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Sugar-mediated physical constraints drive the evolution of pollination drops into nectar

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It is now well established that the chemical composition of ovular secretions in gymnosperms and angiosperms plays a key role in pollination biology, and the evolutionary history of this chemical profile has attracted considerable attention. In this work, for the first time, we focus on the physical properties of ovular secretions and their potential central role in the evolutionary success of angiosperms. Through wettability measurements on model systems, artificial secretions deposited on female cones of *Taxus baccata*, chosen as a representative gymnosperm species, we demonstrate that at the cone apex, characterized by 3D confocal scanning profilometry, a highly hydrophobic interaction arises. This interaction depends on both the nanostructure of the cone surface and the specific sugar composition typical of the pollination drop, enabling the secretion to maintain an almost perfect droplet shape and thereby maximizing the interception of airborne pollen grains. Additional observations performed by optical microscopy on the same solutions revealed that the chemical composition of the pollination drop, that is typically dominated by glucose and fructose and low in sucrose, ensures a high degree of pollen stabilization at the droplet surface, unlike solutions having higher concentration of sucrose, such as those typical of angiosperm nectar, which appear highly unstable. Overall the results point out that the sugar profile of the pollination drop is optimal for maximizing airborne pollen capture and to interact with pollen grains once this has landed on the drop. On the other hand this was most probably a constraint that reduced the possibility of chemical adaptation of pollination drop to interact with new pollinating agents, i.e. insects.

Main

Sugary secretions in plant reproduction: an introduction

Sugary exudates play a central role in plant reproduction, yet their function has been almost exclusively interpreted in biochemical or ecological terms. In seed plants, liquid secretions such as the gymnosperm pollination drop and angiosperm nectar, which have a specific and very different sugar profile, are commonly described as carriers of nutrients, osmolytes, or signaling compounds. Nectar is a sucrose rich solution containing lower amounts of glucose and fructose, whereas the pollination drop is characterized by a much lower total sugar content, dominated by glucose and fructose, with sucrose being scarce or absent[1,2]. The distinct chemical composition of these two secretions (and the reasons underlying it) has long attracted scientific interest. However, little attention has been paid to the fact that these fluids are also physical systems, whose ability to wet, adhere to, or detach from biological surfaces is governed by fundamental physicochemical parameters, such as surface tension, viscosity and wettability, which directly control their functional performance during pollination. Surprisingly, the role of sugar composition in determining these physical properties, and its consequences for effective pollen capture and stabilization, has not been systematically investigated, despite their well documented ability to significantly modulate the physicochemical parameters described above.

Physicochemical behaviour of sugars in aqueous systems

Sugars do not act as surfactants and therefore do not directly reduce liquid–gas surface tension; instead, their primary physical effect is to modulate viscosity and hydration structure, parameters that critically influence droplet behaviour on micro and nanostructured hydrophobic surfaces[3]. Glucose, fructose and sucrose (the main

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sugars present in plant exudates[1,2,4] differ markedly in their hydration properties and molecular architecture, resulting in distinct interactions with water and biological surfaces[5]. While all three sugars increase solution viscosity, this effect follows the order sucrose > glucose > fructose[6], reflecting differences in molecular mass, hydrogen-bonding capacity and conformational flexibility[7]. On nanostructured surfaces, these differences translate into contrasting physical outcomes. Increased viscosity can stabilize a hydrophobic regime by limiting liquid infiltration into surface nanocavities, whereas under conditions of good wettability sugars may instead enhance adhesion by structuring the liquid phase and weakly modifying solid–liquid interactions[3]. Fructose, which forms strong but less ordered hydrogen bonds with water[5], is often dominant in gymnosperm pollination drops[1], suggesting a functional link between hydration properties and droplet performance. Beyond interfacial effects, sugar composition also regulates osmolarity and water fluxes within reproductive fluids. Monosaccharide rich solutions exhibit higher osmolarity than sucrose dominated ones at equal weight concentration, influencing pollen hydration and water balance[8,9]. Plants actively regulate the sugar profile of nectar and related secretions to balance rheological performance, osmotic control and environmental constraints[9,10]. Together, these considerations indicate that sugar composition governs the physical functionality of pollination fluids through coupled effects on viscosity, interfacial behaviour and osmotic regulation, rather than through biochemical interactions alone.

Evolutionary hypothesis and conceptual framework of the study

This study was motivated by an evolutionary hypothesis: that the chemical composition of the pollination drop is not arbitrary, but reflects a long term optimization of the pollination system under specific physical environmental constraints. In particular, we hypothesized that sugar composition plays a decisive role in mediating the interaction between the pollination drop and the cone surface, thereby influencing pollination efficiency in relation to ambient temperature, humidity, and mechanical perturbations. From this perspective, the physicochemical properties of the pollination drop emerge as potential selective targets, linking environmental physics to pollination efficiency and ultimately reproductive success. In gymnosperms, successful fertilization critically depends on the interaction between a liquid secretion and an exposed reproductive surface. The female ovule secretes a small volume of fluid through the micropyle, forming the pollination drop (PD), a spherical droplet that protrudes from the cone surface and serves as the primary interface for intercepting wind-dispersed pollen. The efficiency of this system relies on two tightly coupled physical requirements: (i) the ability of the droplet to maintain a stable, nearly spherical shape under environmental perturbations, and (ii) the capacity to capture and retain pollen grains once they contact the liquid surface. Both requirements are intrinsically controlled by the physicochemical properties of the PD and by its interaction with the cone surface. Here, we demonstrate that these properties are not generic features of aqueous solutions, but emerge from a specific sugar-mediated physical strategy.

Model system and experimental approach

Using *Taxus baccata* (Fig. 1) as a model gymnosperm species, we show that the sugar composition typical of the pollination drop finely tunes the balance between viscous and capillary forces, enabling a stable droplet geometry

