

参赛学生姓名: Meihui Ding

中学: International Department, The

Affiliate High School of SCNU

省份: Guangdong

国家/地区: China

指导老师姓名: Jianing Wu, Yuli Luo

指导老师单位: Sun Yat-Sen University School

of Advanced Manufacturin

论文题目: Discrete Topological Structure and

Dispersal Capability of Spathodea campanulata

Seeds

Discrete Topological Structure and Dispersal Capability of *Spathodea campanulata* Seeds

Meihui Ding

Abstract

Wind dispersal of plant seeds is a key ecological process for maintaining population connectivity and promoting species expansion. As one of the world's top 100 invasive species, the flame tree (*Spathodea campanulata*) possesses winged seeds with significant potential for long-distance dispersal; however, the relationship between seed morphological variation and dispersal function within a single fruit remains unclear. This study used *Spathodea campanulata* seeds to systematically investigate the spatial organization of seed morphology within a seed pod, revealed the regulatory mechanism by which roundness influences flight patterns and dispersal distance, and achieved programmable dispersal distribution of artificial seeds based on this mechanism.

The study first quantified the roundness coefficient (C) of seeds at six layers (L1–L6) within the seed pod through standardized image acquisition and contour extraction. The results showed that seed roundness exhibited a monotonically increasing gradient from the outer to

the inner part of the seed pod ($C_{L1} = 0.791 \rightarrow C_{L6} = 0.849$), exhibiting a structured morphological characteristic of “square on the outside, round on the inside.” Free-fall experiments revealed significant differences in the horizontal dispersion distance among seeds at different layers. Through trajectory analysis, two typical flight modes were identified: disordered tumbling and stable gliding; By solving an overdetermined system of linear equations, we determined that the average roundness in the disordered state was 0.78, while in the gliding state it was 0.89; furthermore, the average dispersion distance in the gliding state (33.71 cm) was significantly greater than that in the disordered state (20.19 cm), thereby establishing a causal chain of “roundness $\rightarrow$ flight mode $\rightarrow$ dispersion distance.”

To validate this causal chain and eliminate the interference caused by the asymmetry of natural seeds, this study used the average contour of natural seeds as a reference and employed a hybrid process combining 3D printing with laser cutting to fabricate artificial seeds that differed only in their roundness ($C=0.78$ and $C=0.89$). Scattering experiments confirmed that the artificial seeds successfully replicated both the chaotic and gliding flight modes and their dispersion distributions. By fitting the data on landing points at multiple heights to a Weibull distribution, a predictive model was established in which the scale parameter increases linearly with height; in mixed-release experiments involving artificial

seeds in different flight modes, the model's predicted frequency distribution of mixed releases highly matched the actual landing points observed in the experiments. These results constitute a complete closed-loop validation, demonstrating that by designing passive flying vehicles with specific geometric features and adjusting their mixing ratios, it is possible to pre-calculate and precisely control the landing distribution of large-scale deployments. This provides a theoretical reference for the programmable control of the overall landing distribution of large-scale distributed passive flying sensors.

Keywords: Flame Tree, roundness coefficient, flight mode, Weibull distribution, 3D printing, laser cutting, programmable control

Table of Contents

Abstract	1
1. Background	5
2. Materials and Methods	8
2.1 Seed Collection and Extraction	8
2.2 Extraction of Seed Contour Data	12
2.3 Scattering Data Collection	14
2.4 Artificial Seed Fabrication	17
3. Results and Analysis	19
3.1 Layered Structure of Seed Pods, Morphological Gradients, and Diffusion Distance	20
3.2 Relationship between Roundness, Flight Pattern, and Dispersal Distance	23
3.3 Programmable Control of Artificial Seed Replication and Dispersal Distribution	28
4. Discussion and Outlook	34
4.1 Aerodynamic Mechanism of How Roundness Controls Flight Mode	34
4.2 Outlook	37
References	40
Acknowledgments	42

1. Background

The long-distance dispersal of plant seeds is a crucial ecological process for completing the plant life cycle, maintaining population connectivity, and promoting species expansion ^{[1][2]}. Among the various dispersal agents, wind plays a significant role in transporting seeds to locations far from the parent plant through horizontal air currents, turbulence, and updrafts, making it one of the key natural agents for plant long-distance dispersal ^{[3][4][5][6]}. To adapt to wind dispersal, plants have evolved a rich variety of seed or fruit appendages (Fig. 1). Among these, winged seeds typically possess flat, lightweight wing-like structures that increase aerodynamic lift, reduce settling velocity, and prolong time in flight, thereby enhancing the seeds' potential for horizontal dispersal ^{[7][8][9]}.



