

Interactions of pollen-stigma interface in fruit trees: A multiscale analysis of adhesion mechanisms

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Abstract: Inspired by sophisticated adhesion strategies in nature, physicochemical properties of pollen from three widely distributed fruit species (apple, pear, and kiwifruit) are investigated, and an novel adhesion mechanism for fruit tree pollination is proposed. Through simulation and measurement of natural pollination process, adhesion force between pollen and stigma is quantified,

with its constituent components deduced theoretically. Herein, composition and hygroscopic capacity of pollenkitt from three species reveal that while van der Waals forces dominate the adhesion between two biological interfaces, the presence of pollenkitt confers an increased binding strength as relative humidity rises. At the microscale, pollen surfaces are characterized, and biological model between pollen surface microstructure and stigma papillae is investigated to reproduce the natural pollination adhesion system. Following the discovery of strikingly similar ridge structures in two Rosaceae pollen species and dense microprotuberances on kiwifruit pollen, various mechanical models of these microstructures with papillae as well as artificial substrates are established. Furthermore, based on electrostatic properties of pollen, the electrostatically enhanced adhesion effect is explored through theoretical analysis and experimental validation. Collectively, this research elucidates a bioadhesion mechanism underlying fruit tree pollination, providing application potential for research in agricultural science and technology, biomedicine, and ecological environment.

Keywords: biological interface; adhesion force; AFM; pollination; electrostatic deposition

1 Introduction

Pollen-stigma adhesion is the initial step of plant sexual reproduction. During its dispersal and transportation from anther to stigma, pollen undergoes multiple cycles of detachment and adhesion on the surfaces of flowers and insects [1, 2], moreover, successful plant fertilization requires firm adhesion to stigma and maintenance of this state for a sufficient duration [3-5]. Typical bioadhesion systems have inspired numerous studies to elaborate on their underlying mechanisms [6, 7], and facilitated the development of high-performance adhesive products by harnessing their operational principles [8-10]. For instance, the van der Waals mechanism of gecko setae provided foundation for developing the first dry adhesive microstructures [11]. This breakthrough triggered a series of subsequent bio-mimetic studies [12, 13], leading to fabrication of reversible adhesives [14]. The

integration of gecko-inspired adhesion with soft robotics has ultimately enabled climbing on complex surfaces [15]. Capillary forces and viscous forces between tree frog toe pads and substrates significantly enhance the adhesion of tree frogs, which has inspired the design of underwater adhesive materials [16]. Mussels can attach rapidly and firmly to solid surfaces in marine environment, through functionalization of polymers in mussel foot proteins, underwater adhesives and medical suture materials have been developed [17-19]. Natural plant pollen has emerged as a promising drug-encapsulated microcarrier [20], inspired by natural pollen, polymer microparticles with tunable surface roughness have been fabricated, which exhibit strong adhesion capacity to the intestinal mucosa and can serve as novel drug carriers [21, 22]. Pollen-induced asthma and allergies are significant factors affecting respiratory health [23, 24], and research on the adhesion properties between pollen and artificial substrates is expected to provide solutions for indoor air purification.

Efficient collection and transportation of pollen are crucial for the survival of both animals and plants. In nature, plants primarily rely on anemophily and entomophily for pollination [25, 26], while artificially intervened pollination aids in the smooth delivery of pollen to stigmas, they share the same objective. Pollen from different plant species exhibits significant variability, with sizes ranging from 10 nm to 100 μm and morphologies spanning from spiny and complex structures to regular olive-shaped forms [27]. However, pollen from the same plant species exhibits intrinsic adaptation for adhesion to stigmatic surface. In *Hypochaeris radicata* L., soft stigmatic papillae provide capillary force to trap spines on pollen surface [2], whereas the smaller, smooth pollen grains of *Actinidia chinensis* Planch. are firmly entrapped by stigmatic papillae until germination occurs [4]. Driven by pollination adaptation during long-term cultivation and domestication, pollen surfaces have undergone a transition from rough to smooth [28]. Pollen of angiosperms commonly contain pollenkit [29-31], a substance that facilitates pollen transport [32], supports pollen adhesion to stigma, and enables rehydration [33, 34]. Pollenkit mainly consists of saturated and unsaturated fatty acids, lipids, carotenoids, flavonoids, proteins, and carbohydrates [35, 36], which renders the process

of characterizing pollen adhesion properties more complex. Non-defatted pollen exhibits significantly higher adhesion values, for instance, pollen from *Taraxacum officinale* rich in pollenkit demonstrates an adhesion force 3 to 6 times greater than that of defatted samples [27]. During peak flowering period, stigma secretes mucus to capture pollen from the air or carried by pollinating insects and prevent its detachment. Capillary mechanism contributed by stigma papillae is expected to promote adhesion [37]. To date, however, the contribution of these potential forces to enhancing pollen adhesion has not been reported, and studies on the physical adhesion properties of pollen remain limited.

In existing studies, inspired by natural bio-adhesion systems such as geckos, tree frogs, and mussels, significant advances have been achieved in adhesives, soft robotics, and medical sutures [12-18]. Current research on pollen adhesion has predominantly focused on model plants such as dandelion and *Arabidopsis thaliana* [27, 34, 37], yet adhesion mechanisms during fruit tree pollination remain largely unexplored. Here, we investigated the pollen-stigma adhesion mechanisms in apple (*Malus domestica* ‘Fuji’), pear (*Pyrus pyrifolia* ‘Niitaka’), and kiwifruit (*Actinidia deliciosa* ‘Hayward’), three species of global distribution, significant economic and ecological value, and relevance to human health. We characterized the morphology of pollen and stigmas, pollen-stigma adhesion structures, quantitatively analyzed van der Waals and capillary bridge forces, and established a mathematical contact model for pollen-stigma interaction. Furthermore, motivated by the widespread application of the charging effect in engineering [38, 39], and in enhancing plant physiology [40-43], we established a pollen charging platform and verified the potential of electrostatically treated pollen to enhance adhesion. This study deepens the understanding of the elaborate adhesion strategies in nature, and through mechanism analysis and model establishment, exhibits unique application potential in fields such as agricultural science and technology, biomedicine, and ecological environment.

2 Experimental

2.1 Sample collection and preparation

To prevent contamination on plant surfaces, flower buds of apple (*Malus domestica* 'Fuji'), pear (*Pyrus pyrifolia* 'Niitaka'), and kiwifruit (*Actinidia deliciosa* 'Hayward') were bagged during large bud stage (Fig. S1(a)). After flower anthesis, flower samples were collected indoors together with paper bags, and several flower buds with separated petals were selected (Fig. S1(b)), as their stigmas were fully developed and remained uncontaminated. Fresh pollen and styles were collected from these buds to observe the natural morphology of pollen grains and stigmatic papillae. After full flower anthesis, pollen is deposited on the stigmatic surface via anemophilous and entomophilous pollination (Fig. S1(c)). Pollinated styles were collected to observe contact structures of pollen on stigmatic surface. Freshly collected pollen was stored at -18°C for subsequent use.

Styles were dissected at their base using a scalpel and fixed on glass slide with scotch tape, and oriented with papillae-containing surface facing upward for atomic force microscopy (AFM) adhesion force measurements. To prevent desiccation during testing, basal end of style was wrapped in tape together with water-saturated paper (Fig. S1(d)).

Freshly collected pollen was immersed in a chloroform-methanol mixture (3: 1), sonicated for 1 min, followed by centrifugation at 6000 rpm for 10 min at 4 °C, this washing procedure was repeated five times until the supernatant became transparent. Pollen samples involved in this study included raw apple pollen (RAP), washed apple pollen (WAP), raw pear pollen (RPP), washed pear pollen (WPP), raw kiwifruit pollen (RKP), and washed kiwifruit pollen (WKP).

2.2 Pollen density and weight measurements

True density of pollen samples was determined by applying gas displacement method based on Archimedes' principle, utilizing Boyle's law with low molecular diameter inert gas (helium). The true volume of pollen sample was accurately determined by measuring the reduction in gas volume of sample test chamber caused by placing the sample into the chamber, thereby obtaining its true

density (true density=mass/true volume; AccuPyc II 1345, USA). A minimal quantity of pollen was transferred using an eyelash onto weighing paper and weighed using a microbalance (XP6, Mettler Toledo, Switzerland; precision: 0.001 mg). Pollen grains on weighing paper were photographed and counted under a microscope (Fig. S2).

2.3 Substrate preparation

A polystyrene (PS, $M_w=200,000$) solution was prepared by dissolving PS in toluene at a 10 wt%, hydrophobic substrates were fabricated by coating silicon wafers with PS solution. Hydrophilic substrates were prepared by etching silicon wafers in piranha solution (sulfuric acid: hydrogen peroxide = 7:3, v/v) for 4 hours. Static water contact angle θ_w of all polymer-coated silicon substrates was measured using a contact angle analyzer (PZ-350SD, Beijing PinZhiChuangSi Precision Instrument, China) to confirm their hydrophobic or hydrophilic properties (Figure S3, Supporting Information). Surface topography of each substrate type was characterized by AFM, scanning three random $10\ \mu\text{m}\times 10\ \mu\text{m}$ areas. Arithmetic average roughness (Ra) and root mean square roughness (RMS) values were obtained (Table S1).