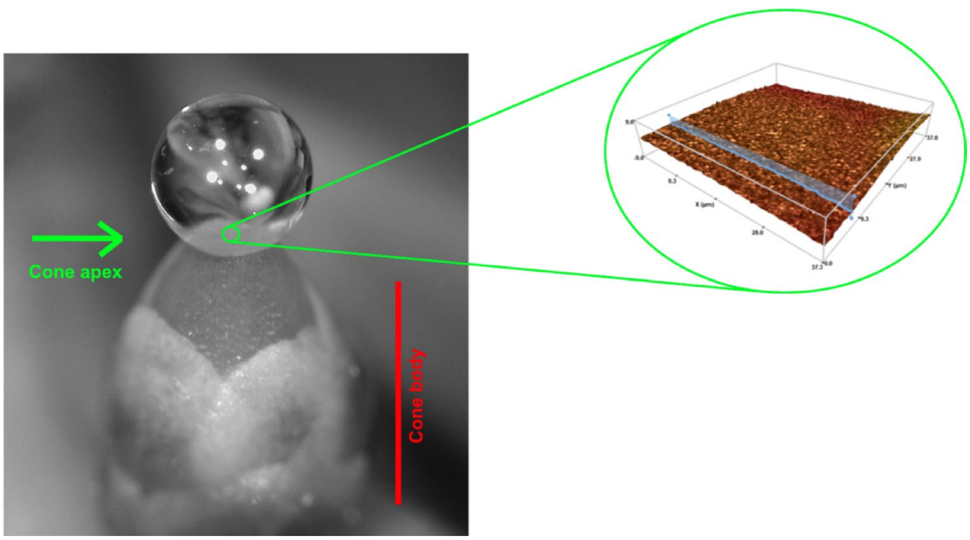

Fig. 1. Female cone of *Taxus baccata* (Taxaceae) containing one ovule that secrets a pollination drop. It is possible to appreciate the large volume of the droplet, which remains perfectly spherical, relative to its small contact area with the surface. The green arrow indicates the cone apex, corresponding to the experimental region where the pollination drop rests and where the surface nanostructure responsible for the observed hydrophobic interaction was characterized. The red bar marks the cone body. The inset shows a three-dimensional confocal image (a) obtained by confocal scanning profilometry of the apical surface, revealing nanoscale roughness that contributes to the droplet–surface interaction.

and efficient pollen stabilization on a nanostructured, hydrophobic cone apex. Crucially, we show that altering the sugar profile, specifically by increasing sucrose content to mimic angiosperm nectar, disrupts this balance, leading to excessive surface tension, reduced wettability, and failure of stable pollen deposition. The interaction between the PD and the female cone is strongly surface-dependent. Through 3D confocal scanning profilometry, we reveal that the apical region of the *T. baccata* female cone exhibits a pronounced nanostructure consistent with a highly hydrophobic regime. Wettability measurements obtained by drop-shape analysis and complementary microscopic observations of pollen deposition dynamics show that the PD analogue maintains a large contact angle at the cone apex while exhibiting a moderate liquid–gas surface tension, a configuration that preserves droplet sphericity while simultaneously preventing the dispersion of pollen captured by the drop. This behavior is imparted by a sugar profile dominated by glucose and fructose and low in sucrose. These results establish that sugar composition controls pollination efficiency primarily through physical, not biochemical, mechanisms. Our findings thus identify a previously overlooked dimension of plant reproductive biology: the physics of sugary secretions as a functional determinant of pollination success. The pollination drop of *T. baccata* emerges as a highly optimized liquid system, in which surface nanostructure and sugar-mediated rheology cooperate to maximize pollen interception and retention under wind-driven conditions. Only in this context do broader evolutionary implications arise. Gymnosperms rely predominantly on anemophilous pollination[11], a strategy that imposes strict physical constraints on the interaction between liquid secretions and exposed reproductive surfaces. By contrast, angiosperms employ nectar primarily to mediate interactions with biotic pollinators. The dominance of sucrose and higher total sugar concentrations in angiosperm nectar, while advantageous for energy transfer and osmotic stability under hot and dry climates[12], produces physicochemical properties that are incompatible with the requirements of gymnosperm style pollen capture. We therefore propose that differences in sugar composition and the physical properties they generate, represent a fundamental constraint shaping pollination strategies, with evolutionary consequences that extend beyond biochemistry to the physics of liquid–surface interactions. Extended biophysical background and theoretical considerations are provided in the Supplementary Information. The choice of *Taxus baccata* as a model system strengthens the broader relevance of our findings, as this species represents a particularly suitable model for investigating the physical behaviour of pollination drops in gymnosperms. In this species, the pollination drop is produced as a single, relatively large droplet protruding from the micropyle, which makes the liquid–air interface easily observable and experimentally accessible. Similar exposed pollination drops are characteristic of many gymnosperms, including members of Taxaceae, Cupressaceae and Pinaceae, where the drop functions as the primary interface for airborne pollen capture and transport (Doyle & O'Leary, 1935; Nepi et al., 2017). The pollination drop of *T. baccata* has been extensively studied in terms of its chemical composition, physiology and role in pollen capture, making it one of the best-characterized gymnosperm reproductive fluids (von Aderkas et al., 2015; Nepi et al., 2017). Its sugar composition, typically dominated by glucose and fructose at relatively low total concentrations, is representative of many gymnosperm pollination drops, which generally differ markedly from the sucrose-rich nectars typical of angiosperms (Nepi et al., 2009; von Aderkas et al., 2015).

Results

Physical framework for interpreting wettability measurements

The functional geometry of the pollination drop depends on its wettability, defined as the tendency of a liquid to spread on or detach from a solid surface. Wettability is conventionally quantified by the contact angle (Supplementary Fig. 2), which reflects the balance between cohesion forces within the liquid and adhesion forces at the liquid–solid interface[13]. When adhesion dominates, droplets spread and display small contact angles, whereas when cohesion prevails, droplets retain a spherical shape and exhibit large contact angles. At the microscopic scale, wettability emerges from the energetic balance among three interfaces: liquid–gas, solid–liquid and solid–gas, whose relative surface tensions determine the equilibrium contact angle[13]. Although surface tension at the liquid–gas interface contributes to droplet cohesion, the strength of liquid–solid interactions is equally critical for determining whether a droplet spreads or remains weakly attached to a surface. The work of adhesion arises from intermolecular interactions acting over nanometric length scales and is therefore strongly reduced on irregular or nanostructured surfaces that limit intimate molecular contact[14]. Nanostructured plant surfaces are well known to exploit this principle to achieve hydrophobic or superhydrophobic regimes, as exemplified by the lotus effect, where hierarchical micro and nanostructures minimize liquid–solid contact and promote droplet sphericity and mobility[15]. In such systems, droplet stability is not an intrinsic property of the liquid alone, but emerges from the interaction between liquid properties and surface architecture. These concepts are directly relevant for interpreting the wettability measurements of pollination-drop analogues on the female cones of *T. baccata*.

Contact angle

The contact angle (CA) measurements obtained at the apex and on the bodies of the female cones of *T. baccata* are reported in Tables 1 and 2, respectively. The contact angle values are presented as the average values between the maximum and minimum angles over the last 60 s of measurement, along with the difference, Δθ, observed between the maximum and minimum angles during the same period (indices may be added if possible). It is evident that the behavior of the droplet in the two regions of the cone is drastically different. All the solutions tested perfectly wet the body of the cone, with a θ angle remaining below 10° at both 20 °C and 40 °C; solutions B and C did not show any behavior different from that of pure water. In contrast, at the apex of the cone, water and the two sugary solutions exhibited significant differences, with a hydrophobic behavior increasing in the order water < solution C < solution B, and in the latter case approaching the superhydrophobic zone. The effect of temperature, as expected, decreases the contact angles for all solutions. Solution B, which mimics angiosperm nectar, shows the most hydrophobic interaction, indicating that the increase in sugar concentration and the

T(°C)	θ H_2O	θ Sol. B	θ Sol. C
20	< 10°	< 10°	< 12°
40	< 10°	< 10°	< 10

Table 1. Contact angles (θ) measured on the body region of the *T. baccata* cone for deionized water (H_2O), solution B (sucrose-rich solution simulating angiosperm nectar) and solution C (glucose–fructose dominant solution simulating the gymnosperm pollination drop), at 20 °C and 40 °C.

