A bioinspired approach to engineer seed microenvironment to boost germination and mitigate soil salinity

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Human population growth, soil degradation, and agrochemical misuse are significant challenges that agriculture must face in the upcoming decades as it pertains to global food production. Seed enhancement technologies will play a pivotal role in supporting food security by enabling germination of seeds in degraded environments, reducing seed germination time, and boosting crop yields. So far, a great effort has been pursued in designing plants that can adapt to different environments and germinate in the presence of abiotic stressors, such as salt, soil salinity, heat, and drought. The technology proposed here seeks a different goal: To engineer the microenvironment of seeds by encapsulation, preservation, and precise delivery of biofertilizers that can boost seed germination and mitigate abiotic stressors. In particular, we developed a biomaterial based on silk fibroin and trehalose that can be mixed with rhizobacteria and applied on the surface of seeds, retrofitting currently used techniques for seed coating, i.e., dip coating or spray drying. A micrometer thick transparent robust coating is formed by material assembly. The combination of a polymorphic protein as S and of a disaccharide used by living systems to tolerate abiotic stressors provides a beneficial environment for the survival of nonspore forming rhizobacteria outside the soil and in anhydrous conditions. Using Rhizobium tropici CIAT 899 and Phaseolus vulgaris as working models, we demonstrated that rhizobacteria delivered in the soil after coating dissolution infect seedlings’ roots, form root nodules, enhance yield, boost germination, and mitigate soil salinity.

Significance

In a world that strives to accommodate population growth and climate pattern changes, there is a compelling need to develop new technologies to enhance agricultural output while minimizing inputs and mitigating their effects on the environment. In this study, we describe a biomaterial-based approach to engineer the microenvironment of seeds through the preservation and delivery of plant growth promoting rhizobacteria (PGPRs) that are able to fix nitrogen and mitigate soil salinity. PGPRs are encapsulated in silk–trehalose (ST) coatings that achieve bacterial preservation and delivery upon sowing. The biomaterial choice is inspired by a recent finding that a combination of proteins and disaccharides is key for anhydrobiosis. This simple technology is effective to boost seed germination and mitigate soil salinity.

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Competing interest statement: A patent application that includes the technology reported in this manuscript has been filed through the Technology Licensing Office of the Massachusetts Institute of Technology. B.M. has a financial interest in Cambridge Crops, Inc., which uses S-based coatings to extend food shelf-life.

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technology that combines biodegradation with encapsulation, preservation, and controlled release of payloads that can boost seed germination and mitigate stressors.

In this study, we developed a biomaterial-based approach to engineer seed coatings that can boost germination and mitigate abiotic stressors, such as soil salinity. In particular, we designed a biomass-based approach to engineer seed coatings that can boost abiotic stressors, such as soil salinity. The mixture can be mixed with rhizobacteria and applied on the surface of seeds, retrofitting currently used techniques for seed coating, such as dip coating or spray drying. S is a structural protein that is well known for its application in textiles and that has been reinvented as a naturally derived technical material with applications in regenerative medicine, drug delivery, implantable optoelectronics, and food coating (13, 14). The structural protein is purified from cocoons into a water suspension using a water-based process that uses chaotropic agents as LiBr to break the inter- and intramolecular hydrogen bonds that cross-link S molecules into fibers (15). Upon removal of the ions via dialysis, S has the form of nanomicelles in water suspension that are stable for a period of time that ranges from days to months, depending on concentration, pH, and molecular weight (16, 17). Material assembly is driven by water removal and formation of new intra- and intermolecular hydrogen bonds. This process can be engineered to obtain several materials formats, including transparent robust membranes that have been used to extend the shelf life of perishable crops (18). The combination of a diblock copolymer-like structure with hydrophobic repetitive amino acid sequences spaced out by hydrophilic negatively charged nonrepetitive sequences make S polymorphic as the protein can be obtained in random coil or β-sheet rich structures, enabling the fabrication of silk materials that are water soluble or water insoluble, respectively (19, 20). The S structure also provides a distinct environment that can preserve labile compounds ranging from antibiotics to growth factors, enzymes, and viruses by mitigating oxidative stress, providing sufficient hydration, and maintaining biomolecules configuration in anhydrous conditions (21).