Figure 1. Typical Winged Seed Morphologies

Previous studies on wind dispersal of seeds have largely focused on interspecific comparisons, examining how parameters such as seed mass, projected area, wing lift, and settling velocity among different plant species influence dispersal distance or flight trajectories ^{[10][11][12][13][14]}. In contrast, relatively little attention has been paid to morphological differences among seeds within the same species, or even within the same plant or the same fruit ^[15]. In fact, seeds produced by the same plant are not entirely uniform; seeds within the same fruit or pod often exhibit variation in size, mass, and shape. However, such intraspecific or intraindividual morphological differences have yet to be specifically incorporated into the analytical framework in many studies ^[15].

The flame tree (*Spathodea campanulata*, also known as the African tulip tree) is a highly invasive tropical tree species (Fig. 2A) listed by the IUCN Invasive Species Specialist Group as one of the “World’s 100 Most Invasive Alien Species” ^{[16][17]}. Flame tree seeds are relatively light and possess broad, membranous wings on their outer surface, relying primarily on wind for dispersal ^[18]. Previous studies have estimated the dispersal distance of its seeds; results indicate that under the strong trade winds of Tahiti, seeds released by a single flame tree located on a steep cliff edge may traverse the entire island of Tahiti ^[19]. Further regional atmospheric trajectory simulations also indicate that this species has significant potential for interregional and even inter-island dispersal, with

the model predicting a maximum dispersal distance of up to 1,364 km ^[20].

These characteristics make the flame tree an ideal model for studying the mechanisms of wind-mediated dispersal of membranous-winged seeds.



Figure 2. (A) *Spathodea campanulata* tree. (B) Seed pods of *Spathodea campanulata*. (C) Seeds of *Spathodea campanulata*.

In our preliminary observations, we found that seeds within the same pod of the flame tree (Fig. 2B) exhibit significant individual variation in planform morphology: some seeds are nearly square, while others exhibit a higher degree of circularity (Fig. 2C). This stable morphological diversity raises a core scientific question: Do morphological differences among seeds within the same pod correspond to different wind-dispersal capabilities? If such a correlation exists, what qualitative relationship governs the relationship between seed geometry and horizontal dispersal distance? Can we utilize this qualitative relationship to achieve preliminary control over the dispersal patterns of micro-passive flying vehicles?

To address these questions, this study proposes the following hypothesis: Since flame tree seeds are ultra-thin (average thickness $4\ \mu\text{m}$) planar structures, we hypothesize that the seeds' planar geometric characteristics are the key physical variables influencing their horizontal dispersal distance, and that this influence is achieved by regulating the seeds' flight patterns. To test this hypothesis, we designed a systematic research approach comprising “morphological quantification—stratified dispersal—flight pattern induction—geometric parameter extraction—artificial seed replication,” aimed at revealing the intrinsic relationship between the morphological variation of flame tree seeds and wind-driven dispersal efficiency, elucidating the potential dispersal functions of the internal morphological diversity within seed pods, and providing a theoretical basis for the aerodynamic design of biomimetic passive micro-air vehicles.

2. Materials and Methods

2.1 Seed Collection and Extraction

The flame tree seed pods required for this study were collected in mid-June 2025 from plants in the green belts of urban parks surrounding the Shenzhen Campus of Sun Yat-sen University. Flame trees are widely cultivated in this region as ornamental street trees, with a sufficiently large population to facilitate systematic sampling. During collection,

specialized landscaping high-reach pruners (with an extended telescoping pole, maximum extension length approximately 5 m) were used to cut intact seed pods attached to branches at various heights (Fig. 3A). To prevent seed loss from interfering with subsequent experiments, this study collected only seed pods with intact, uncracked pericarp.

The collected seed pods were elongated and boat-shaped, resembling slightly curved bananas, with lengths ranging from 20 to 30 cm. Maturity could be clearly distinguished by surface color: immature seed pods were bright green, with smooth, firm skin (Fig. 3B); mature seed pods were grayish-black, with dry, hardened pericarp (Fig. 3C). Some overripe seed pods had naturally split along the dorsal suture, exposing the seeds inside; such pods were excluded during collection. To preserve the freshness of the seed pods and seeds as much as possible, the collected seed pods were immediately placed in breathable sampling bags and transported to the laboratory within one hour.

Upon arrival at the laboratory, mature grayish-black seed pods with intact, uncracked pericarp were selected for seed extraction (Fig. 3D).

Before extracting the seeds, the seed pods were allowed to split naturally to minimize mechanical damage to the seeds caused by manual removal.