2.4 Morphological characterization of pollen

The Surface topography of pollen was characterized by AFM (Dimension FastScan Bio, Bruker, USA) with SNL-10 probe (Bruker, USA), the cantilever had a spring constant of 0.35 N/m, a length of 120 μm , a thickness of 0.6 μm , and the probe featured a tip height of 2.5 μm , a half-open angle of $15\pm 2.5^\circ$, and a tip radius of 13.2 nm. Samples included raw pollen and washed pollen.

2.5 Pollen-modified tipless cantilever

Due to the significant differences in material properties between probe and pollen grains, surface energy between them does not accurately reflect that of actual pollen, therefore, pollen grain was functionalized onto a tipless cantilever (Fig. S4), adhesion forces between pollen and stigma were measured by pollen-modified probe. Ion-cleaned tipless cantilever was placed on the microscope stage with its front side facing upward; Two glass capillaries with an approximate inner diameter of

15 μm were pulled using a multi-pipette puller (PMP107, MDI, USA), and mounted separately on the micromanipulator arm of a micromanipulation system (TransferMan 4r, Eppendorf, Germany) and a pneumatic microsyringe; a pneumatic microsyringe was used to aspirate epoxy adhesive (UHU, Germany) that had been pre-cured for 15 minutes; under microscope, capillary was positioned near the center of tipless cantilever, and an appropriate amount of adhesive was dispensed, considering pollen size, the coverage area of adhesive must not exceed 20 μm ; pollen grain was picked up using micromanipulator and precisely placed onto adhesive-coated region of tipless cantilever; after modification, the assembly was cured at room temperature for 24 hours.

2.6 Adhesion force measurement

Adhesion force between pollen-modified probe and sample was measured by acquiring force curves in Ramp mode, interaction force depends on the distance between the two surfaces; by varying the distance between them, the change in interaction force as a function of probe displacement can be measured. Force-displacement curves were further elaborated in Section S2.

2.7 Cryo-SEM Assays

Observations were conducted using cryo-SEM (FlexSem1000, Hitachi Ltd, Tokyo, Japan), at -90°C to investigate contact structure of pollen-stigma in native state. Before fabricating pollen-modified probes and after conducting adhesion force tests, cryo-SEM observations were required to verify whether pollen grains on cantilever were damaged. Samples were mounted on metal stubs using carbon tape, and an accelerating voltage of 10.0 kV was applied prior to imaging.

2.8 Pollen Composition Assays

Raw and washed pollen were placed on glass microscope slides. Fluorescence images of pollen were acquired using a confocal fluorescence microscope (Olympus IX83-FV3000) equipped with an FITC channel, which was fitted with a 60 $\times$ oil immersion objective. For EGFP, the excitation wavelength was set at 488 nm, with an emission collection range of 500-540 nm. SERS spectra were collected using confocal micro-Raman spectrometer (Renishaw inVia), a 785 nm laser was selected with an

output power of 300 mW. Spectral acquisition was performed with a 20× objective lens and a 10× eyepiece, with an exposure time of 10 s and a laser power setting of 1%. Raw and washed pollen were dried for 24 hours, approximately 2 mg of dried samples was mixed with pure potassium bromide (KBr) at a 1:100 mass ratio, ground thoroughly in an agate mortar, dried again. Fourier transform infrared (FTIR) spectrometer (Thermo Fisher Scientific Nicolet iS20, USA) was employed, with a test wavenumber range set to 4000-400 cm^{-1} .

3 Results and discussion

3.1 Structure of pollen-stigma contact

Geometric structures of pollen-stigma of apple (Fig. 1(a)), pear (Fig. 1(e)), and kiwifruit (Fig. 1(i)) in their native states were observed using cryogenic scanning electron microscopy (cryo-SEM) (Figs. 1(d), 1(h) and 1(l)). Meanwhile, morphologies of styles (Figs. 1(b), 1(f), and 1(j)) and anthers (Figs. 1(c), 1(g) and 1(k)) were analyzed. Distal ends of styles in all three species were densely covered with papillae, forming the pollination-receptive region, i.e., the stigma. Successful pollination is associated with a series of plant physiological mechanisms, including pollen germination, pollen tube competition, and stigma receptivity. A single apple flower requires 100-200 pollen grains to achieve pollination [44], a pear flower needs 150-250 pollen grains [45], while kiwifruit requires more than 10,000 pollen grains to attain complete fruit set [46]. As described in Experimental section, true density of three pollen types were measured five times at room temperature, providing useful data for pollen research (Tables S2, S3 and S4), true densities of apple, pear, and kiwifruit pollen were $1.3520 \pm 0.0004 \text{ g/cm}^3$, $1.3482 \pm 0.0004 \text{ g/cm}^3$, and $1.3292 \pm 0.0003 \text{ g/cm}^3$, respectively. Scaling of stigmatic papillae area with pollen requirements for successful pollination. Distribution of papillae varies notably: confined to style tip in pear style (Fig. 1(f)), extending basipetally in apple style (Fig. 1(b)), and colonizing about 2/3 of style in kiwifruit (Fig. 1(j)), liquid was observed on surface of fresh stigmas (Fig. S6). Because of self-incompatibility, most apple and pear cultivars require cross-pollination. Although kiwifruit possesses degenerate stamens, its pollen is non-viable, necessitating

strict cross-pollination. Anther senescence in these three plants is followed by dehiscence, releasing substantial amounts of pollen (Figs. 1(c), 1(g) and 1(k)). Interestingly, pollen morphologies are all characterized by elongated ellipsoid shape, bearing three equally spaced colpi on surface (Figs. 1(d) 1(h) and 1(l)).

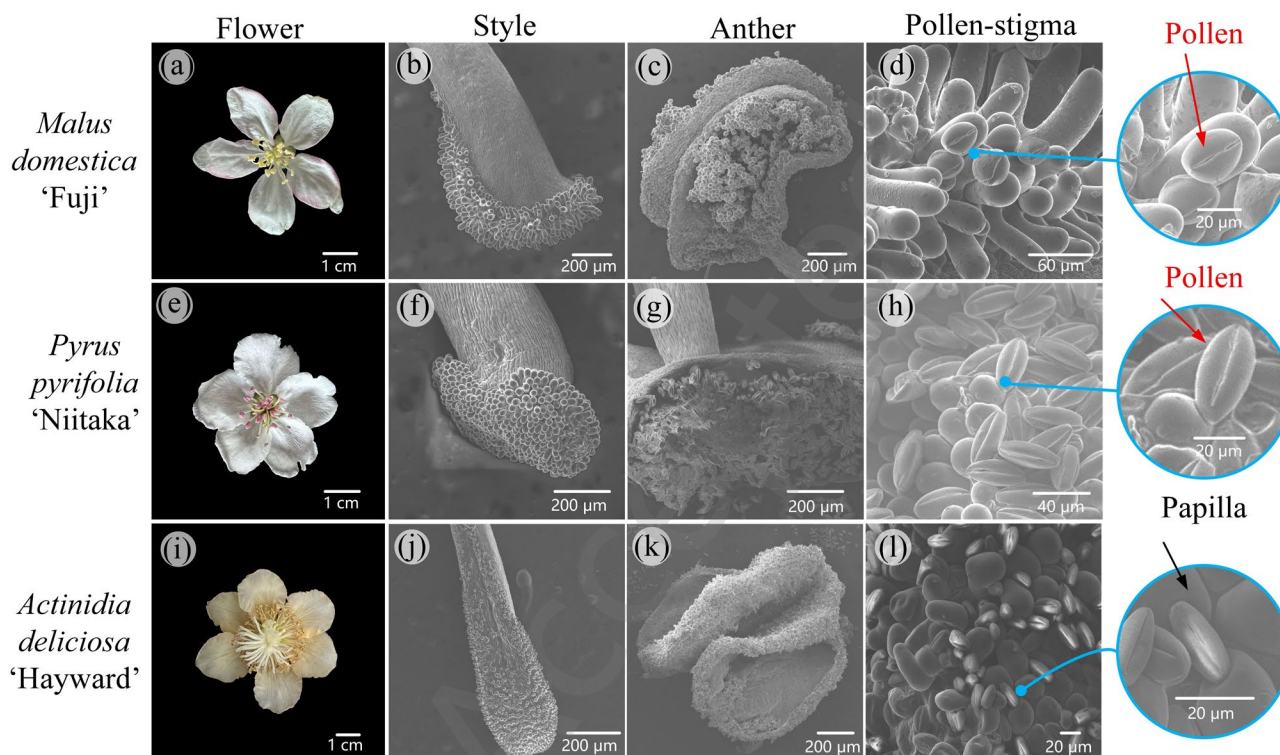


Fig. 1 Images of floral organs of apple (*Malus domestica* 'Fuji'), pear (*Pyrus pyrifolia* 'Niitaka'), and kiwifruit (*Actinidia deliciosa* 'Hayward'). (a, e, i) Flowers. (b, f, j) Styles. (c, g, k) Anthers. (d, h, l) Contact structure of pollen-stigma.