Trehalose is a nonreducing disaccharide in which the 2 glucose units are linked via an α,α-(1,1)-glycosidic bond. This disaccharide has been isolated from all domains of life including plants, animals, fungi, yeast, archaea, and bacteria (22). Trehalose is also industrially produced as it is used in the food, cosmetics, and pharmaceutical industries. This disaccharide can serve as a signaling molecule, as a reserve carbohydrate, and as a stress protectant (e.g., drought, cold, and salt stress) (23). Accumulation of trehalose occurs both intra- and extracellularly (22, 24, 25). There are 2 competing, but not mutually exclusive, hypotheses about the mechanism of trehalose-driven cellular protection; (i) the vitrification hypothesis suggests that trehalose forms a glasslike matrix within cells, physically preventing protein denaturation, protein aggregation, and membrane fusion, (ii) the water replacement hypothesis posits that hydrogen bonds between water and cellular components are replaced by trehalose as cells dry, which would also prevent protein denaturation, aggregation, and membrane fusion (26). Recently, it has been shown that a particular class of proteins known as intrinsically disordered proteins also contributes to anhydrobiosis. For example, a mixture of water-soluble proteins rich in hydrogen bonds and disaccharides is a successful strategy that anhydrobiotic organisms, such as tardigrades, have evolved to survive desiccation (27). Inspired by these recent findings, we have investigated a biomaterial formulation that synergistically use the coating-forming, payload encapsulation, preservation, and biodegradation capabilities of S with the ability of trehalose to offer protection from osmotic and desiccation stresses in rhizobacteria to develop a seed-coating technology that can boost germination and mitigate abiotic stressors, such as soil salinity.

**Formulation of ST Biomaterials.** Li et al. (28) have recently reported how the preservation of biomolecules in S formulations correlates with matrix β-relaxation as it does in sugar-based dry formulations. It was also found that inclusion of sugars, such as sucrose in S-based materials enhances the protein stabilizing performance as they can act as antiplasticizers that suppress β-relaxation and decelerate degradation rates. In Fig. 1, we report the effects of trehalose on S matrices. Molecular dynamic simulations were used to investigate the molecular mobility of a S-like system made by 18 (GAGSGA)2 peptides organized in a β-sheet configuration when suspended in water or in a water–trehalose mixture (Fig. 1D). Time evaluation of the RMSD of the atomic position from the original conformation indicated that trehalose reduces the dynamics of the 18 peptide systems and correlates with the general knowledge that sugars form a matrix around proteins that lock them in the original conformation by slowing down protein dynamics. Experimentally, we have demonstrated that trehalose does not interfere with S assembly as its addition to S suspensions does not impart any modification to the random coil structure assumed by S nor does it drive protein assembly. Circular dichroism (CD) spectra of S and ST water suspensions depicted that the protein maintained a random coil structure (indicated by the negative bands near 195 nm and low ellipticity above 210 nm) (29) when exposed to increasing concentrations of trehalose, up to 75 dry wt% (Fig. 1B). Dynamic light scattering (DLS) was used to measure the hydrodynamic radius of S nanomicelles in S and ST water suspensions (Fig. 1C). No statistically significant difference (P > 0.05) was found in the measured nanomicelles diameters at increasing trehalose concentrations, indicating that trehalose does not influence the assembly of S molecules in water. Attenuated total reflection–FTIR (ATR–FTIR) was used to evaluate the effects of trehalose on S polymorphism upon drying (Fig. 1D). All of the spectra of S films obtained using an increasing concentration of trehalose had an amide I resonance centered at 1,647 cm−1, indicating that the structure of S molecules was not affected by trehalose and possessed a random coil configuration (30). Interestingly, methods, such as water annealing that are commonly used to drive the random coil to β-sheet transition in assembled S molecules were still effective in crystallizing S at high concentrations of trehalose. This phenomenon suggests that the replacement of hydrogen bonds between S molecules and water with inter- and intramolecular hydrogen bonds may be thermodynamically favorable even in the presence of trehalose and that the structural rearrangements are less cooperative. This also means that hydration and volume change despite the trehalose-induced vitrification of the protein. Nanoindentation mechanical tests conducted on S films containing increasing concentrations of trehalose showed that films’ hardness and Young’s modulus increased as the trehalose concentration increased. The inclusion of large quantities (up to 75 wt%) of the disaccharide imparted an antiplasticizing effect, which followed the rule of mixture and resulted in a more brittle final material, especially at trehalose concentrations >50 dry wt% (Fig. 1E). However, when water annealing postprocessing was applied to enhance films’ β-sheets content, the hardness and Young’s modulus of ST materials did not follow the rule of mixture. Hardness increased for trehalose concentrations up to 25 dry wt% [i.e., ST(3:1)] and then decreased in films with a trehalose content of 50 and 75 dry wt% [i.e., ST(1:1) and ST(1:3), respectively]. Young’s modulus of ST materials increased for ST(3:1) films and then plateaued for larger trehalose contents. In SI Appendix, Fig. S1, we report the characterization of films obtained by mixing S with sucrose, a disaccharide that was not considered in this study for seed-coating applications given its large use as a food ingredient. CD, DLS, and ATR-FTIR analyses showed that sucrose did not modify S folding and assembly behavior, similar to what found for trehalose (SI Appendix, Fig. S1 A–D). However, nanoindentation measurements showed that the rule of mixture can predict mechanical properties when sucrose is incorporated in S materials, even when water annealing is applied. These data suggest a difference in the effects of vitrification imparted by trehalose.
and sucrose on silk materials; trehalose possesses higher glass transition temperature ($T_g \sim 393 \text{ K}$) when compared to sucrose ($T_g \sim 348 \text{ K}$) and can form a more homogenous network with proteins (26, 31). As a result, the trehalose brittle matrix is disrupted by $S$ random coil to β-sheets structural changes during water annealing, yielding a weaker material for trehalose concentrations >25 dry wt%. Nonetheless, ST materials showed mechanical properties on the order of currently available seed coatings (Young’s modulus of $10^{-1}$–$10^1 \text{ GPa}$) (32).