To facilitate natural splitting, the mature seed pods were placed in a constant-temperature forced-air oven for drying. The drying temperature is set to 45 °C , with a duration of 48 h. Under these conditions, the

lignified pericarp of the seed pods gradually loses water and shrinks, naturally splitting along the dorsal suture, and the seeds inside are gradually exposed as the pericarp splits open (Fig. 3E). This gentle drying protocol effectively induces the seed pods to burst while avoiding damage to the morphology of the seed wings caused by high temperatures.

After baking and bursting, the seed pod pericarp has naturally split along the dorsal suture, but some seeds remain enclosed within the seed coat. Gently pry open the pericarp along the crack with both hands to expose the multiple layers of seeds attached to the central midrib. Then, using pointed forceps, peel away the septal tissue layer by layer, starting from the outermost layer (Fig. 3F). Each layer of seeds is interconnected by thin wings, forming a natural layered structure. During the procedure, grasp the edge of the septum with forceps and gently remove the entire layer of seeds, along with the connecting tissue, transferring it to a sheet of white paper. The advantage of this method is that each extracted seed layer retains its original interconnected state, and the relative spatial arrangement of seeds within each layer is fully preserved, allowing for clear tracing of the original attachment position of each seed within the seed pod. During the peeling process, each layer is immediately labeled with its sequence number (designated L1, L2, ..., L6 from outer to inner) to ensure clear and traceable attribution of the interlayer spaces.

The extracted seeds were transferred to sealed specimen boxes and stored at room temperature away from light to prevent condensation from affecting the morphology of the seed wings. In this study, 9–10 morphologically intact seeds were selected from each of the six layers for subsequent contour parameter extraction and free-fall experiments. All samples retained their original layer numbers, allowing for a one-to-one correspondence between image measurement data, landing point data, and spatial positions within the seed pod for each individual seed.



Figure 3. (A) Harvesting *Spathodea campanulata* seed pods at high altitudes. (B) Immature seed pod. (C) Mature seed pod. (D) Seed pod before baking. (E) Seed pods after baking. (F) Layer-by-layer extraction of seeds.

2.2 Extraction of Seed Contour Data

To accurately quantify the planar geometric morphology of seeds, this study established a standardized contour data extraction workflow consisting of “image acquisition—grayscale conversion—threshold segmentation—boundary selection—coordinate extraction.”

The seeds to be tested were laid flat on a white background with their flat surfaces facing upward, ensuring they were neither curled nor folded. A flat-surface image of each seed was captured using the macro mode on a smartphone. When acquiring each raw image, a physical scale bar was placed in the same imaging plane as the seed being tested and recorded simultaneously (Figure 4A).

After importing the images into ImageJ, the “Set Scale” calibration was first performed based on the pixel length corresponding to the scale bar in the image to establish a conversion relationship between pixel units and actual length, thereby ensuring that measurement results for different seed images have consistent physical dimensions.

Next, the acquired color images were imported into ImageJ 1.54p software. First, the command Image → Type → 8-bit was executed to convert the RGB color images into 8-bit grayscale images (Fig. 4B). This step compresses the brightness value of each pixel in the image into the grayscale range of 0–255, providing single-channel brightness

information for subsequent threshold segmentation and eliminating the interference of color information on boundary recognition.

Next, the Image → Adjust → Threshold command is executed to perform threshold segmentation on the grayscale image (Figure 4C). By adjusting the upper and lower threshold limits, the seed region (target) is separated from the background: pixels below the threshold are classified as background (black), while those above the threshold are classified as the seed region (white).

After threshold segmentation is complete, the "Analyze → Analyze Particles" function is used to detect connected regions. The software automatically identifies and selects the outer contour boundary of the seed region (Figure 4D).

Once the boundary is selected, execute Analyze → Analyze Particles; the software will automatically generate a sequence of two-dimensional coordinates for each pixel along the contour boundary (Figure 4E). This coordinate sequence is exported in text format and contains the (x, y) pixel coordinates of each point on the boundary, which are used for the calculation of the roundness coefficient.

Through the above process, this study extracted a complete dataset of contour coordinates from approximately 60 seeds across six layers (L1–L6). All data were archived by layer and individual ID to ensure

layer-by-layer correspondence with the drop point data from the scattering experiment.