T(°C)	θ H_2O	θ Sol. B	θ Sol. C
20	123° ± 1	142° ± 1	129° ± 1
40	112° ± 1	126° ± 6	117° ± 1

Table 2. Static contact angles (θ) measured on the apical region of the *T. baccata* cone for deionized water (H_2O), solution B (sucrose-rich solution simulating angiosperm nectar) and solution C (glucose–fructose dominant solution simulating the gymnosperm pollination drop), at 20 °C and 40 °C. Reported θ values correspond to the mean between the maximum and minimum contact angles recorded over the final 60 s of the measurement window. Contact angles were measured on three independent droplets and reported as mean ± standard .

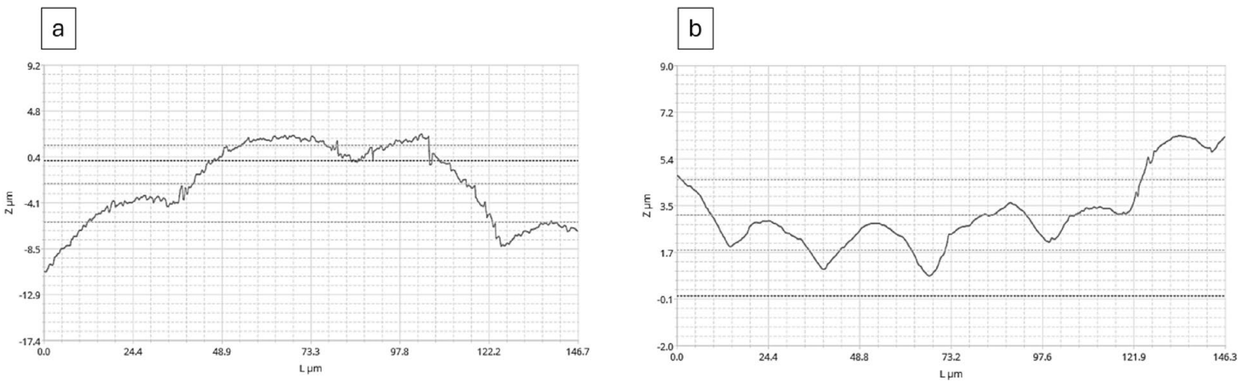

Fig. 2. Roughness profiles obtained by confocal scanning profilometry on the apical region (**a**) and on the body (**b**) of the female cone of *Taxus baccata*, highlighting differences in surface topography between the two regions.

presence of sucrose enhance the physicochemical properties that lead to a reduction in wettability at the apex of the cone (in contrast, no effect is observed on the body of the cone).

Surface characterization

3D confocal and interferometric profilometry was performed on the female cones of *Taxus baccata* surfaces before the CA measurements. The roughness (Sa) of the samples, both in the apical area and on the body, is in the micrometer range, 4–6 µm (Fig. 2a and b), but a second roughness scale is observed only in the apical areas 2D profile, where it is on the nanometric scale, 200–400 nm (Fig. 3a and b). These measurements revealed a topography based on two roughness scales that can explain the high hydrophobicity found in all the samples in the apical area and the low hydrophobicity observed in the body area, where nanoroughness was not detected.

Surface tension

Surface tension is a general interfacial property that quantifies the energetic cost associated with the creation of an interface between two phases. More broadly, it reflects the imbalance of intermolecular forces experienced by molecules located at an interface compared to those in the bulk phase[13,14]. In biological systems, several interfacial tensions may be relevant simultaneously, including liquid–gas (γ_{LG}), solid–liquid (γ_{SL}) and solid–gas (γ_{SG}) interfaces, whose combined balance determines wettability and droplet behaviour on structured surfaces. In the present study, surface tension measurements specifically refer to the γ_{LG}, which governs droplet cohesion and contributes to the ability of the pollination drop to maintain a stable, exposed geometry. Importantly, γ_{LG} is also highly sensitive to the presence of surface-active impurities, which readily adsorb at the interface and induce time-dependent relaxation phenomena[16]. The surface tension values (Table 3) found for the sugar solutions did not show any relaxation phenomena, highlighting the absence of adsorption phenomena and therefore also

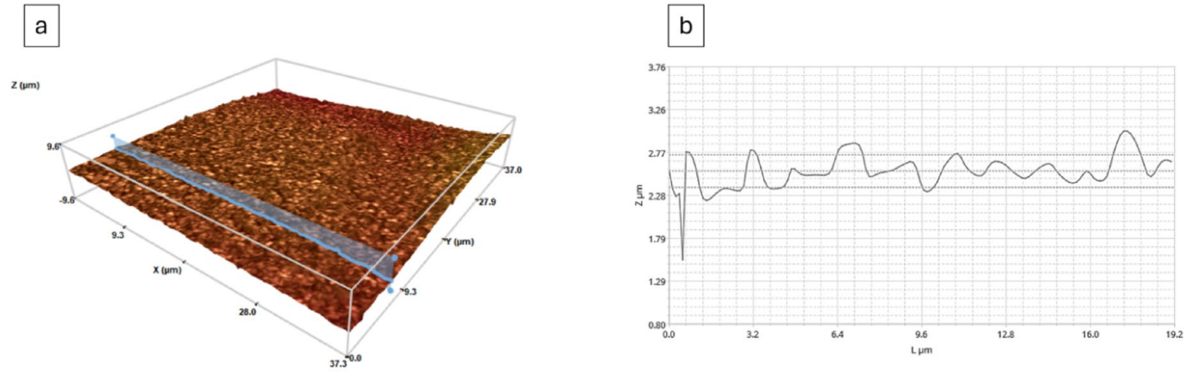

Fig. 3. Three-dimensional confocal image (**a**) and corresponding roughness profile (**b**) acquired by confocal scanning profilometry on a detail of the apical surface of the cone, revealing nanoscale roughness (Sa = 315 nm).