Coating Assembly and Biofertilizer Encapsulation and Release Performance. $S$ assembly is driven by water evaporation and results in a sol–gel-solid transition process that yields a transparent material. The resulting film has a roughness of a few nanometers (measured by atomic force microscopy on flat films) and a thickness that can be controlled by modifying solution rheological parameters (33). At constant solid matter content, inclusion of trehalose in $S$ suspensions decreases solution viscosity ($SI$ Appendix, Fig. S2), which, however, remains on the order of $10^{-4}$ Pas, thereby enabling the application of $S$ suspensions on complex geometries, such as spheroids by retrofitting existing technologies commonly used for seed coating. Contact angle (9) measurements also showed that decreases at trehalose concentration, given the higher hydrophilicity of the disaccharide when compared to $S$ ($SI$ Appendix, Fig. S2). When using borosilicate glass beads with a diameter of 5 mm as a model for seeds, dip coating, and spray drying of $S$ suspensions enabled the encapsulation and delivery of payloads, such as PGPRs via formation of micrometer thick coatings that biodegrade when exposed to water (Fig. 2). Given the transparency of silk materials, we used GFP-producing PGPRs, such as GFP-modified $R. \text{ tropici CIAT 899 (GFP-CIAT 899)}$ to evaluate the encapsulation, preservation, and delivery of rhizobia. $\text{CIAT 899}$ is a broad host-range rhizobial strain and the most successful symbiont of $P. \text{ vulgaris}$ (34, 35). $\text{CIAT 899}$ provides high tolerance to environmental stresses, such as high temperature, acidity, and salinity, and its potential use as a biofertilizer is highly desirable but hindered by the low survivability of gram-negative bacteria during the desiccation and rehydration steps required for coating formation and inoculation (12, 36). In Fig. 2, we report fluorescent images of glass beads coated with ST materials using dip-coating and spray drying techniques. When compared with the negative controls, it is possible to see how the GFP-CIAT 899 was successfully encapsulated in the coating materials as glass beads fluoresced when excited with a blue light. Spray-coated beads exhibited brighter fluorescence, which suggests the achievement of an enhanced encapsulation of GFP-CIAT 899. However, dip-coating methods are often preferable due to the easier implementation at scale. SEM was used to evaluate the thickness of the coatings obtained as a function of increasing relative concentration of trehalose in $S$ matrices (i.e., dry mass remained constant). SEM micrographs revealed that coatings thickness was on the order of a few micrometers ($5 \pm 2 \mu m$) and depicted the presence of bacteria in the vitrified polymer matrix (Fig. 2B). Successful encapsulation and release of GFP-CIAT 899 on glass beads as a function of ST mixture-coating material (i.e., increasing the relative content of trehalose) was then evaluated via streaking of resuscitated bacteria on an agar plate using a colony counting method (Fig. 2C). Given the coating thickness ($t$), the spherical geometry of the substrate ($r$), the known concentration of bacteria in the coating solution ($C_b$), and assuming a homogenous dispersion of bacteria and the formation of a homogenous coating, it is possible to estimate the
number of bacteria encapsulated in the coating \( N \) by multiplying \( C_b \) times the volume of the coating spherical shell \( V \),