Adhesion structure at pollen-stigma interface correlates with the relative size between pollen and papillae. Apple pollen and papillae are similar in size (Fig. 1(d)); in pear, pollen exceeds papilla dimensions (Fig. 1(h)); while in kiwifruit, papillae are substantially larger than pollen grains (Fig. 1(l)). Nevertheless, consistent with the intrinsic adaptive traits of each plant's pollen-stigma compatibility (Fig. S7), distinct liquid was observed on papillae of apple and pear stigmas. Some pollen grains adhered to the papilla surfaces, while the rest were firmly held by capillary bridges formed by papillae, this phenomenon particularly evident in kiwifruit stigmas. Additionally, kiwifruit

possesses flexible papillae, and plastic deformation of papillae surface was observed upon contact (Fig. S7(c)).

3.2 Surface characteristics of pollen

Fresh pollen was collected and stored at -18°C , and washed pollen was prepared as described in Experimental Section. Prior to cryo-SEM observation sample surfaces were sputter-coated with 10 nm thick Au-Pd layer (LEICA EM ACE200). Before washing, pollen surfaces of apple and pear (both belong to Rosaceae subfamily) exhibited irregular textures; after washing, these surface textures became more distinct and displayed micropores that were absent on fresh pollen (Figs. 2(a) and S8(a)). While surface characteristics of kiwifruit pollen remained largely similar after washing, the dense surface coating observed initially was removed, and micropores that were absent on fresh pollen became apparent (Fig. S9(a)). We hypothesize that this plant-derived surface material is pollenkitt, a substance commonly found in entomophilous pollen [47], though no previous studies have reported the surface substance involved in this study. To verify this hypothesis, pollen surfaces were observed by confocal fluorescence microscopy (CLSM) (Fig. 2(b)). Since one of carotenoids (β -carotene) in pollenkitt exhibits autofluorescence with an excitation wavelength of 488 nm [48], images were captured before and after washing. Distinct fluorescence emitted by carotenoids was observed on all raw, untreated pollen grains, whereas pollen that had been washed to remove surface coating exhibited no fluorescence (Figs. 2(b), S8(b) and S9(b)). However, for a more definitive identification of pollenkitt, pollen was collected from unopened flowers directly into clean containers and analyzed immediately without frozen storage, Raman spectra were obtained for both washed pollen and pollen extracts (Figs. 2(c) S8(c) and S9(c)). Intense peak around 1370 cm^{-1} (CH_3 symmetric bending) observed in washed apple pollen (WAP), which is assigned to lipids, and the same peak was also detected in washed pear pollen (WPP) and washed kiwifruit pollen (WKP). Intense peaks around 2904 cm^{-1} and 2941 cm^{-1} (C-C stretching) only observed in Raman spectra of washed pollen, are assigned to carbohydrates [49]. Intense peaks (1004 cm^{-1} , 1520 cm^{-1} , 1150 cm^{-1})

of the Raman spectra of pollen extract are assigned to carotenoids, known component of pollenkitt [50]. This finding is consistent with observations from CLSM and cryo-SEM, demonstrating that the surface substances removed from pollen is pollenkitt. Furthermore, fourier transform infrared (FTIR) spectra of the three pollen samples were measured before and after washing (Fig. S10). It was found that washing did not alter main chemical structure of pollen, as all characteristic structural peaks indicated by arrows were retained. However, a decrease in peak area of specific amide bands in three pollen samples after washing indicates that the washing treatment removed lipids tightly bound to proteins.

In prior reported evidence, significant morphological differences were observed in ragweed, dandelion, and sunflower pollen before and after washing, where the treatment revealed more distinct microstructural features such as conical spines or grooves microstructures. Notably, dandelion pollen has been reported to possess a pollenkitt content as high as 60 wt% [24, 27]. Thus, we hypothesize that pollen investigated in this study contains a relatively lower proportion of pollenkitt. Cryo-SEM is insufficient for quantitative characterization of pollen surfaces, AFM was employed to quantitatively analyze surface roughness at the nanoscale, where $4 \times 4 \mu\text{m}$ areas on pollen surface were randomly selected for scanning. Surface of raw apple pollen (RAP) exhibits distinct groove microstructures (Fig. 2(d)), with a width ranging from 230 to 330 nm, the arithmetic mean roughness (Ra) is 51.09 ± 7.07 nm, and the root mean square roughness (RMS) is 64.73 ± 9.99 nm. After washing to remove pollenkitt, surface morphology of WAP becomes smoother (Fig. 2(e)), with an Ra of 30.2 ± 4.22 nm and an RMS of 38.56 ± 3.64 nm. The difference of surfaces between RAP and WAP is particularly evident in Fig. 2(g). Similarly, considerable alterations in surface roughness were observed in both pear and kiwifruit pollen following pollenkitt removal (Figs. S8(d), S8(e), S9(d) and S9(e)), with the most pronounced difference noted in kiwifruit pollen (Table S5).

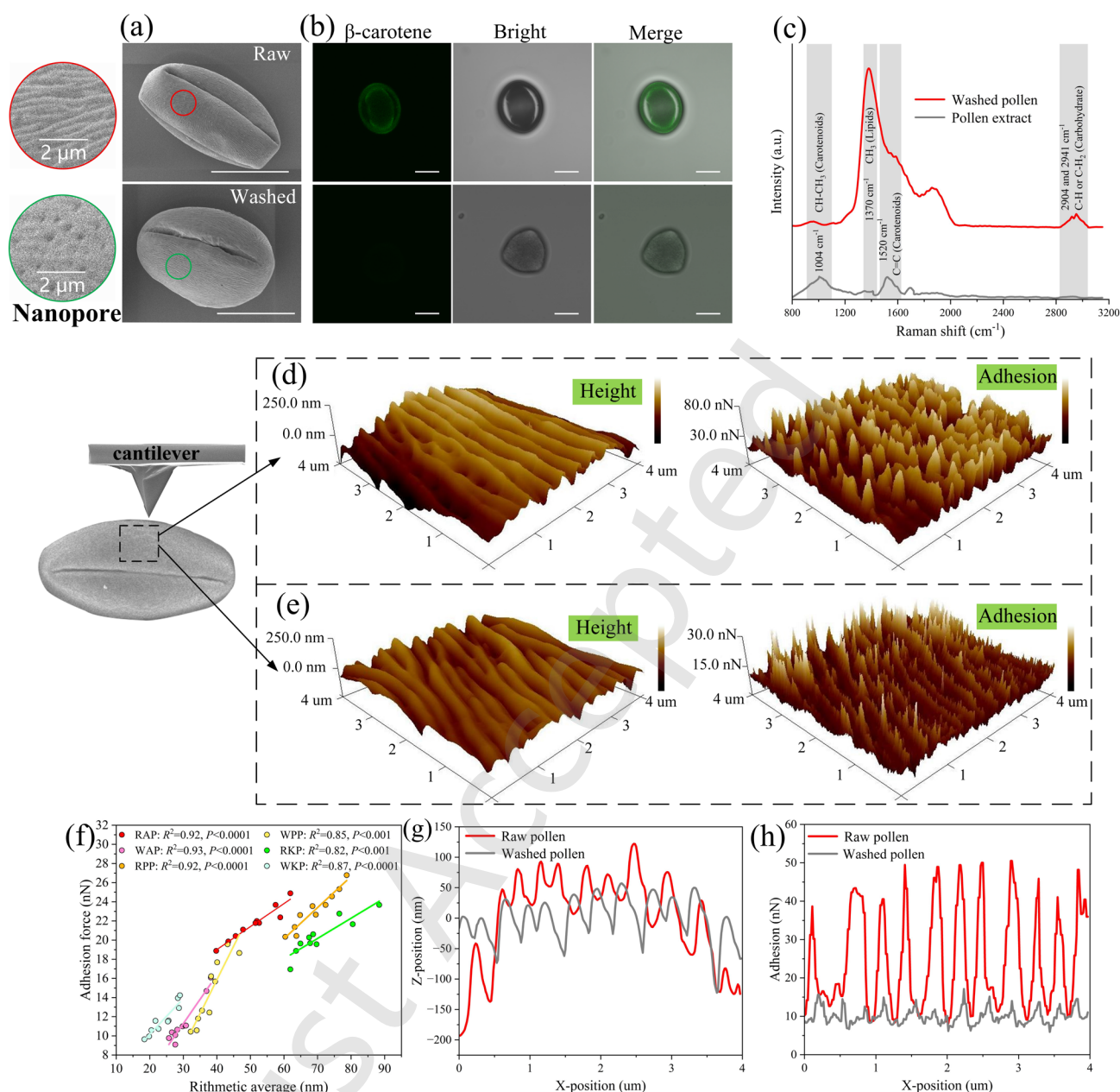


Fig. 2 Morphology and composition analysis of pollen surface. (a) Cryo-SEM images of apple pollen surface morphology before and after washing, pollen samples were sputter-coated with Au-Pd, bar is 20 μm . (b) Fluorescence micrographs of apple pollen before and after washing, bar is 20 μm . (c) Raman spectra of WAP and pollen extract, 785 nm laser excitation. Surface topography of RAP (d) and WAP (e), and adhesion force distribution between pollen and probe, 4 $\times$ 4 μm . (f) Relationship Between the arithmetic average roughness of pollen surface and adhesion force. (g) Comparison of surface roughness between RAP and WAP. (h) Comparison of adhesion force between (RAP and WAP) and probe.

