pH-dependent conversion [12].

(2) Supplying latex constituents to wounds. To validate the results from the *in vitro* experiments in a more natural setting, one could add the latex constituents at ecologically relevant concentrations directly into the exuding latex. While this approach is feasible above-ground, it is difficult to implement below-ground, where plant–microbe interactions are most intense due to the rich soil microbiota.

(3) Exploit natural variations in latex accumulation. Species often exhibit intraspecific variation in latex constituents. This variation can be exploited to test whether latex mediates plant–microbe interactions in two ways. First, intraspecific genetic variations in latex constituents can be correlated to microbial colonization using common garden experiments. Although this approach is applicable to a wide range of plants – and has revealed that latex can defend plants against herbivores [1] – the approach has not been widely used to infer defensive function of latex against microbes. Second, plant genotypes can be crossed and inbred to generate mapping populations with which genetic loci altering plant–microbe interactions can be identified without a priori assumptions. While generating mapping populations is time consuming, several mapping populations in latex-bearing plants already exist, for instance, in the rubber tree *Hevea brasiliensis*.

(4) Alter the accumulation of latex constituents through genetic engineering. One of the most powerful approaches to study plant–microbe interactions is to knock down, knock out, or knock in latex constituents and subsequently study the root microbiome upon wounding [4]. Ideally, wounds are inflicted by both herbivores and mechanical damage, as manipulating latex constituents can alter herbivore behavior and, thereby, the plant microbiome. While genetic engineering is, to date, applicable to only a small set of latex-bearing plants (e.g., *Taraxacum* species), establishing methods to genetically modify other latex-bearing plants and improving existing genetic engineering platforms will be critical to test whether latex defends plants against microbes.
An inherent problem of genetically modifying the amount of metabolite accumulation is that the flux through other pathways is often altered. To overcome this issue, one could change not the absolute accumulation of latex constituents but rather their localization, as many latex constituents are produced in both laticifer and non-laticifer cells. This requires identifying specific transporters, which is challenging but likely feasible in the future using single-cell analysis.