\[
N = C_b \cdot V = C_b \cdot \left( \frac{4}{3} \pi R^3 - \frac{4}{3} \pi r^3 \right) \approx C_b \cdot (4\pi r^2 t),
\]

where \( R = (r + t) \) and \( 4\pi r^2 t \) is an approximation for the volume of a thin spherical shell obtained as the surface area of the inner sphere multiplied by the thickness \( t \) of the shell. Using \( r = 0.25, t = 0.0005 \) cm, and \( C_b = 10^{10} \) cm\(^3\), then \( N \approx 3.9 \times 10^6 \), which indicated a 1 logarithmic reduction of GFP-CIAT 899 culturability during the coating and resuscitation procedures (circa \( 10^5 \) CIAT 899 were resuscitated from ST coatings as shown in Fig. 2C).

Using phytagel as a model for soil moisture content, we investigated ST films biodegradation and release of GFP-CIAT 899 using a ChemiDoc MP Imaging System. Time-lapse images of the materials indicated that an increasing relative content of trehalose accelerated material reswelling such that structural integrity was lost within 10 min. Additionally, fluorescence microscopy images taken on glass beads coated with ST materials encapsulating GFP-CIAT 899 showed bacteria release in phytagel a few minutes after materials were in contact with the artificial soil (SI Appendix, Fig. S3 and Movie S1).

**Preservation of CIAT 899 in ST Coatings.** PGPRs, such as CIAT 899, are nonspore forming bacteria with limited viability outside the soil and poor survival postdissication (37). Long-term storage of rhizobacteria in seed coatings is one of the major bottlenecks that hinders the large-scale use of these biofertilizers in agricultural practice (38, 39). Application of PGPRs directly in soil and handling of living bacteria require tools and expertise that are not largely available, and thereby the successful encapsulation of PGPRs in seed coatings is seen as a key step to translating the beneficial effects of biofertilizers from bench to field. To assess the potential use of ST materials as seed-coating technology to encapsulate, preserve, and deliver PGPRs, viability and culturability studies were conducted on CIAT 899 embedded in silk, trehalose, and their mixtures at \( T = 23 \) °C and relative humidity (RH) of 25% and 50% for up to 4 wk. GFP-CIAT 899 preserved in sodium chloride and polymers (e.g., methylcellulose [MC] and polyvinylpyrrolidone [PVP]) found in commercially available seed coatings were used as controls. Fig. 3 shows that ST materials outperformed silk, trehalose, MC, and PVP in preserving GFP-CIAT 899. Interestingly enough, water annealing of silk and ST materials (labeled with A at the end of the sample names in Fig. 3) did not enhance preservation as previously reported for biomolecules, such as antibiotics, enzymes, and growth factors (40, 41), but appeared to be detrimental. S films anneal into a water-insoluble material when left at room temperature and very high RH as the random coil to \( \beta \)-sheet transition is thermodynamically favored (42). This process, commonly named water annealing, causes a partial rehydration and a second drying of the materials which may have stressed and damaged GFP-CIAT899. Vial ability measurements (Fig. 3, Top row) obtained with alamarBlue staining showed that ST(1:3) provided the best environment for GFP-CIAT 899 preservation at both RH levels considered. At week 4 post film formation, more than 25% of GFP-CIAT 899 encapsulated in ST(1:3) films were found to be metabolically active when preserved at RH = 25%. Higher humidity levels decreased viability to \( \sim 5% \) at week 4, indicating that the coating performance suffers from the hygroscopic nature of the materials used. AlamarBlue was indicative of GFP-CIAT 899 bacteria that were alive (i.e., active metabolic state and intact membrane) postresuscitation. However, in order to survive in a competitive environment, such as the rhizosphere and to form nodules with the host plants, PGPRs need to be able to form colonies. GFP-CIAT 899 reculturability was investigated by streaking resuscitated bacteria on agar plates as a function of storage material,
time, and RH (Fig. 3, Bottom row and SI Appendix, Figs. S4 and S5). Culture media was not added to resuscitate bacteria in order to better simulate soil conditions where no recovery time would occur. GFP-CIAT 899 colony counting indicated lower viability levels when compared to results obtained with alamarBlue metabolic activity assay, suggesting that a large quantity of GFP-CIAT 899 was viable but nonculturable (VBNC). The VBNC state in PGPRs was previously described as a side effect of desiccation using several encapsulation matrices, including nitrocellulose filters where viability dropped to 4.0% after 1 wk and to less than 2% after 4 wk at RH = 22% (43).