After pollenkitt removal, microscopic undulations on pollen surface are significantly reduced, and more notably, a substantial change in adhesion force was observed. As illustrated by adhesion force distribution maps between apple pollen and probe (SNL-10), in RAP, adhesion force between surface protrusions and probe was approximately 50 nN, while it measured about 9 nN in groove valleys (Fig. 2(d)); for WAP, adhesion force at surface protrusions decreased to approximately 14 nN, and that in groove valleys was around 6 nN (Fig. 2(e)). Figure 2(h) provides an intuitive comparison of pollenkitt's contribution to adhesion force. Prior studies have reported that pollenkitt endows pollen with considerable viscosity [51], where this substance is also referred to as pollen wall or pollenkitt. After pollenkitt removal, adhesion force decreased by up to 47% in WAP and by at least 37% in WPP (Fig. S8(g)). Ten measurements of adhesion force between each pollen type and the probe were performed separately, revealing that adhesion forces of both raw and washed pollen demonstrated a dependence on surface roughness (Fig. 2(f)).

3.3 Measurement of pollen-stigma adhesion

To analyze the adhesion mechanism between pollen and stigma during pollination, pollen grains, as modified on tipless cantilever as described in Experimental section, were brought into contact with fixed stigma (Fig. 3(a)). Probe was retracted at a speed of 300 nm/s, while force was recorded as a function of distance. A typical force-distance curve is presented in Fig. 3(c), indicating that the curves overlap during probe approach to sample and retraction (stages 3-4 in Section S2 and Fig. S5), it can be confirmed that no significant plastic deformation occurred on the pollen surface. The long-distance retraction segment of force curve reveals characteristics of stretching of stigmatic papillae as pollen moves away and the thinning of liquid bridge [48].

Our previous study demonstrated that successful pollination is determined by pollen viability and stigma receptivity [4], and initial adhesion of pollen on stigmatic surface lays the foundation for these physiological processes. Therefore, we focused on adhesion strength at short time scales. Figure 3(d), 0 s indicates that pollen grains were immediately retracted after contacting stigma, while

subsequent time points (e.g., 5 s, 30 s, 60 s, 180 s) represent the duration of contact. In instantaneous contact (0 s), adhesion force between apple pollen and stigma was 80.96 nN (89.95 nN in pear pollen). With increasing contact duration (up to 3 minutes), adhesion force progressively increased in both cases. Interestingly, the most significant enhancement occurred within 60 s; for instance, apple pollen exhibited a 9.44% increase at 60 s compared to instantaneous contact (5.48% for pear). In contrast, when contact time was further extended by 120 s, adhesion force of apple pollen only increased by 4.45% (1.29% for pear). Based on observed trends in adhesion force, it can be preliminarily inferred that the initial pollination stage (<1 min) plays a decisive role in determining whether pollen grains remain adhered to stigma. This conclusion is also applicable to kiwifruit pollen, which exhibited a 50.79% increase in adhesion force within the first 60 s, followed by a mere 0.52% increase thereafter. Unlike the Rosaceae pollen, kiwifruit pollen underwent a wider range of force increase in 0~60 s (60.78~91.65 nN), and this phenomenon must be interpreted in conjunction with the distinctive surface characteristics. Surfaces of apple and pear pollen are densely covered with ridges (Figs. 2(d) and S8(d)). In adhesion force tests, brief pollen-stigma contact can be reasonably equivalent to contact between the most prominent ridge and stigmatic papilla, and adhesion force depends on ridge characteristics. Both apple and pear pollen show nearly identical force progression patterns with their respective stigmas. This functional similarity corresponds to their analogous surface patterns, a structural conservation within the Rosaceae family. Kiwifruit pollen surface features protrusions of varying sizes (Fig. S9(d)). With longer contact, more protrusions engage in adhesion process, and leading to a rise in adhesion force, the second jump observed in force curves between kiwifruit pollen and stigma confirmed our hypothesis (Fig. S11).

Given structurally complex nature of stigma, it is appropriate to substitute the stigma in Fig. 3(a) with substrates of distinct properties, to investigate composition of pollen-stigma adhesion, quantify the contribution of pollen-kitt, analyze dependence of pollen adhesion on relative humidity (RH) [37]. Fabricated as detailed in Experimental section, parameters of piranha-etched Si and PS-coated Si are

summarized in Table S1. Piranha-etched Si served as hydrophilic substrate (contact angle: $14.56 \pm 0.38^\circ$; Ra: 0.27 ± 0.03 nm; RMS: 0.89 ± 0.20 nm), while PS-coated Si functioned as hydrophobic substrate (contact angle: $94 \pm 0.49^\circ$; Ra: 0.88 ± 0.12 nm; RMS: 1.59 ± 0.15 nm). RH was maintained 15%~75% by placing AFM in a chamber filled with humidity-controlled N₂. Compared with pollen's surface characteristics, substrate with minimal roughness had a negligible impact on adhesion force. Adhesion force increased with RH for all three raw pollen. While van der Waals force prevailed under dry (15% RH) conditions [52], the combined effects of substrate's hydrophilicity from piranha-etched Si and the rising contribution of capillary forces enhanced adhesion at higher RH [53]. Although pollenkitt contributes significantly to adhesion (Figs. 2(d) and 2(e)), its removal surprisingly enhanced the adhesion force of pollen-Si. This counterintuitive result can be attributed to the larger surface features of washed pollen (Figs. 2(e), S8e and S9(e)), where the exposure sharper ridge crests or microprotuberances after washing likely increases the real contact area and thus the van der Waals contribution under dry conditions, which can outweigh the loss of viscous pollenkitt layer. The contribution of pollenkitt to adhesion is revealed by comparing the humidity-induced adhesion increase before and after washing treatment. For raw apple, pear, and kiwifruit pollen, adhesion at 75% RH increased by 52.94%, 55.89%, and 300.39%, respectively, compared to 15% RH. In contrast, washed pollen showed markedly smaller increases of 37.52%, 33.23%, and 99.18%. The adhesion of pollen-PS substrate differed significantly before and after washing. With pollenkitt present, adhesion force increased with RH, though remaining lower than that on piranha-etched Si. In contact of washed pollen-PS substrate, the non-wetting PS surface prevented capillary bridge formation even at high RH, and adhesion force was consistently dominated by van der Waals interactions. The hygroscopic properties of pollen clarifies this trend (Table S6). At 15% RH, single RAP grain measured 13.13 ± 0.24 ng versus 12.59 ± 0.32 ng for WAP; at 75% RH, masses reached 13.42 ± 0.31 ng and 12.69 ± 0.27 ng, respectively. Under high RH, raw pollen absorbed 2.9 times more moisture than washed pollen, which is consistent with pollenkitt's

role in limiting water loss during dispersal and transportation. Additionally, cryo-SEM images further confirm liquid bridge formation on raw pollen after 4 h deposition on Si wafers, showing clear pollenkitt transfer to the substrate (Fig. 3(j)), while the contact zone of washed pollen remained extremely clean (Fig. 3(k)).

Regarding practical orchard deployment, field microclimate variations significantly dictate pollen-stigma adhesion efficiency. Because the hygroscopic pollenkitt induces strong capillary forces that multiply adhesion at high RH (75%), pollination operations are best executed in the early morning or late afternoon under moderate temperatures and high moisture. Conversely, rapid evaporation during hot, dry middays prevents capillary bridge formation, leading to weak adhesion and high risks of wind-induced detachment. For arid orchards, activating a micro-misting system prior to pollination can artificially cool and humidify the canopy. This intervention leverages the pollenkitt's adhesion-boosting mechanism and promotes pollen germination [33, 34], thereby securing highly efficient pollen capture and successful fruit set [40, 43].