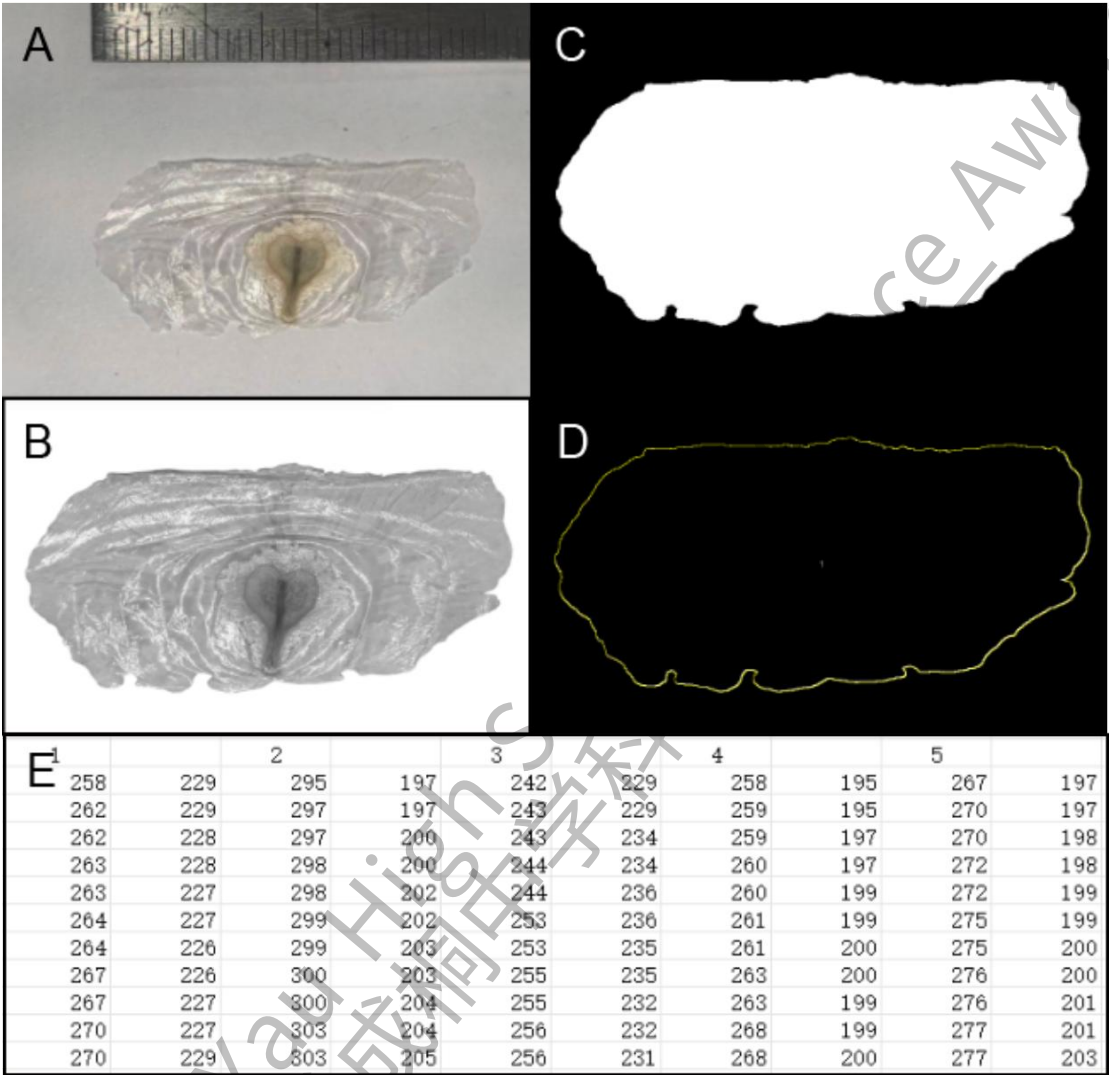


Figure 4. (A) High-resolution photograph of a seed. (B) 8-bit grayscale conversion. (C) Threshold segmentation. (D) Boundary selection. (E) Contour coordinate data.

2.3 Scattering Data Collection

To quantify the horizontal dispersal capacity of seeds with different geometric shapes, this study established a standardized indoor, windless free-fall testing platform. The experiment was conducted in a sealed laboratory; doors, windows, and ventilation systems were shut off during

the experiment to minimize interference from environmental airflow on the falling trajectories. A fully enclosed tent was set up inside the laboratory to serve as the experimental area, with the release point located at its center; the vertical projection of this point on the floor served as the origin for horizontal displacement measurements(Figure 5A). During release, the experimenter used tweezers to pick up a single seed, placed it at the release point, ensured the seed remained in a horizontal orientation, and then released it, allowing it to fall freely from a state of rest. After each seed was released, the experimenter waited until it had completely landed and come to rest before releasing the next one, to avoid interference from collisions between seeds in the air or on the ground.