In our experiments, silk, trehalose, and ST mixtures produced a statistically significant increase in viability relative to PVP and MC, which are commercially used in seed-coating formulations. Additionally, ST(1:3) preserved GFP-CIAT 899 better than other ST mixtures and with similar performance to pure trehalose, indicating that the disaccharide is the key ingredient in the ST mixture to achieve bacterial reculturability postdesiccation. ST(1:3) was then chosen as the best performing coating because it integrates beneficial trehalose vitrification with the ability of S to provide sufficient mechanical robustness, adhesion, and controllable degradation to the end material. Annealing of S at the point of material fabrication may also be used in the future to control (in a time-dependent manner) the coating biodegradation and consequent release of PGPRs in the surrounding environment.

**Intrinsic vs. Extrinsic Trehalose.** Several rhizobium species, such as *Rhizobium Eti* are reported to synthesize, uptake, and degrade trehalose (44). The disaccharide accumulates in the cells as an osmoprotectant in response to increasing osmotic pressure of the medium through the otsAB, treS, and treZY synthetic pathways while internal translocation is regulated by permease proteins, such as a trehalose–maltose ABC transporter, encoded by the trehalose transport and utilization (thu) operon (thuEFGK) (44). For CIAT 899, it has been reported that trehalose synthesis is osmoregulated (45), suggesting the involvement of trehalose in the osmotolerance of this strain. However, it is still unknown if CIAT 899 has ABC transporter proteins capable of translocating trehalose as only evidence for a sorbitol/mannitol ABC transporter have been reported (45). To further investigate the mechanism that underpins stabilization of CIAT 899 in ST materials, we measured intrinsic trehalose content for CIAT 899 incubated in a 1 dry wt% trehalose solution and a 0.09 dry wt% NaCl solution for 1 h. The 1-h time point was used to mimic the amount of time CIAT 899 is in contact with ST materials during solution handling and coating formation. The study showed that, within 1 h, the CIAT 899 intrinsic trehalose concentration was not affected by extrinsic trehalose present in the forming ST materials (Fig. 4A). This finding suggests that the stabilization process induced by ST coatings leverages extracellular phenomena, such as vitrification rather than being driven by intracellular translocation of trehalose to provide intrinsic osmotic protection.

![Fig. 3. Preservation of CIAT 899 in silk, trehalose, and their mixtures. Data were collected at weeks 1, 2, and 4 for samples stored at 23 °C and at (A) 25% (B) 50% RH. In the Top, viability indicates the percentage of bacteria that were metabolically active and had intact membranes as investigated by alamarBlue analysis. In the Bottom, viability was measured as the percentage of bacteria that were culturable into colonies (colony counting analysis). Data are a pooled average ±SD of n = 5 replicates across 10 samples, and a single factor Anova test was used. Silk (S), trehalose (T), ST, xx indicates the relative weight ratio between the 2 biopolymers, annealed 6 h (A), methyl cellulose (MC), and polyvinylpyrrolidone (PVP).]