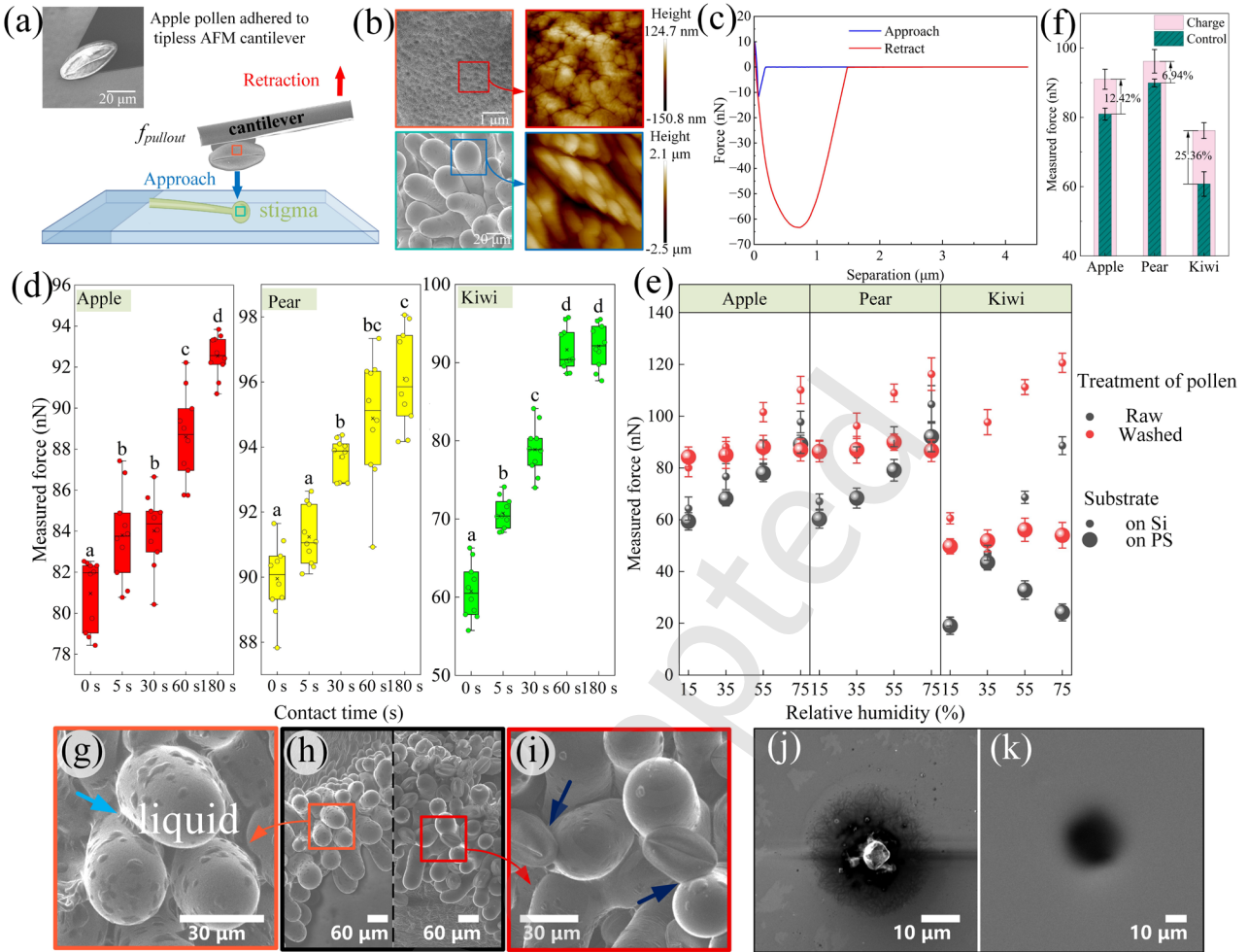


Fig. 3 Adhesion force measurement and analysis of pollen-stigma adhesive structures. (a) Schematic illustration of adhesion test using a pollen-modified tipless cantilever and stigma, the schematic diagram of the stigma is reproduced with permission from Figdraw. (b) Magnified view showing pollen and stigma surface morphology. (c) Schematic of AFM force curve (blue: approach; red: retract). (d) Adhesion force between pollen and stigma in apple, pear, and kiwifruit was measured as a function of contact time, specifically at 0 s, 5 s, 30 s, 60 s, and 180 s; Statistical differences were calculated by one-way ANOVA, different letters indicate statistically significant differences determined by Tukey's multiple comparison test ($P < 0.05$). (e) Adhesion force of apple, pear, and kiwifruit pollen, both before and after cleaning, was measured between piranha-etched silicon wafer substrates and polystyrene-coated substrates as a function of RH (15%, 35%, 55%, and 75%). (f) Comparison of adhesion forces between apple, pear, and kiwifruit pollen (before and after charging) and their respective stigmas. (g) Magnified view of stigmatic papilla. (h) Cryo-

SEM image of pollen-stigma adhesion. (i) Magnified view of the pollen-stigma interface. (j) Deposit of RAP on silicon wafer. (k) Deposit of WAP on Si wafer.

3.4 Composition analysis of adhesion force

3.4.1 Van der Waals force and capillary force

The contact geometry between pollen and interfaces is species-specific, determined by the dimensions and morphology of pollen surface features. Corresponding adhesion force is given by Eq. 1:

$$F_{adhesion} = F_{vdw} + F_{capillary} \quad (1)$$

where F_{vdw} is the van der Waals force of short-range contact, $F_{capillary}$ is the capillary force arising from the meniscus contact structure composed of pollen-medium-interface.

The densely distributed spherical protrusions on kiwifruit pollen form a characteristic sphere-on-flat contact geometry (Figs. S9(d) and S12(b)), and sufficient spacing allows van der Waals attractions between adjacent protrusions to be neglected [54]. Thus, the adhesion can be approximated using Hamaker model:

$$F_{vdw} = \frac{AR_{protrusion}}{6D^2} \quad (2)$$

where A is the material-dependent nonretarded Hamaker constant, taken as 8.5×10^{-20} J for pollen [27], D is the cutoff separation distance, taken as 0.165 nm, $R_{protrusion}$ is radius of protrusions on kiwifruit pollen. Statistically, value of $R_{protrusion}$ ranges from 30 to 50 nm, the calculated van der Waals force between a single protrusion ($R_{protrusion} = 40$ nm) and stigma is 20.08 nN. Washing reduces protrusion density (Fig. S9(e)) but increases $R_{protrusion}$ to around 120 nm, elevating the van der Waals force to 53.76 nN on piranha-etched Si and 54.60 nN on PS-coated Si (Section S3 and Table S7).

Pollenkitt filling the gap between pollen and stigma (Figs. 1(l) and S7(c)) results in a capillary force composed of surface tension and Laplace pressure component (Eq. 3). This force can be calculated based on meniscus geometry (Fig. 4a). Surface tension is given by Eq. 4.

$$F_{capillary} = F_{tension} + F_{Laplace} \quad (3)$$

$$F_{tension} = 2\pi R\gamma \sin \varphi \sin((\varphi + \theta_1)) \quad (4)$$

where R is the characteristic contact radius of pollen, its value equals $R_{protrusion}$, and γ is the surface tension of pollenkitt, taken as 45 mJ/m^2 , and θ_1 is the contact angle between pollenkitt and pollen surface, and φ is the filling angle of pollenkitt [27]. The Laplace pressure-induced force is determined by Eq. 5:

$$F_{Laplace} = \pi R_1^2 \Delta P \quad (5)$$

$$\Delta P = \gamma \left(\frac{1}{R_2} + \frac{1}{R_1} \right) \quad (6)$$

$$R_1 = R \sin \varphi \quad (7)$$

$$R_2 = \frac{D + R(1 - \cos \varphi)}{\cos(\theta_1 + \varphi) + \cos \theta_2} \quad (8)$$

where ΔP is the Laplace pressure, estimated by the Young-Laplace equation (Eq. 6), and R_1 is the azimuthal radius (Eq. 7), R_2 is the meridional radius (Eq. 8), and θ_2 is the contact angle between the pollenkitt and interface. Based on cryo-SEM images, pollenkitt spreading on stigma papilla exhibits acute angles, justifying our assignment of θ_1 as $10\text{-}30^\circ$, while the extreme conditions of 0° and 90° also evaluated. The maximum theoretically calculated capillary force is 24.82 nN (Fig. 4(b)), yielding a maximum resultant force of 44.9 nN , which is approximately one-third lower than AFM measurement (Fig. 3(d)). This discrepancy is considered reasonable, as the process of contact, separation, and recontact between pollen and stigma was observed via force-distance curves (Fig. S11). With a radius of $\sim 120 \text{ nm}$ (Fig. S9(e)), the protrusion of WKP produces a van der Waals force of 62.4 nN , the calculated value agrees well with the adhesion force measured at $15\% \text{ RH}$ (Fig. 3(e)). As RH increased, capillary forces provided an additional adhesive contribution (Fig. 4e). Notably, the van der Waals force depends on the Hamaker constant A [52, 54], as detailed in Section S4.