After the seeds landed, red circular markers (30 mm in diameter) were first placed at all landing points to mark their locations. Next, a 1.0-meter-long standard ruler was placed within the experimental area to serve as a reference for subsequent image scale conversion. The complete distribution of landing points was captured using a top-down photographic approach. The camera was mounted approximately 2.0 meters directly above the release point, with the optical axis perpendicular to the ground and the field of view covering the entire area of seed landing points as well as the ruler. During shooting, the camera position was kept level to minimize positional measurement errors caused by image distortion.

The top-down images were first imported into ImageJ for processing. A “Set Scale” calibration was performed based on the pixel length corresponding to the 1.0 m ruler in the image to establish a conversion relationship between pixel units and actual length. Subsequently, the vertical projection of the center of the release point on the ground was marked as the coordinate origin $(0,0)$. The center of each red-marked circle was clicked in sequence, and the pixel coordinates of that landing point relative to the origin were recorded. ImageJ’s “Measure” function automatically output the true coordinates (x,y) of each landing point.

The coordinate data for all landing points were exported in text format and imported into MATLAB for subsequent analysis and visualization (Figure 5B). Each layer of seed particles corresponds to a set of landing point coordinate data; combined with their morphometric data, this establishes a database of correspondences between “layer position—morphometric parameters—landing point coordinates.” This dataset is used for subsequent calculations of diffusion distance, plotting probability density distributions, and statistical modeling analysis.

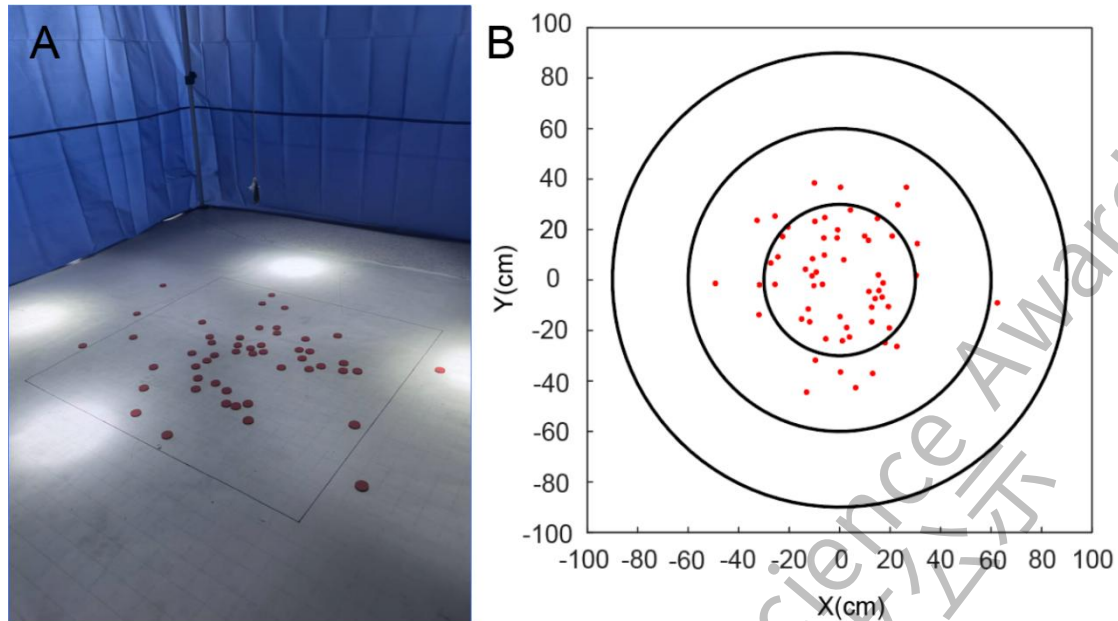


Figure 5. (A) Drop-test site diagram.

(B) Scatter plot of landing positions generated in MATLAB.

2.4 Artificial Seed Fabrication

To independently verify the causal effects of geometric features on flight patterns and dispersal distance, and to eliminate confounding factors associated with natural seeds—such as mass, density, thickness, and surface texture—this study employed a hybrid process combining PLA printing and laser cutting to fabricate artificial seeds. This approach allows for independent control of the seeds' planar geometric contours and internal mass distribution while ensuring that all artificial seeds share consistent material, thickness, density, and mass.

During fabrication, a PEI (polyetherimide) film was first laid flat on the 3D printer's build plate, ensuring the film's surface was smooth and wrinkle-free to provide a stable substrate for subsequent printing (Fig.