T(°C)	Surface tension H_2O (mN/m)	Surface tension sol. B (mN/m)	Surface tension sol. C (mN/m)
20	72.6 ± 0.3	73.4 ± 0.5	72.6 ± 0.7
40	69.8 ± 0.4	71.3 ± 0.3	70.5 ± 0.4

Table 3. Liquid–gas surface tension of aqueous solutions used in the study. Liquid–gas surface tension values measured for deionized water (H_2O), solution B (sucrose-rich solution simulating angiosperm nectar) and solution C (glucose–fructose dominant solution simulating the gymnosperm pollination drop), at 20 °C and 40 °C. The measurements reported correspond to stable equilibrium values recorded over the final 60 s of of the measurement interval. Each value represents the mean ± standard deviation of three independent measurements.

indicating the absence of any surface-active impurities in the starting substances supplied and that the observed effects arise from intrinsic bulk properties. As expected, surface tension values measured at 20 °C are consistently higher than those recorded at 40 °C. Solution B displays the highest surface tension across both temperatures. Notably, whereas pure water and solution C exhibit identical values at 20 °C, solution C undergoes a smaller reduction in surface tension at 40 °C.

Optical microscopy analysis

Figure 4a–c show the state of the system formed by *Taxus baccata* pollen on a water droplet (system A) immediately after deposition, 30 s, 90 s, and 5 min after the deposition, respectively. Images in Figs. 5 and 6 follow the same chronological order for systems B and C, corresponding to solution B and solution C, respectively. In both system A and B, the pollen grains tend to slide from the apex of the droplet toward its base. However, system B destabilizes almost immediately: within just 30 s most pollen grains have already migrated to the droplet margins. In contrast, system A exhibits a more gradual destabilization. The pollen grains generally remain on the surface, moving laterally while staying in focus, and progressively drift away from the central region, corresponding to the droplet apex. Only in rare cases individual grains penetrate the droplet interior; when this occurs, they move out of focus and disappear from view.In system C, which contains the pollination drop mimicking solution (PD), the dynamics are the opposite of those observed in systems A and B. Over time, a clear stabilization of the system occurs: pollen grains accumulate at the apical region of the droplet and remain stably positioned at the droplet apex, forming compact clusters rather than dispersing, and migrate toward the droplet apex instead of its periphery. In this condition, grains appear to remain primarily at the air–liquid interface. Although a slight partial immersion of a limited number of grains cannot be entirely excluded, no clear penetration of pollen into the bulk of the droplet was observed.

Structural characterization of pollen and pollen surface

Taxus baccata pollen grains are small, with diameters ranging from 10 to 25 µm in the dehydrated state and 21–25 µm when hydrated. In the dehydrated condition, pollen grains appear irregular in shape (Fig. 7a), becoming ellipsoidal to spheroidal upon hydration (Fig. 7b). The grains are inaperturate, lacking distinct germination apertures. SEM analysis revealed that the pollen surface exhibits a scabrate exine with microgemmate ornamentation (Fig. 7c). Quantitative measurements indicate that individual microgemmae have diameters ranging from approximately 0.20 to 0.88 µm, with a mean characteristic size of 0.32 µm, and are densely distributed across the pollen surface. This micrometre-scale surface structuring increases the number of potential contact points between the pollen grain and the air–liquid interface and is expected to influence wetting behaviour and interfacial stability. In particular, the presence of numerous surface asperities may promote contact-line pinning and contribute to the observed stabilization of pollen grains at the droplet interface, highlighting the coupled

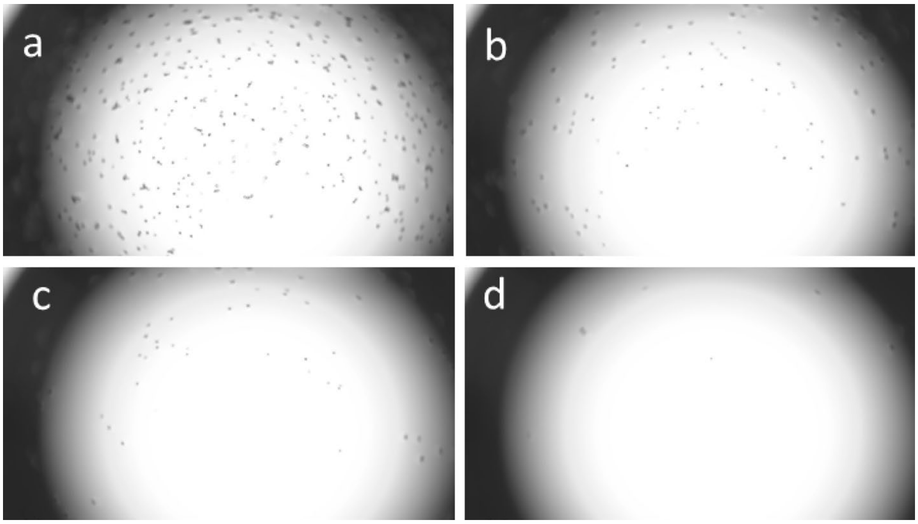

Fig. 4. Images (**a**–**d**) show the state of the system formed by *Taxus baccata* pollen on a water droplet immediately after deposition (**a**), 30 s (**b**), 90 s (**c**), and 5 min (**d**) after the deposition.

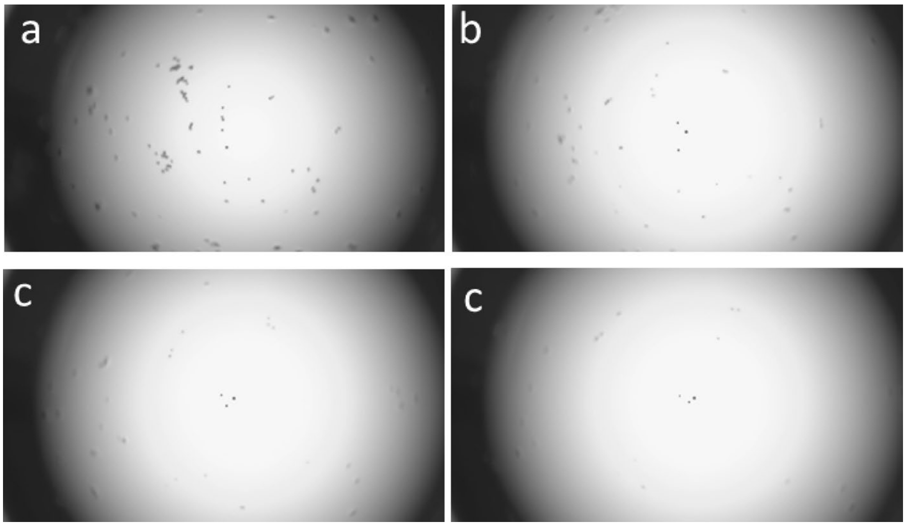

Fig. 5. Images (**a**–**d**) show the state of the system formed by *Taxus baccata* pollen on a droplet of solution B, solution simulating angiosperm nectar (15% sucrose, 7.5% glucose, 7.5% fructose, % w/w in deionized water), immediately after deposition (**a**), 30 s (**b**), 90 s (**c**), and 5 min (**d**) after the deposition.

role of pollen surface microstructure and liquid physicochemical properties in determining pollen–droplet interactions.