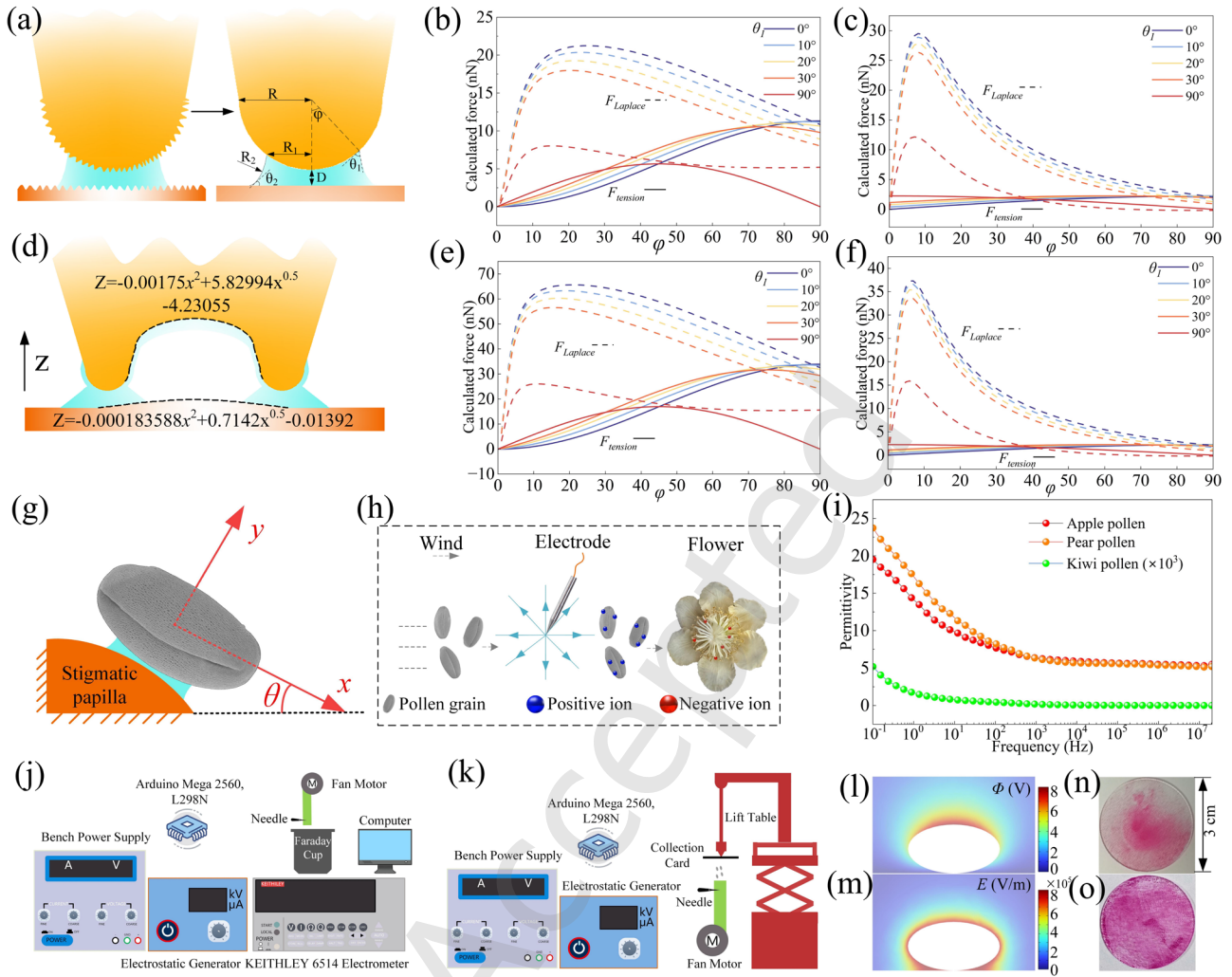


Fig. 4 Analysis of forces between pollen and various substrates. (a) Contact model of pollen surface microstructure and interface. (b) Calculated capillary force between a 40-nm-radius protrusion on kiwifruit pollen surface and substrate. (c) Calculated capillary force between a 15-nm-radius ridge on apple pollen surfaces and substrate. (d) Computational model for cavity suction at pollen-stigma contact interface. (e) Calculated capillary force between a 120-nm-radius protrusion on kiwifruit pollen surface and substrate. (f) Calculated capillary force between a 25-nm-radius ridge on apple pollen surfaces and substrate. (g) Contact model of pollen-stigma interaction for estimating viscous and electrostatic forces. (h) Schematic illustration of the pollen electrification principle. (i) Permittivity of apple, pear, and kiwifruit pollen over frequency range of 0.1 Hz to 1 MHz. (j) Schematic illustration of measurement for pollen charge quantification. (k) Schematic illustration of adhesion assessment for charged pollen. (l) Electric potential and (m) electric field intensity of charged pollen simulated by COMSOL. (n) Deposition of pollen without electrostatic treatment on collection card. (o) Deposition of pollen electrostatically treated on collection card.

Distinct nanoscale ridge structures were observed on surfaces of both apple and pear pollen, both before and after washing (Figs. 2(d), 2(e), S8(d) and S8(e)). Since the adhesion of a single ridge (radius R_{ridge}) is governed by van der Waals force, it can be modeled as a cylinder-on-plane interaction using Hamaker model (Fig. S12(a)):

$$F_{vdw} = \frac{A\sqrt{R_{ridge}}}{8\sqrt{2}a^{5/2}} \cdot L_{ridge} \quad (9)$$

where R_{ridge} is the radius of ridge-like structure on both apple and pear surface (determined by SEM and AFM), L_{ridge} is the length of ridge-like structure. Given their highly similar surface features, apple and pear pollen are discussed together. The average contact radius of ridge crests on RAP is 15.14 nm (approximately 25.24 nm after washing). Using Eq. 9, the van der Waals force for the raw pollen-stigma was estimated to be 67.17 nN. For WAP, corresponding forces with piranha-etched Si and PS-coated Si substrates were 73.1 nN and 74.2 nN, respectively which agree well with adhesion forces measured at 15% RH (Fig. 3(e)). The contact model in Fig. 4(a) is also applicable to estimating the capillary force between pollen ridges of apple or pear and the stigma (Eq. 10), where protrusion represents the cross-section of a ridge with radius R_{ridge} in contact with interface.

$$F_{capillary} = 2L_{ridge}\gamma \sin(\varphi + \theta_1) + \Delta PS_{ca} \quad (10)$$

where for a cylinder, $1/R_1=0$, thus, the Laplace pressure $\Delta P=\gamma/R_2$, and the projected contact area $S_{ca}=2R\sin\varphi L_{ridge}$. The increase in RH leads to calculated contribution of capillary force to adhesion (Figs. 4(c) and 4(f)). For pear pollen, the mean contact radius of the pollen ridge of RPP was 16.54 nm (approximately 24.21 nm for WPP). The combined forces of capillary force and van der Waals force before and after washing were 99.51 nN and 118.98 nN, respectively (Fig. S13), which are consistent with the measured values in Fig. 3(e), confirming that the calculated adhesion force values fall within a reasonable range.

It is reasonable to propose that the initial pollen-stigma adhesion determines whether physiological process of pollination can be initiated. 2 hours after pollination, robust adhesive structures were

observed on stigma (Fig. S7), and azimuthal radius and meridional radius were estimated from SEM images to be approximately 4000 nm and 300 nm, respectively, with a liquid bridge height of 800 nm. Van der Waals forces become negligible under such height. As elaborated in Section S4 (ESM), when separation distance exceeds 100 nm, the van der Waals force decreases by six to seven orders of magnitude, here, if adhesion force is dominated by capillary force, the value theoretically calculated using Eq. 3 is 1.244×10^4 nN, which is hundreds of times greater than pollen gravity, is sufficient to overcome pollen's own weight and keep it adhered to stigma. The force calculations above represent ideal values perpendicular to pollen-stigma contact surface. However, from a work perspective, separating the two normally against capillary force requires work ΔW . If an imaginary external force is applied to twist pollen away from capillary bridge until complete detachment, the path over which work is done equals the perimeter of capillary bridge contact line, required external force is 395.59 nN, which likewise far exceeds the pollen's own gravity, demonstrating the inherent adaptive design of pollen-stigma contact.

3.4.2 Suction force induced by pollen surface cavity

Above, the force analysis was based on AFM simulations of short-term contact between pollen and stigma or substrates. In following section, combined with SEM images, the forces present after pollen deposited on stigma under natural conditions are analyzed.