6A). Next, PLA discs with a radius of 3.5 mm and a height of 0.08 mm

are printed on the surface of the PEI film to serve as seed trays for the artificial seeds (Fig. 6B). Due to the poor adhesion between PLA and the PEI film, even the ultra-thin 0.08-mm-thick PLA discs can be easily and intactly peeled off the PEI film. Figure 6C shows the PLA seed discs after printing but before separation from the film, while Figure 6D shows one of the PLA seed discs after separation from the film.

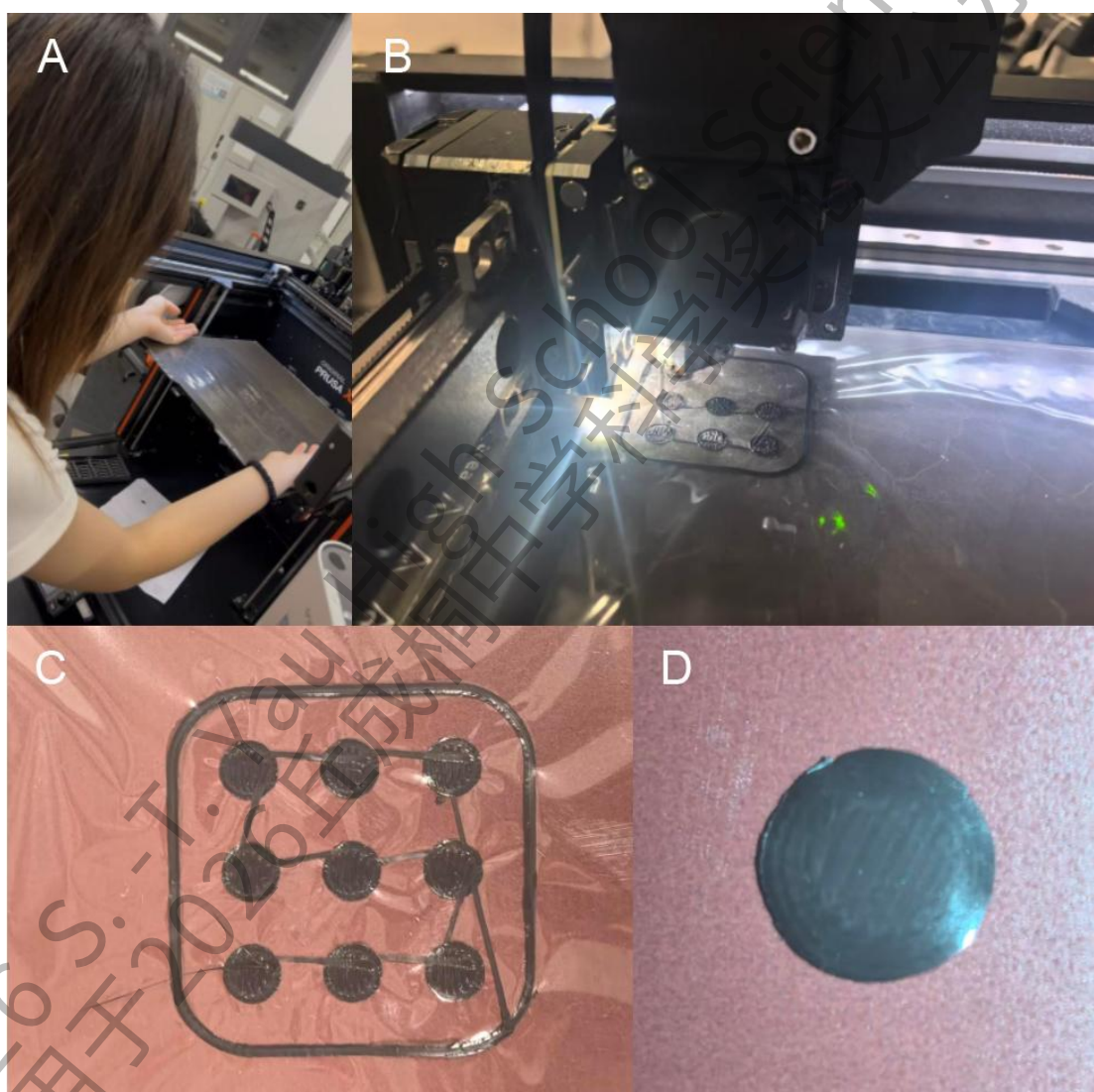


Figure 6. (A) Polyetherimide film laying. (B) 3D printing process of the seed disc. (C) All printed seed discs after printing. (D) A single seed disc separated from the film.