Discussion

Nanostructured cone surface and wettability control of the pollination drop

The results presented provide a clear picture, highlighting the presence of a specific strategy in *T. baccata* (used as a model for gymnosperms) aimed at generating highly hydrophobic conditions exclusively at the pollination drop secretion site, located at the apex of female cones. This adaptation ensures the stabilization of a large, spherical droplet. Roughness measurements taken at the apex and along the cone body demonstrate that this property arises from the presence of nanometric surface architectures at the apical region, which are absent from the rest of the cone. Contact angle measurements were performed using pure water, a solution mimicking the pollination drop (10% w/w hexoses), and a solution simulating angiosperm nectar (30% w/w carbohydrates, sucrose-dominant). The results indicate that sugar composition significantly influences the interaction with the surface, with the highest hydrophobicity observed for the sucrose-dominant solution. The liquid-gas surface tension (γ_{LG}) measured at 20 °C was identical for pure water and the hexose solution, whereas it was slightly higher for the sucrose-dominant solution. At 40 °C, the surface tension of all solutions decreased, but at this temperature, the surface tension of the hexose solution was slightly higher than that of pure water, though

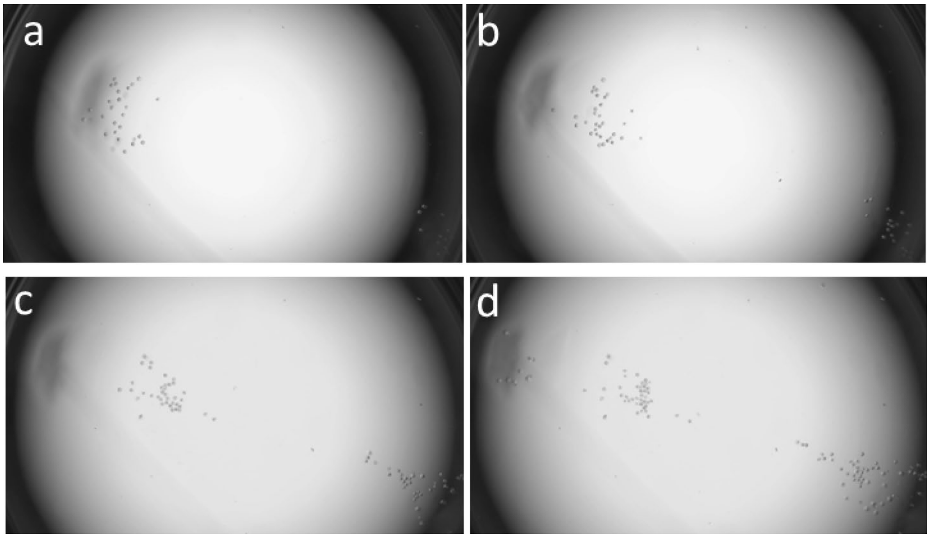

Fig. 6. Images (**a**–**d**) show the state of the system formed by Taxus baccata pollen on a droplet of solution C, solution simulating gymnosperm pollination drop (2.5% fructose, 2.5% glucose, % w/w in deionized water), immediately after deposition (**a**), 30 s (**b**), 90 s (**c**), and 5 min (**d**) after the deposition.

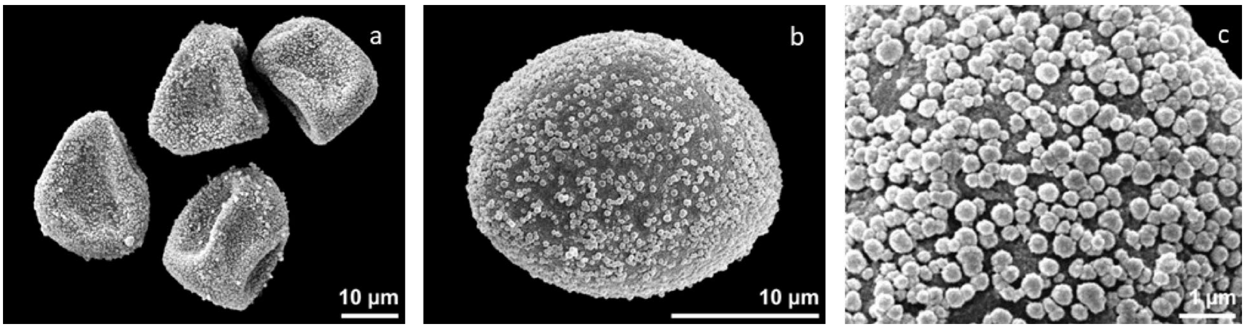

Fig. 7. Morphology of *Taxus baccata* pollen grains observed by scanning electron microscopy (SEM). (**a**) Morphology of dehydrated *Taxus baccata* pollen grains - SEM image showing the irregular shape of dehydrated pollen grains. In the dry state, pollen grains exhibit variable outlines due to dehydration-induced collapse of the pollen wall. (**b**) Morphology of hydrated *Taxus baccata* pollen grains - SEM image showing hydrated pollen grains. Upon hydration, the grains become ellipsoidal to spheroidal and recover a more regular morphology. (**c**) Surface microstructure of *Taxus baccata* pollen - SEM image showing the scabrate exine with dense microgemmate ornamentation. Individual microgemmae range from approximately 0.20 to 0.88 µm in diameter and are distributed across the pollen surface, creating numerous surface asperities that may influence wetting behaviour and interfacial interactions with liquid droplets. SEM images were obtained from the publicly available PalDat database (2000 onwards, www.paldat.org).

still lower than that of the sucrose-dominant solution. The slight variations in liquid-gas surface tension suggest that the observed changes in contact angle must be due to solid-liquid interfacial interactions, likely linked to increased viscous forces, which are maximal in the sucrose-dominant solution[6]. The maximization of hydrophobic interactions through enhanced viscous forces, rather than by increasing the liquid–gas surface tension, is crucial for the plant, as a higher liquid–gas surface tension would prevent the stable deposition of pollen on the PD.