![Fig. 4. Interplay between trehalose and CIAT 899. (A) Bacteria were cultured for 1 h in 1% dry wt% trehalose solution to measure cellular uptake of extrinsic trehalose. Intrinsic levels of the disaccharide were found to be not statistically significantly different (P > 0.05) when compared to the control (0.09 dry wt% NaCl solution). Data are a pooled average ±SD of n = 7, and a single factor Anova test was used. (B) CIAT 899 and CNF42 were cultured in 0.4% minimal sucrose solution and 0.4% minimal trehalose solution. Growth profiles of CIAT 899 show the ability to translocate and metabolize trehalose and to use it as a carbon source. Data are a pooled average ±SD of n = 7.](image-url)
CIAT 899, we measured the ability to translocate and metabolize trehalose when compared to a rhizobium strain as _R. etli_ CNF42, which is well known to possess the _thu_ operon that can translocate and utilize trehalose (Fig. 4B) (46). The study was conducted by cultivating CIAT 899 and CNF42 in minimal media using trehalose as a carbon source and sucrose as a positive control. Optical measurements (OD600) showed that CIAT 899 could proliferate in trehalose minimal media as well as CNF42, indicating the ability of CIAT899 to translocate and metabolize trehalose and suggesting that, in the future, longer preexposure to trehalose may lead to enhance preservation performance.

**P. vulgaris Germination Boost and Mitigation of Saline Soil Conditions.** _P. vulgaris_ seeds were dip coated with ST(1:3) encapsulating CIAT 899, dried, and stored for 24 h before planting (Fig. 5A). Dip coating was used as it is a cheap, high throughput, and low technology method easily accessible to all farmers (47). Among all of the materials investigated, the ST(1:3) mixture ratio was used given its superior performance in terms of mechanical properties, solution viscosity, and CIAT 899 preservation. Coating processing was designed to coat each seed with 10⁷ CIAT 899 bacteria, following requirements generally imposed by policy makers for biofertilizers (48). CIAT 899-coated _P. vulgaris_ were grown over a 2-wk period of time in saline (8-ds/m) and nonsaline (4-ds/m) soil using ST(1:3)-coated seeds with no CIAT 899 as the control. Saline soil was established by adding NaCl to topsoil. The CIAT 899-coated _P. vulgaris_ seeds exhibited a statistically significant improvement in germination rate for 4- and 8-ds/m soils in comparison to the control seeds. Over the 2-wk investigation period, CIAT 899-coated _P. vulgaris_ seeds grew into seedlings that were taller and possessed longer and more articulated roots in comparison to the control seeds (Fig. 5B). Visual inspection and fluorescence microscopy were used to assess nodule formation. The right panel of Fig. 5B depicts how the GFP-CIAT 899-coated _P. vulgaris_ seeds germinated into plants that were colonized by GFP-CIAT 899 as indicated by the presence of nodules that exhibited a strong GFP fluorescence. Interestingly enough, the effectiveness of the CIAT 899-ST (1:3) coating in boosting seed germination and producing stronger seedlings was more evident in the high-salinity 8-ds/m soil.

**Conclusion**

To summarize, we developed a biomaterial formulation capable of precisely coating seeds with biofertilizers and releasing them in the soil to boost seed germination and mitigate soil salinity. The bio-inspired approach that we describe combines a disaccharide well known for its key role in anhydrobiosis with a structural protein that imparts mechanical robustness, ease of fabrication, adherence, conformability, and controlled biodegradation. The rhizobium strain used in this paper survived encapsulation in the biomaterial coating, was preserved over time, and was successfully released in the soil to form symbiotic nodules with the host roots. ST-coated seeds yielded plants that grew faster and stronger in the presence of saline soil. More broadly, our study opens the door to the application of advanced materials to precision agriculture, introducing concepts that are germane to drug delivery and biomaterials design to a field that needs to implement innovative technologies to enhance food production while minimizing inputs and mitigating environmental impacts. Using this approach, it is now possible to define applications where biomaterials can be used to engineer the seed microenvironment to precisely deliver nutrients, hormones, and beneficial biomolecules to seedlings, paving the way for a more sustainable and effective delivery of fertilizers and pesticides.

**Data Availability Statement.** All data discussed in the paper will be made available to readers upon request to B.M.

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