Considering the microstructures of apple and pear pollen surfaces (Figs. 2(d) and 8(d)) and morphology of pollen deposited on papillae after pollination (Figs. S7(a) and S7(b)), enclosed cavities are formed between them. Capillarity draws liquid into these cavities (Fig. 5(a)), and under the influence of gravity or adhesion, a partial vacuum can develop as air is displaced [55], which pulls pollen into tighter contact with papilla (Fig. 4(d)). Assuming a linear elastic deformation at pollen-contact surface:

$$V_{(p)} = V_0 + k(P - P_0) \quad (11)$$

where V_0 is the initial volume in cavity, and P is the air pressure in cavity, P_0 is the standard atmospheric pressure, taken as 101325 Pa, k is the volume deformation coefficient, $k=3(1-\nu)V_0/E$, E is the Young's modulus of pollen, taken as 3×10^8 Pa (via indentation test), ν is the Poisson's ratio, taken as 0.35. $P_0 \cdot V_0 = P_0 \cdot V_{(P_0)} = nRT = m_0/M \cdot RT$, $P \cdot V_{(P)} = m/M \cdot RT$, n is the amount of air, R is the air constant, m is the current air mass in the cavity, M is the molar mass of air. Pressure induced by cavity volume reduction is:

$$PV_{(P)} = \frac{m}{m_0} P_0 V_0 \Rightarrow P(V_0 - kP - kP_0) = \frac{m}{m_0} P_0 V_0 \quad (12)$$

$$P = \frac{-(V_0 - kP_0) + \sqrt{(V_0 - kP_0)^2 + 4k \frac{m}{m_0} P_0 V_0}}{2k} \quad (13)$$

Based on relatively regular ridge distribution on apple and pear pollen surfaces, and the topographic data of adjacent ridges and stigmatic papillae measured by AFM probe. The cross-sectional area of cavity on apple pollen was obtained via fitting contour profile as $4.6573 \times 10^3 \text{ nm}^2$ (Fig. 4(d)), for an assumed cavity length of 1000 nm, initial volume V_0 of cavity is $4.66 \times 10^{-21} \text{ m}^3$. The estimated suction force generated by the pressure difference induced by cavity volume variation are summarized in Table S8, which indicate that different degrees of volume reduction, the cavity are expected to produce a suction force of several nanonewtons. The cavity formed between adjacent ridge structures on the surface of pear pollen is shown in Fig. 5(b). Due to the size difference of the structures, the cavity can generate an attractive force of approximately 20 nN (Fig. 5(c)). Although volume variation in cavity could not be directly observed during the short-term contact in AFM tests, this hypothesis remains valid based on final three-phase contact structure of pollen on papilla.

The biomechanical mechanism of cavity-induced suction has also been documented in other biological adhesion systems. During investigations into the wet adhesion of the bee arolium, air pockets at the contact interface were directly visualized using SEM [55], leading to the formulation of a solid-liquid-gas three-phase interfacial model. That study elucidated that the pressure differential,

arising from volumetric changes of the gas within the sealed cavities, generates supplementary suction, thereby significantly enhancing the bee's attachment stability on vertical substrates. Despite morphological disparities between the hexagonal framework of arolium and ridge microstructures on pollen surface, the fundamental physical principle underlying suction generation remains identical: both depend on the pressure gradients within enclosed micro-cavities. This cross-species analogy lends indirect experimental credence to the pollen-papilla cavity suction model proposed herein, suggesting that microstructure-mediated cavity suction is likely a ubiquitous reinforcing mechanism across biological adhesion systems. **However, direct in-situ micro-pressure measurement of the cavity suction remains technically challenging and is an important subject for future research.**

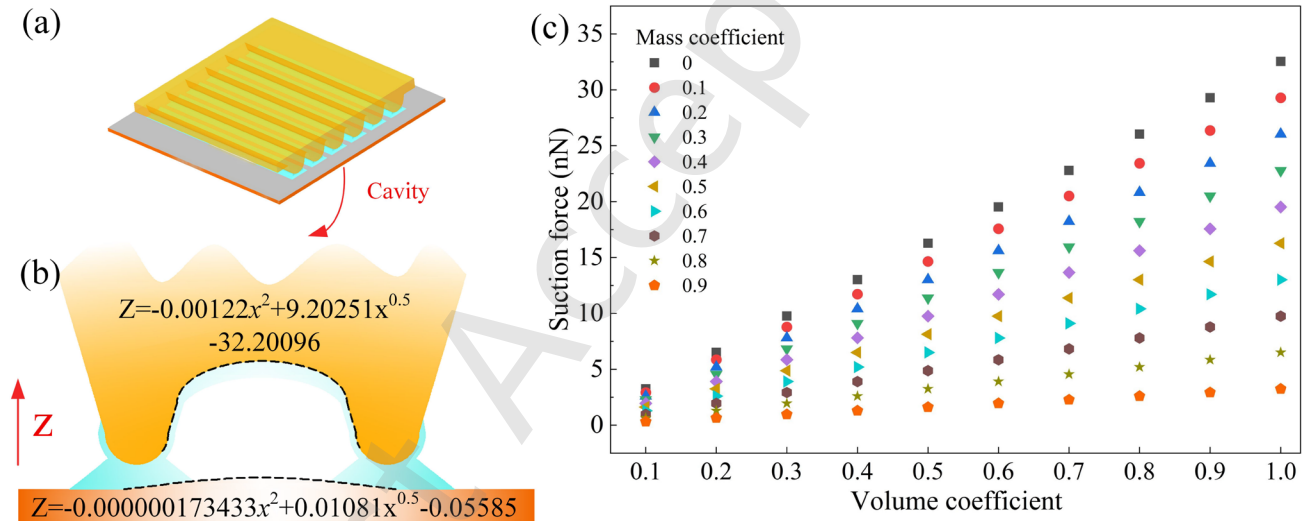


Fig. 5 Theoretical model of suction force induced by cavities generated by microstructures on pollen surfaces.

(a) Contact model between pollen and interface. (b) Cavities formed between pear pollen and the interface. (c) Calculated suction force induced by cavities on the pear pollen surface.

3.4.3 Viscous force of pollenkitt after pollen deposits on stigma

Considering the final state of pollen-stigma contact morphology after pollination, some pollen grains are firmly clamped by adjacent papillae (Figs. 3(i) and S7), while others adhere to papillae through limited contact areas. For this seemingly unstable contact pattern, we independently analyzed the viscous force mediated by pollenkitt (Fig. 4(g)). Pollen deposit on papillae with a spacing of δ , taking long axis of pollen as the x -axis, which forms an angle θ with the horizontal direction, and the

y -axis perpendicular to x -axis, the Navier-Stokes equation in x -direction simplifies under assumption of steady-state laminar flow of pollenkitt in a rectangular coordinate system to:

$$\rho(u_x \frac{\partial u_x}{\partial x} + u_y \frac{\partial u_x}{\partial y} + u_z \frac{\partial u_x}{\partial z}) = \rho f_x - \frac{\partial p}{\partial x} + \mu \nabla^2 u_x \quad (14)$$

According to actual scenario of pollen adhesion, we first develop a generalized flow model based on the following assumptions: pollenkitt is considered an incompressible Newtonian fluid; pollen grain is regarded as a rigid sphere undergoing constant-velocity translation along papilla surface; the flow is assumed laminar, with inertial effects neglected; a no-slip condition is applied at both papilla interface and pollen surface; and only gravitational and viscous forces are considered. Taking the inclined interface as a fixed reference frame, the pollenkitt flow varies exclusively in x -direction, i.e., $u=u(x)$, $u(y)=u(z)=0$. By applying this general model to the static equilibrium condition, where the relative velocity is set to zero, the viscous force resisting gravitational sliding can be estimated. Consequently, upon simplification of Navier-Stokes equations, under steady-state conditions where $\partial u/\partial t=0$, the momentum equation in the x -direction simplifies to:

$$\mu \frac{d^2 u}{dy^2} = \frac{\partial p}{\partial x} - \rho g \sin \theta \quad (15)$$

$$\tau(\delta) = \frac{\mu v}{\delta} - \frac{\rho g \sin \theta}{2} \delta \quad (16)$$

After pollination, adhesion between pollen and stigma is typically static, which differs from the repeated process of adhesion to detachment exhibited by bees or geckos on surfaces [6, 55]. Therefore, after pollen deposits on stigma, its velocity relative to pollenkitt is 0 ($v=0$), according to Eq. 16, shear stress acts in the opposite direction of x -axis (Fig. 4(g)) and is negative (Section S6 in the Electronic Supplementary Material (ESM)). Consequently, viscous force of pollenkitt prevents pollen from sliding down under gravity. The magnitude of viscous force is determined by the density of pollenkitt and spacing. From SEM image estimations, the liquid bridge between pollen-stigma has an azimuthal radius of 4000 nm, a meridional radius of 300 nm, and a height of 800 nm, using a pollenkitt density of 948 kg/m³ [48], and an inclination angle $\theta=20^\circ$, the viscous force resisting

pollen sliding is calculated to be 4.787 pN. When the pollenkitt viscous model is re-derived using power-law and Bingham constitutive equations, the shear stress at the pollen surface remains invariant (Eqs. 16, S19, and S24). This is because, during static contact between pollen and stigmatic papillae ($v=0$), the shear stress is completely independent of non-Newtonian rheological parameters. Consequently, the non-Newtonian characteristics of the pollenkitt do not alter the magnitude of viscous force. **It should be noted, however, that this conclusion applies strictly to the static pollination status, for dynamic scenarios involving high-speed pollen impact or sliding motion, the non-Newtonian rheological properties of pollenkitt should be taken into account.**

Notably, the adhesion force (comprising Van der Waals and capillary forces) between the pollen-stigma acts as normal force at contact interface (also known as the pull-off force), which maintains a firm attachment between them. The static viscous force of pollenkitt is four orders of magnitude smaller than both the AFM-measured adhesion force and pollen gravity, being profoundly smaller than the tangential component of gravity at contact interface, this minimal viscous resistance implies that the pollen grain can undergo gravity-driven micro-adjustments to smoothly achieve the optimal position and orientation for germination.