Capillary–viscous balance governing pollen stabilization on the droplet surface

The previous assumption was confirmed by the second set of experiments, in which optical microscopy revealed that only solution C (which simulates the PD) stabilizes the pollen–drop system. This stabilization arises from a delicate balance of forces maintained by its specific sugar composition. A possible explanation for the observed phenomenon is as follows. Both water and solution C exhibit identical surface tension values at 20 °C; however, at 40 °C, the surface tension of solution C decreases less markedly. This indicates that the presence of small concentrations of fructose and glucose mitigates the effect of perturbations (such as vibration or temperature increase) on surface tension. Water, in contrast, shows the lowest viscosity among the three tested liquids. The stability of the system follows the order C > A > B, which can be interpreted in terms of the balance between

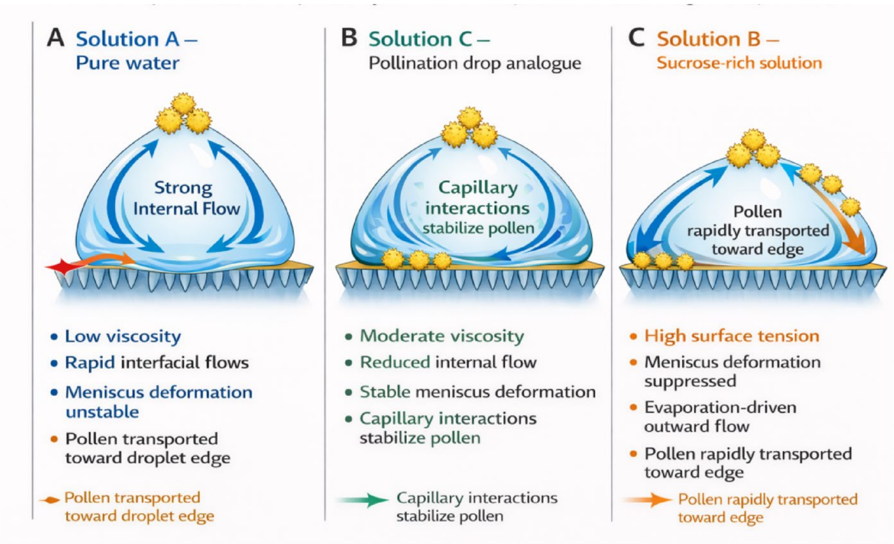

Fig. 8. Schematic representation of pollen dynamics on droplets of different sugar compositions.

capillary and viscous forces acting at the droplet interface. When a pollen grain lands on the droplet surface it locally deforms the air–liquid interface, creating a small depression whose curvature depends on the balance between surface tension γ and gravitational forces. The characteristic deformation length scale is the capillary length

$$\ell_c = \sqrt{\gamma / \rho\, g}$$

where ρ is the liquid density and g the gravitational acceleration (therefore denser solutions, such as B, decrease the length of the deformation). Particles adsorbed at the interface generate local meniscus distortions that can interact with one another through capillary forces, producing the well-known capillary interaction mechanism described for particles at fluid interfaces[17–19]. The microgemmate ornamentation of the *Taxus baccata* pollen exine (~ 0.3 μm) lies within the characteristic scale of surface asperities known to induce contact-line pinning and capillary multipole interactions between particles adsorbed at fluid interfaces. Such irregularities produce anisotropic distortions of the air–liquid interface that generate quadrupolar capillary interactions, which can promote the aggregation and stabilization of particles at the droplet surface, commonly known as the Cheerios effect[20]. However, the persistence of these interfacial depressions depends strongly on the hydrodynamic stability of the droplet. In liquids of low viscosity, such as pure water (system A), small perturbations caused by environmental vibrations or evaporation-driven convection can rapidly disrupt the meniscus around the particle. The relative importance of viscous and capillary forces is described by the capillary number

$$\mathrm{Ca} = \frac{\mu\, U}{\gamma}$$

where μ is the dynamic viscosity and U a characteristic interfacial velocity. In water, the low viscosity results in rapid interfacial flows that destabilize the capillary depressions after approximately 90 s, causing the pollen grains to slide toward the droplet edge. In solution C, the presence of small concentrations of fructose and glucose slightly increases viscosity while leaving surface tension nearly identical to that of pure water. The higher viscosity reduces the velocity of thermally or mechanically induced flows and therefore lowers the effective capillary number, allowing the interfacial depressions to persist long enough for capillary interactions to stabilize the pollen at the droplet apex. In contrast, solution B exhibits both higher viscosity and higher surface tension due to its high sucrose content. While the increased viscosity would in principle damp interfacial motion, the much higher surface tension suppresses the deformation of the droplet surface required to generate the meniscus around the particle. As a result, pollen grains cannot create stable interfacial depressions and immediately slide toward the droplet edge. Moreover, although the overall evaporation rate of sugar solutions is generally lower than that of pure water due to reduced water activity, evaporation in sessile droplets is spatially non uniform and is strongly enhanced near the contact line. This produces a compensatory radial flow from the droplet apex toward the edge that transports particles along the interface[21,22]. In highly concentrated solutions such as system B, evaporation induces strong concentration and density gradients near the droplet edge, which amplify internal convective flows and favor the outward transport of particles toward the contact line. In solution C, which contains much lower sugar concentrations, these gradients remain weak and the resulting radial flows are significantly reduced. As a consequence, capillary interactions between pollen grains are able to dominate the dynamics at the droplet surface, allowing the particles to remain trapped near the apex rather than being transported toward the droplet edge. A schematic representation of the described mechanisms is shown in Fig. 8.

Functional consequences of sugar composition for droplet stability and pollen capture

It is interesting to observe that at 40 °C, the contact angle of the solution mimicking angiosperm nectar is nearly identical to that of the pollination drop solution measured at 20 °C. This experimental evidence suggests that a sugar solution analogous to angiosperm nectar, when placed on the nanostructured surface of a *Taxus* cone, compensates for the increased wettability caused by a 40 °C temperature rise, similar to what a pollination drop would experience. This consideration is particularly significant as it strongly supports the hypothesis that the chemical modifications between the pollination drop and nectar originally arose as a physiological compensation mechanism, driven by climate change, to preserve reproductive success. However, as demonstrated by our experiments, the increase in sugar content and the emergence of sucrose, although ideal for maintaining a spherical droplet shape, ultimately do not confer the same functional fitness as the system characterized by low concentrations of glucose and fructose. The reduced wettability associated with a higher surface tension results in a lower capacity of the system to support the stable adhesion of pollen grains. We propose that this trade-off between maintaining an optimal spherical shape of the pollination drop and preserving the rheological parameters required for efficient pollen deposition and probably also for osmotic homeostasis, internal fluid dynamics, and overall water balance (if the solution mimicking angiosperm nectar were composed solely of glucose and fructose, its osmolarity would be 1.664 Osm/L, with a viscosity of approximately 1.60 mPa.s at 40 °C, conversely, the sucrose-dominant solution (solution B) has an osmolarity of 1.27 Osm/L but a significantly higher viscosity, 1.79 mPa.s, which represents a disadvantage for fluid transport and thus pollen hydration) represented an evolutionary bottleneck for gymnosperms in hot and arid climates. This evolutionary constraint likely drove a shift in pollination strategies: the higher sugar content and the predominance of sucrose became the key innovations that enabled the development of entomophilous pollination, a strategy more versatile and resilient than the anemophilous one. The earliest angiosperm flowers had very small petals and a structural organization closely resembling that of gymnosperm cones[23,24]. Evolution subsequently favored traits that enhanced the attraction of pollinators, driving the transition of angiosperms toward entomophilous pollination as their predominant strategy.