Once the seed tray has been printed, the seed film must be cut. First, lay a 3- μm -thick PI (polyimide) film flat on the work area of the laser cutter (Fig. 7A). Next, import the 2D vector diagram of the seed film's outline into CutLabX, the laser cutter's control software (Fig. 7B). After clicking "Start," the laser will cut along the outer edge of the seed outline (Fig. 7C). Once cutting is complete, use tweezers to peel the artificial seed away from the film scrap to obtain the complete seed membrane (Fig. 7D).

Finally, the seed tray and seed membrane are bonded together to produce a complete artificial seed (Fig. 7E).

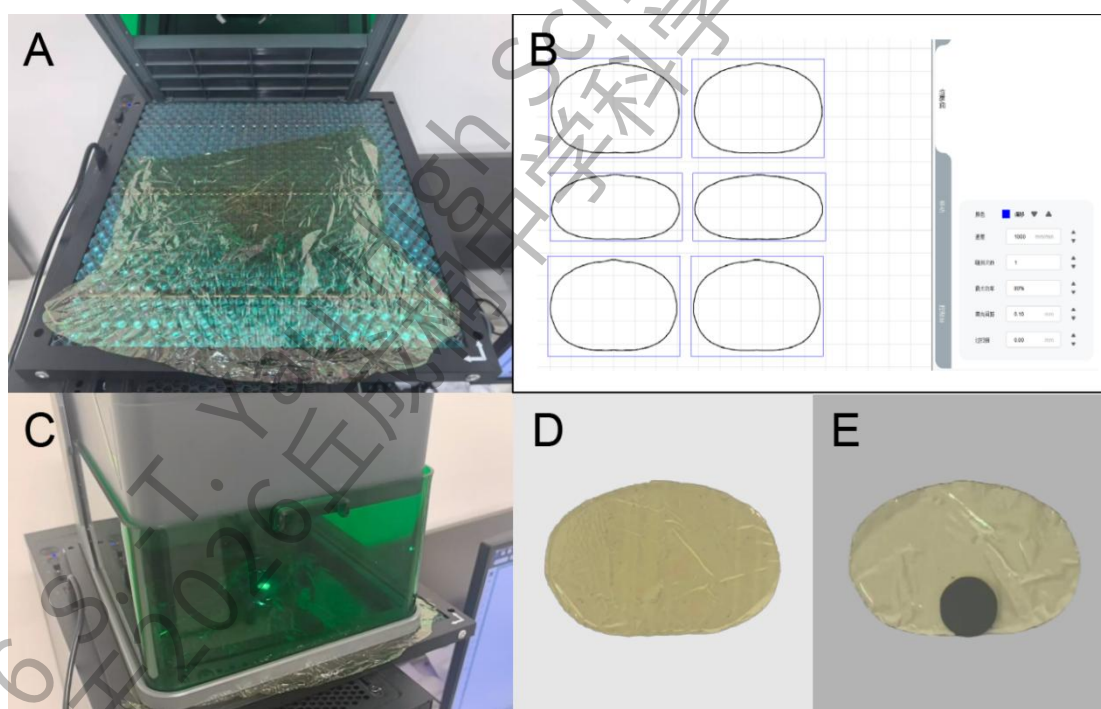


Figure 7. (A) Polyimide film laying. (B) CutLabX operation interface. (C) Laser cutting process. (D) Cut seed membranes. (E) A single artificial seed.

3. Results and Analysis

3.1 Layered Structure of Seed Pods, Morphological Gradients, and Diffusion Distance

To investigate whether morphological differences among seeds within a seed pod follow structured spatial patterns, this study first conducted a systematic quantitative analysis of seed attachment positions and geometric morphology. Using the central midrib of the seed pod as a spatial reference, seeds were classified into six layers (L1 to L6, Fig. 8C) based on their attachment positions from the outer to the inner region, and morphological parameters were calculated for seeds in each layer. This study employed the roundness coefficient (C) as a quantitative measure of shape, calculated as follows: First, the coordinates of all pixels along the seed contour were extracted, and the geometric center of the contour (i.e., the arithmetic mean of all boundary point coordinates) was calculated; then, the Euclidean distance from each pixel on the contour boundary to this geometric center is calculated individually, yielding a sequence of radial distances; next, the arithmetic mean $\bar{r}$ and the sample standard deviation σ of this sequence are determined; finally, the roundness coefficient C is defined as follows:

$$C = \bar{r} / (\bar{r} + \sigma)$$

This metric describes the circularity of a shape based on the statistical dispersion of the radial distances: when the contour is an ideal

circle, the distances from all boundary points to the center are equal, and the standard deviation $\sigma = 0$; at this point, $C = 1$, reaching its maximum value. When the contour deviates from a circle, the amplitude of variation in the radial distances along the boundary increases, σ rises accordingly, and the value of C decreases (Figure 8A).