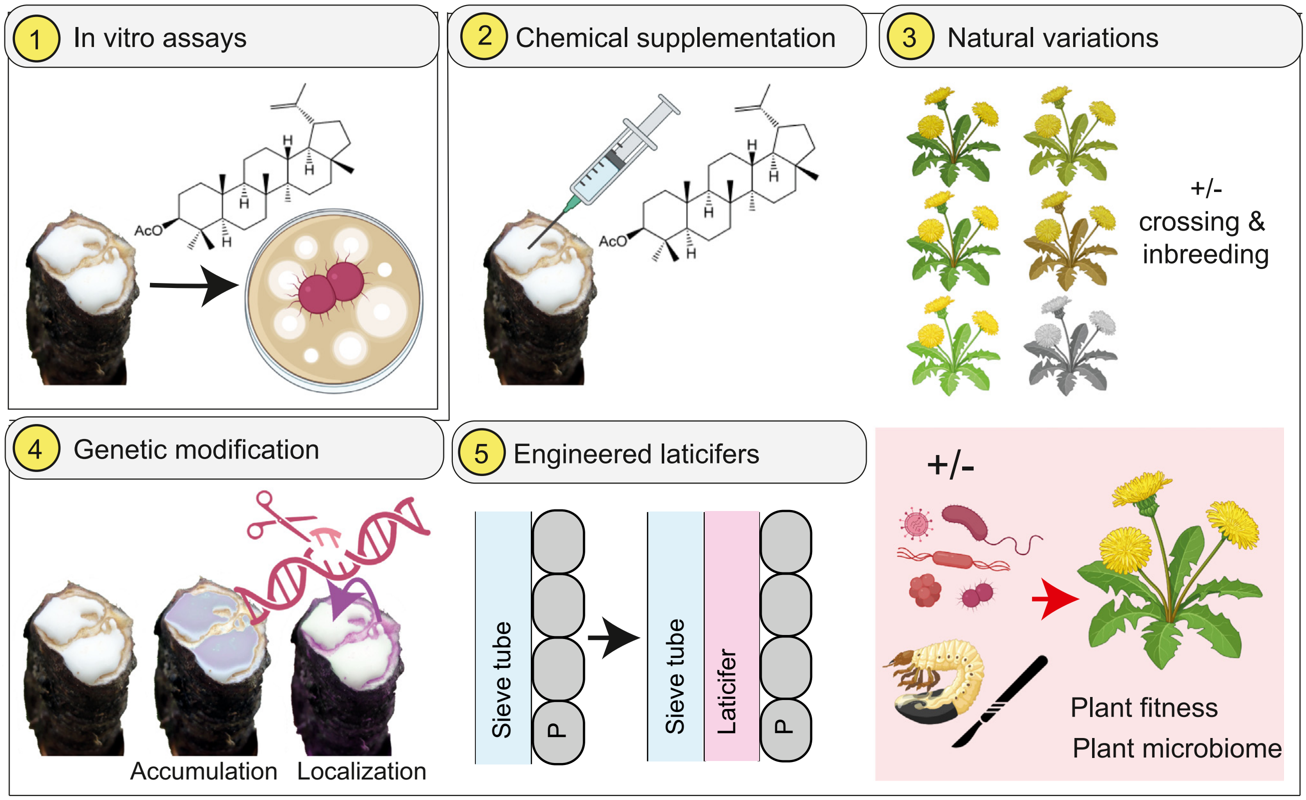

Figure 2. To test whether latex defends plants against microbes upon wounding requires manipulation of the latex constituents and the plant microbiota while measuring plant fitness. (1) Testing the growth-inhibitory activities of purified latex constituents is an ideal first step to understand their direct impact on microbial growth. (2) Adding latex constituents to exuding latex can test whether latex constituents have a tangible effect on plant–microbe interactions *in planta*. (3) Intraspecific genetic variation can be exploited to associate a latex constituent or a genetic locus to the colonization of plants by pathogenic microbes. This approach is particularly powerful if genotypes are crossed and subsequently inbred to generate a mapping population. (4) Genetically modifying the total amount of latex constituents, or modifying their site of accumulation, can reveal whether latex constituents defend plants against microbes. (5) Engineering laticifers in plants which lack them could reveal how the gain of laticifers can alter the plant´s interaction with pathogenic and beneficial microbes during evolution. Abbreviation: P, parenchyma cell. The illustration was generated using BioRender.com. Picture credit: Meret Huber.

(5) Engineering laticifers. Perhaps the most significant approach to study whether latex defends plants against microbes is to engineer laticifers in a species that does not naturally produce them. Such an endeavor is, admittedly, challenging and will be realizable only if one can identify the factors controlling laticifer identity, their initiation and growth inside the plant tissue, as well as the production of latex constituents [13]. While none of these processes have been elucidated to date, interspecific and intraspecific comparisons in combination with single-cell analysis may allow the identification of a core set of the genes required for laticifer formation [14]. If laticifers can be engineered in a species lacking them, one could study how the gain of laticifers altered plant defense against microbes during plant evolution and whether laticifers have environment-dependent trade-offs, for instance, whether laticifers disrupt the plant´s interaction with symbiotic microbes – a hypothesis that has been rarely tested. Furthermore, engineered laticifers could spur molecular farming of economically important polymers, for instance natural rubber.

To determine whether latex constituents defend plants against microbes, it is critical that the *in planta* approaches (2–5) are accompanied by measurements of plant fitness upon wounding and manipulations of the microbiota [15] – only then can we infer a defensive function.

Concluding remarks

While latex seals wounds, and can reduce microbial growth, evidence that these processes benefit plant fitness is scarce. The key to filling this knowledge gap is to test latex and its constituents not only *in vitro* but also *in vivo*, and to manipulate both latex constituents and the plant microbiota while measuring plant fitness. Developing and refining genetic engineering tools will be crucial to realize this endeavor and to decipher the role of plant secretory structures in mediating complex trophic interactions in nature.

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AI disclosure

During the preparation of this work the author used ChatGPT in order to improve English grammar. After using this tool/service, the author reviewed and edited the content as needed and takes full responsibility for the content of the publication.

Declaration of interests

No interests are declared.

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