Ephedra as a model transitional system linking pollination drops and nectar

The hypothesis that the chemical-physical characteristics required to maintain a spherical shape and efficient adhesion were key factors in the evolutionary success of the pollination drop's sugar profile is supported by the chemical characterization of the pollination drop in *Ephedra*[1,25]. Indeed, is possibly the only known gymnosperm whose pollination drop contains exclusively sucrose, and notably, it is one of the few gymnosperms that flowers at the beginning of summer. Moreover, *Ephedra* produces one of the largest pollination drops, approximately 1 μL, compared to the $\sim$250 nL of *Taxus*, which is already among the species with the most abundant secretion[25]. *Ephedra* exhibits morphological and physiological traits that are transitional between gymnosperms and angiosperms[26–29] and is therefore often regarded as a key evolutionary model. Its female cones are relatively large compared with those of most other anemophilous gymnosperms, and display a structure reminiscent of primitive flowers. In some species (*Ephedra distachya*, *E. foeminea*), the bracts (modified leaves that protect or accompany a reproductive organ) become red and sugary at maturity, releasing sweet secretions that attract insects or birds, a behavior that is almost entomophilous rather than anemophilous. This supports the hypothesis that the driving force behind the evolution of the flower lies in the physicochemical properties of nectar. Indeed, even among gymnosperms, species with a pollination drop similar in composition to nectar tend to develop cone morphologies that approach the floral condition[26–28].

Conclusions

For the first time, we investigated the system composed of the pollination drop and the female cone of a model gymnosperm, *Taxus baccata*, focusing on the physicochemical properties of the drop and its interaction with the cone surface. Experimental measurements demonstrated that this system maintains a delicate physicochemical balance that maximizes the probability of successful pollination by preserving a spherical droplet shape through a highly hydrophobic interaction with the apical portion of the female cone. This high hydrophobicity is achieved through two key elements: the nanostructured surface of the cone apex and the viscous forces imparted by the specific sugar composition of the pollination drop. It was also shown that the maximization of hydrophobic interactions through viscous forces, rather than through modulation of the liquid-gas surface tension is functionally advantageous for effective pollen deposition. Indeed, when the sugar composition typical of the pollination drop was replaced with that of an angiosperm nectar, richer in sucrose and overall more concentrated, we observed a decrease in wettability (i.e., an increase in hydrophobicity) and a rise in surface tension, preventing the effective deposition of conspecific pollen on the droplet. Conversely, a solution reproducing the composition of the pollination drop conferred high stability to pollen grains at the droplet apex. Overall, our experimental evidence provides a novel perspective on the evolutionary dynamics that led to the dominance of angiosperms, suggesting that sucrose dominance and the increase in total sugar content may have initially represented an adaptation to counteract the increased wettability caused by the high temperatures of the Cretaceous period[30](which would have negatively affected the maintenance of the droplet shape). At the same time, the higher sugar content likely enhanced interactions with animal pollinators, offsetting the disadvantage for pollen deposition and thereby promoting a new pollination strategy based on biotic vectors and novel morphological structures, the flowers. Although the experimental analysis involved only a single model species, the strength and consistency of the results strongly support the conclusion that the physicochemical properties of sugary secretions in gymnosperms and angiosperms played a guiding role in shaping plant evolution under the influence of physical environmental drivers such as temperature and humidity. The evolutionary interpretation proposed here is supported by a large body of ecological research showing that the physicochemical properties of plant secretions can shape plant reproductive strategies.

In particular, the ecological relevance of the physicochemical properties of plant secretions has long been recognized in studies of angiosperm nectar. Frameworks such as optimal foraging theory and nectar economics models demonstrate that nectar concentration, viscosity and sugar composition influence pollinator behaviour, including handling time, energetic reward and foraging efficiency[30–33]. These studies show that the chemical and rheological properties of sugary secretions can play a significant evolutionary role in mediating plant–pollinator interactions. However, in angiosperms these relationships are mainly expressed through interactions with animal pollinators. In contrast, gymnosperm pollination drops evolved in a much earlier reproductive context, where the secretion primarily interacts with airborne pollen rather than with animals. In this framework, the rheological and interfacial properties of the pollination drop may have represented an even more fundamental constraint, directly controlling pollen capture, stabilization and transport. Although the present study focuses on a single model species, the underlying physicochemical mechanisms described here, namely the balance between capillary forces, viscosity and droplet stability, are expected to apply broadly to gymnosperm pollination drops and potentially to other plant secretions exposed to the atmosphere. Importantly, these mechanisms do not depend solely on liquid properties, but also on the nanostructured architecture of the cone apex and on the microgemmate surface features of the pollen grains, which together govern interfacial deformation and particle stabilization. The evolutionary scenario proposed here should therefore be regarded as a hypothesis grounded in experimentally demonstrated physical mechanisms. While further comparative and phylogenetic studies will be necessary to test its generality across taxa, the mechanistic framework presented in this work has been fully elucidated and is based on a model species that is highly representative of gymnosperm reproductive biology.

Methods

Physical framework for interpreting wettability measurements

The functional geometry of the pollination drop depends on its wettability, defined as the tendency of a liquid to spread on or detach from a solid surface. Wettability is conventionally quantified by the contact angle (Supplementary Fig. 2), which reflects the balance between cohesion forces within the liquid and adhesion forces at the liquid–solid interface[13]. When adhesion dominates, droplets spread and display small contact angles, whereas when cohesion prevails, droplets retain a spherical shape and exhibit large contact angles. At the microscopic scale, wettability emerges from the energetic balance among three interfaces: liquid–gas, solid–liquid and solid–gas, whose relative surface tensions determine the equilibrium contact angle[13]. Although surface tension at the liquid–gas interface contributes to droplet cohesion, the strength of liquid–solid interactions is equally critical for determining whether a droplet spreads or remains weakly attached to a surface. The work of adhesion arises from intermolecular interactions acting over nanometric length scales and is therefore strongly reduced on irregular or nanostructured surfaces that limit intimate molecular contact[14]. Nanostructured plant surfaces are well known to exploit this principle to achieve hydrophobic or superhydrophobic regimes, as exemplified by the lotus effect, where hierarchical micro and nanostructures minimize liquid–solid contact and promote droplet sphericity and mobility[15]. In such systems, droplet stability is not an intrinsic property of the liquid alone, but emerges from the interaction between liquid properties and surface architecture. These concepts are directly relevant for interpreting the wettability measurements of pollination-drop analogues on the female cones of *T. baccata*.