3.4.4 Electrostatically enhanced adhesion

In this study, corona charging was selected to electrify pollen grains (Fig. 4(h)). High voltage generates an ion field around the sharp electrode, any passing pollen acquire charge through ion bombardment [56]. The saturation charge of pollen is given by Eq. 17 [39]:

$$q = \frac{3\varepsilon_r}{\varepsilon_r + 2} 4\pi\varepsilon_0 R_p^2 E_0 \quad (17)$$

where is the ε_r relative permittivity of pollen, which was measured using Novocontrol Concept 80 (Novocontrol Technologies, Germany) on pelletized pollen samples (Fig. 4(i)), R_p is the equivalent radius of pollen grains, ε_0 is the vacuum permittivity, E_0 is the applied electric field intensity. Using Eq. 17, with an applied electric field of 4×10^5 V/m, the calculated saturation charges for apple, pear, and kiwifruit pollen are 1.85×10^{-14} C, 1.74×10^{-14} C and 1.12×10^{-14} C, respectively. To measure the

actual charge of pollen, a measurement system was constructed (Fig. 4(j)). An electrostatic generator (Zhaoqing Hechuang Technology, China) was connected to a sharp needle to generate a high-voltage electrostatic field, an adjustable power supply provided electricity to the Arduino Mega 2560, L298N, and a fan, which blew pollen through electrostatic field, and charged pollen subsequently fell into a Faraday cup, and measured using a KEITHLEY 6514 Electrometer (Keithley Instruments, Cleveland, OH, USA). The measured actual charges for a single apple, pear, and kiwifruit pollen grain were $(1.56 \pm 0.02) \times 10^{-14}$ C, $(1.05 \pm 0.01) \times 10^{-14}$ C, $(1.11 \pm 0.02) \times 10^{-14}$ C, respectively.

$$n \cdot D = \rho_q \quad (18)$$

$$D = \varepsilon \cdot E \quad (19)$$

$$-n \cdot (\varepsilon \nabla \phi) = \rho_q \quad (20)$$

Assuming a uniform charge distribution on pollen surface, the charge density ρ_q is given by q/S . By combining Gauss's law (Eq. 18), the constitutive equation relating the electric displacement vector D and the electric field intensity E (Eq. 19), and the electric potential equation (Eq. 20), while setting the electric potential of papilla $\phi=0$ (grounded), the electric potential field can be calculated. Then, electric field on pollen surface is derived from the fundamental relationship between electric field and electric potential $E=-\nabla\phi$. As illustrated in Fig. 4(g), a small portion of pollen adheres to papilla via contact with pollenkitt, while the remaining portion is exposed to air. Here, approximating charged pollen as a point charge and calculate electrostatic force using Coulomb's law is no longer appropriate. According to the Maxwell stress tensor formula, the i -th force component acting on the medium can be calculated by integrating the Maxwell stress tensor T_{ij} over the surface S [38].

$$F_i = \varepsilon \oint_S T_{ij} n_j dA = \varepsilon \int_S (E_i E_i - \frac{1}{2} \delta_{ij} E_i E_j) n_j dA \quad (21)$$

Based on aforementioned contact model and boundary conditions, simulations of electrical potential (Fig. 4(l)), electric field (Fig. 4(m)), and electrostatic adhesion force between charged pollen and

papilla were performed using COMSOL Multiphysics software. Simulated electrostatic forces between charged pollen (apple, pear, and kiwifruit) and papillae were 13.59 nN, 9.85 nN, and 18.19 nN, respectively. These values are slightly higher than the electrostatic contribution to adhesion force measured via AFM (Fig. 3(f)). This discrepancy is presumably attributed to charge transfer occurring during the contact between the pollen-modified probe and papilla in AFM measurements.

To validate the beneficial effect of electrostatic force in pollen adhesion, a charged pollen collection system (Fig. 4k) was established, enabling precise control of pollen spraying at 1 mg or 2 mg per discharge, and charged pollen was blown towards a collection card mounted on a lifer (Figs. 4(n) and 4(o)), and deposition rates were statistically compared before and after charging. In pollination experiments, since the successful pollination of kiwifruit requires a pollen quantity a hundred times greater than that of apples and pears, collection cards (Figs. 4(n) and (o)) were sized at 3 cm, which was determined based on style region of kiwifruit flowers (Fig. 1(i)). In present study, apple and pear pollen exhibit a pale yellow color, while kiwifruit pollen is milky white, making it difficult to observe on collection card, therefore, lycopodium powder was used in spraying tests. In our previous study, we optimized the structural design of the pollinator and performed pollen deposition experiments, the deposition rate of uncharged pollen was 34.69%, with more deposited in the center (Fig. 4(n)); in contrast, deposition rate of charged pollen reached 76.35% and exhibited a uniform distribution (Fig. 4(o)). For the field validation of electrostatic pollination, kiwifruit was chosen because its successful pollination requires a much higher pollen load than the other two investigated species [44-46]. Pollen trajectories were captured using a custom-built pollen particle tracking system equipped with a high-speed camera (Revealer S1315) operating at 5000 frames per second (Fig. S14). By first focusing the macro lens on pollinator outlet, the flight behavior of pollen particles exiting tube was evaluated, and an airflow velocity of 3 m/s was identified as the optimal operating condition for stable pollen delivery (Fig. S15). Subsequent imaging focused on the flowers allowed continuous visualization of pollen capture by flower surface. Rflow-based analysis of the

mean velocity field showed that, in absence of electrostatic charging, pollen particles were more strongly dispersed and were more readily transported away by the airflow along petals (Figs. S16(a) and S16(b)). This dispersion became particularly evident after pollen reached flower, as pollen on both lateral sides gradually moved away from flower surface under non-electrostatic pollination (Fig. S17). By contrast, electrostatic pollination promoted pollen retention through electrostatic attraction between charged pollen and flower, thereby improving pollen capture (Fig. S18). Deposition imaging further confirmed that electrostatic pollination produced substantially greater particle deposition on flowers, especially in the stigma region (Fig. S19), a distribution pattern favorable for fertilization and fruit set [40, 43]. Quantitative analysis further showed that electrostatic pollination improved pollen-use efficiency by more than 29% on average relative to non-electrostatic pollination (Section S7 in the ESM). **However, that this method has inherent limitations: pollen loss may occur during flower collection, style excision, and transfer to weighing paper, thereby introducing measurement errors.**

It should be noted that the current study focuses on three specific fruit species (apple, pear, and kiwifruit), which presents a limitation in sample diversity. While these species effectively represent two distinct types of surface microstructures (ridge structures and microprotuberances) to establish the foundational adhesion models, the universality of proposed bioadhesion mechanisms requires further validation. Future investigations incorporating a broader spectrum of crop samples, such as pollen with reticulate or echinate ornamentations, species with differing pollenkitt capacities (e.g., anemophilous vs. entomophilous plants), and fruits from other diverse taxonomic families, will be essential. Such expansions will help refine the mechanical models and confirm broad applicability of these physicochemical and electrostatic adhesion principles across different agricultural systems.

4 Conclusions

In this paper, we selected three economically vital fruit species with wide global distribution (apple, pear, and kiwifruit), to investigate pollen-stigma adhesion mechanism, the contribution of pollenkitt

to adhesion, and the influence of relative humidity. Meanwhile, we quantified the adhesion force of pollen-stigma through experiments and theoretical calculations, and discussed the potential forces involved. Within the same species, pollen and stigma adhere effectively, pollen grains can be clamped by adjacent papillae, and more importantly, can deposit on stigmatic surface through minimal contact area with papillae. The dominant adhesion forces evolve over time, following initial contact, the formation of robust capillary bridges provides immense adhesion force that far exceeds the pollen's own gravity; viscous force of pollenkitt is significantly lower than the adhesion force and pollen gravity, which allows pollen to smoothly fine-tune a suitable position and angle on stigma for germination, demonstrating a highly adaptive biological design for reliable pollination. The cavity-induced suction further enhance the binding strength between pollen-stigma. Electrostatic forces contribute significantly to adhesion, the application of electrostatic charge remarkably enhances pollen-stigma adhesion forces. Additionally, charged pollen exhibits improved viability and a more uniform, edge-dense distribution, which is highly advantageous for targeting papillae concentrated at the stylar apex. In conclusion, this work characterized the physicochemical properties of pollen, providing valuable data for biomaterials research. We elucidated adhesion mechanism underlying fruit tree pollination, this static adhesion strategy derived from nature holds promise for application in pollen removal from the air and asthma prevention. Meanwhile, the findings offer potential value across mechanistic elucidation, model establishment, agricultural technology, and ecological environmental management.

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Author contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by [Junyu Sun], [YanJun Fang] and [Liyu Chen]. The first draft of the manuscript was written by [Junyu Sun] and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

The data that support the findings of this study can be downloaded from xxxxxxxx / are available from the corresponding author upon reasonable request.

Competing interests

The authors have no competing interests to declare that are relevant to the content of this article.

Electronic Supplementary Material (ESM)

Electronic Supplementary Material: Supplementary material (add a brief description) is available in the online version of this article

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