Experimental design

Our experimental design comprises two complementary approaches. First, we quantified wettability using the drop-shape analysis technique in a laboratory system that closely reproduces the natural pollination environment of *T. baccata*. Specifically, solutions mimicking both the pollination drop and angiosperm nectar were deposited on mature female cones of *T. baccata*, and the wettability and surface tension of both systems were measured at two temperatures, 20 and 40 °C (this last temperature as possible Cretaceous scenario). This choice is motivated by the fact that the radiation of angiosperms is generally traced back to the early Cretaceous, a period characterized by intense climatic changes, including a marked increase in mean global temperatures of up to 15–20 °C and increased atmospheric aridity[2,34]. It is worth recalling that wettability is intrinsically temperature-dependent and typically decreases as temperature increases, owing to the reduction in liquid–gas surface tension and changes in interfacial interactions, effects that are particularly relevant for small droplets interacting with structured biological surfaces[3,18]. In addition, the surface of the cone was characterized by 3D confocal profilometry at both the apex and lateral regions. In a second set of experiments, *T. baccata* pollen grains were deposited onto drops of the same solutions, and the stability of the resulting systems was examined under an optical microscope.

Artificial secretions

For the laboratory experiments, three solutions were prepared with the following compositions:

solution A—deionized water.
solution B—15% sucrose, 7.5% glucose, 7.5% fructose (% w/w) in deionized water.
solution C – 2.5% fructose, 2.5% glucose (% w/w) in deionized water.
The carbohydrates (99.5% purity) were purchased from Sigma Aldrich S.r.l.
Solution B simulates the nectar of angiosperms[4], while solution C simulates the PD[1,2].

Plant material

Untreated *Taxus baccata* pollen, with a diameter ranging from 20 to 30 μm, was kindly provided free of charge by Pharmallegra S.r.l. The pollen originated from Lednice, Breclav, South Moravia (N 48°47′, E 16°48′; altitude 174 m). Branches of Taxus baccata L. bearing female cones were collected in March 2024 from the Botanical

Garden of the University of Siena (Siena, Italy). In the lab, the cones were excised and immediately placed in Petri dishes lined with wet filter paper.

Drop-shape analysis

For the evaluation of the contact angle (CA) of the samples, measurements were carried out by the ASTRAview drop-shape tensiometer[35], developed at CNR-ICMATE, using solution A, MilliQ high-purity-grade water produced by an ion-exchange microfiltration system (Milli-Pore, Burlington, MA, USA), solution B and C. The measurement was performed after placing a drop of liquid produced through a steel capillary (volume 3–5 µL) on the apex and body of the cone, acquiring contact angle values at a frequency of 1 Hz. All measurments were conducted at 20 and 40 °C mantained by a thermostatic chamber. The measurements were repeated at least three times, taking care, in the case of solutions B and C, to wash and dry the substrate by ventilating it with air at room temperature to avoid the effect of any adsorption phenomena that could have affected subsequent measurements. CA were determined using sessile-drop measurements combined with drop shape analysis. Images of the droplets were recorded after deposition and a stabilization time to allow the system to reach a quasi-equilibrium configuration. The droplet profile was extracted from the images and fitted using standard contour-fitting procedures based on the Young–Laplace equation, which describes the shape of a liquid interface under the balance of capillary and gravitational forces. In this approach the CA is obtained from the slope of the fitted droplet contour at the three-phase contact line, rather than from a single geometric measurement.Because the fitting procedure uses the entire droplet contour, the resulting contact angle represents a parameter describing the equilibrium droplet configuration determined by the balance of interfacial tensions according to Young's equation. Drop shape analysis is widely used for quantitative wettability characterization and typically provides uncertainties on the order of ~ 0.6° for static contact angles and a few degrees for dynamic measurements when appropriate imaging and fitting procedures are applied[36].

Surface tension

Surface tension measurements were performed using drop-shape analysis in pendant drop configuration, a non-invasive technique that specifically probes the liquid–gas interfacial tension γ_{LG}. In this approach, γ_{LG} is obtained by fitting the equilibrium shape of a liquid droplet suspended from a capillary, which results from the balance between gravitational forces and capillary cohesion acting at the liquid–gas interface. This method is particularly suitable for aqueous sugar solutions because it avoids contact with solid substrates, thereby minimizing artefacts associated with adsorption or solid–liquid interfacial effects[16]. Surface tension measurements were carried out by Drop Shape Method (pendant drop) at temperatures of 20 and 40 °C in a cell equipped with a thermostatic chamber in the presence of humidity to avoid evaporation with consequent variation of the initial concentrations. The measurements reported correspond to stable equilibrium values recorded over the final 60 s of of the measurement interval. While γ_{LG} alone does not determine wettability, its independent measurement is required to disentangle the relative contributions of liquid cohesion and solid–liquid interactions in shaping droplet behaviour on nanostructured biological surfaces.

3D confocal profilometry

The surface roughness (Sa) and structure of the samples, apex and body of the seed, were assessed using 3D confocal and interferometric profilometry (Sensofar S-NEOX, Terrassa, Spain). The 3D profilometry, because of its quick and non-destructive use and characterization in compliance with ISO 25,178, was selected to enable a large, scanned surface. For each sample, 3D profilometer images and related profile, were acquired.

Optical microscopy analysis

The stability of the pollen–drop system was examined using optical microscopy. Three types of systems were analyzed (each tested in triplicate), consisting of pollen grains and 2 µL droplets, a volume typical of the pollination drop in *T. baccata*[37–39], prepared using solutions A, B, and C. The droplets were dispensed with a micropipette onto standard disposable polystyrene Petri dishes, providing a hydrophobic substrate. *Taxus baccata* pollen grains were collected from their storage container using a metallic needle and gently transferred onto the droplet surface by lightly tapping the needle above the droplet. This procedure allows pollen grains to fall from above under gravity, mimicking the random arrival of airborne pollen during natural wind pollinationImages of each pollen–drop system were taken at 30 s intervals until equilibrium was reached. The purpose of this experiment was to evaluate the stability of pollen deposition on droplets with different sugar compositions. Each observation was repeated four times to ensure reproducibility. Images were captured using a Zeiss Axiovert 5 inverted microscope equipped with 20× and 40× objectives and connected to a Zeiss Axiocam 208 color digital camera. All observations were performed at room temperature (25 °C) in a laboratory environment with monitored temperature but without active humidity control.

Structural characterization of pollen and pollen surface

Scanning electron micrographs of pollen grains and detail of pollen surface have been taken from PalDat (2000 onwards, www.paldat.org).

Data availability

The key data supporting the findings of this study are included in this published article and its Supplementary Information files. Additional data generated during the study, including raw and intermediate experimental data, are available from the corresponding author upon reasonable request.

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Emanuele Giordano: Conceptualization; Methodology; Investigation; Formal analysis; Data curation; Writing – original draft.Gianni Betti: Formal analysis; Writing – review & editing.Daniele Calabrese: Investigation; Data curation; Writing – original draft.Cecilia Del Casino: Formal analysis; Writing – original draft.Michele Ferrari: Formal analysis; Writing – original draft.Francesca Cirisano: Formal analysis; Writing – original draft.Tecla Gasperi: Formal analysis; Writing – review & editing.Massimo Nepi: Conceptualization; Writing – review & editing. All authors read and approved the final manuscript.

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Declarations

Competing interests
The authors declare no competing interests.

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