The results show that seed roundness exhibits a monotonically increasing spatial gradient distribution from the outer to the inner part of the seed pod (Figure 9A). Specifically, from the outermost to the innermost layer, the average roundness of seeds in the six layers is as follows: $C_{L1} = 0.791$, $C_{L2} = 0.755$, $C_{L3} = 0.768$, $C_{L4} = 0.785$, $C_{L5} = 0.813$, and $C_{L6} = 0.849$. Overall, seed roundness gradually increases from the outer to the inner layers.

These results quantitatively reveal, for the first time, the spatial organization patterns of seed morphology within the flame tree seed pods: seeds are not arranged randomly but exhibit a structured gradient characterized by a gradual transition from square shapes on the outer layer to round shapes on the inner layer, indicating that morphological differences are not the result of random developmental noise but rather structural features influenced by the spatial arrangement within the seed pod.

To visually illustrate the continuous morphological transition from square to circular within the seed pod, Figure 8B presents contour images

of representative seeds from the outer layer (L1), middle layer (L4), and inner layer (L6). It can be seen that the contours of outer-layer seeds are angular with significant variation in radial distance; the contours of inner-layer seeds are smooth and approach a perfect circle; and the middle layer exhibits a transitional morphology.

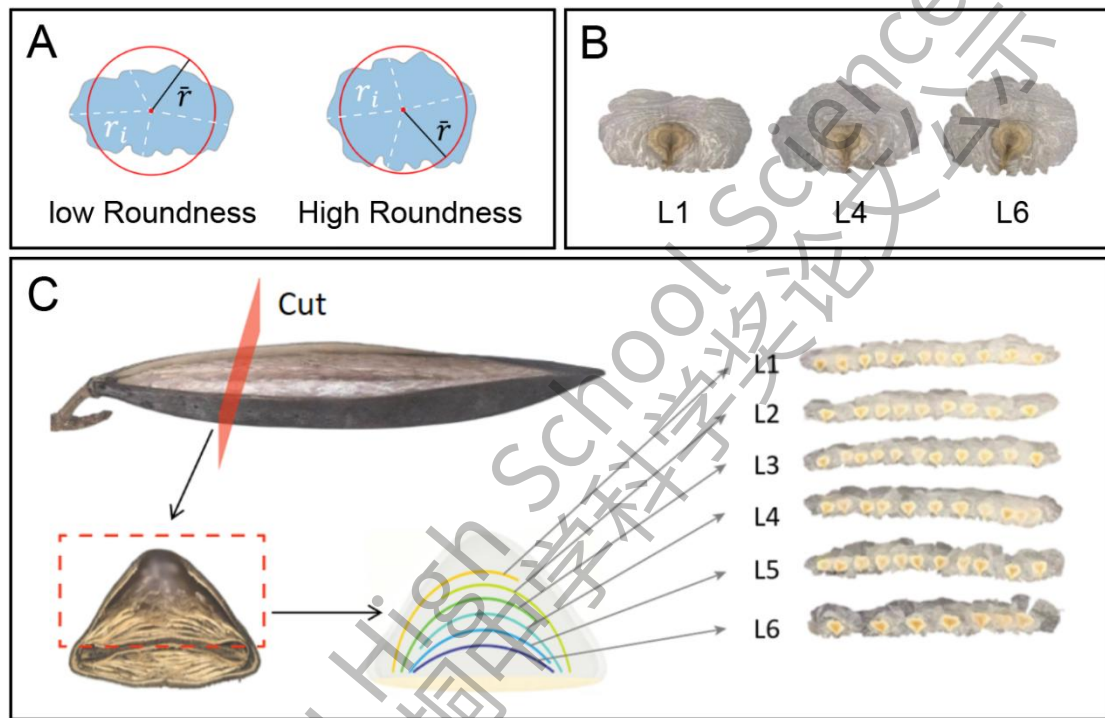


Figure 8. (A) Definition of circularity. (B) Morphology of seeds at typical layer positions. (C) Schematic of the layered structure in a seed pod cross-section.

We then measured the average dispersion distance of seeds from different layers at a height of 1.0 m. The results (Figure 9B) show that the dispersion distances were as follows: $D_{L1} = 25.36$ cm, $D_{L2} = 19.43$ cm, $D_{L3} = 21.44$ cm, $D_{L4} = 19.43$ cm, $D_{L5} = 26.60$ cm, and $D_{L6} = 21.32$ cm.

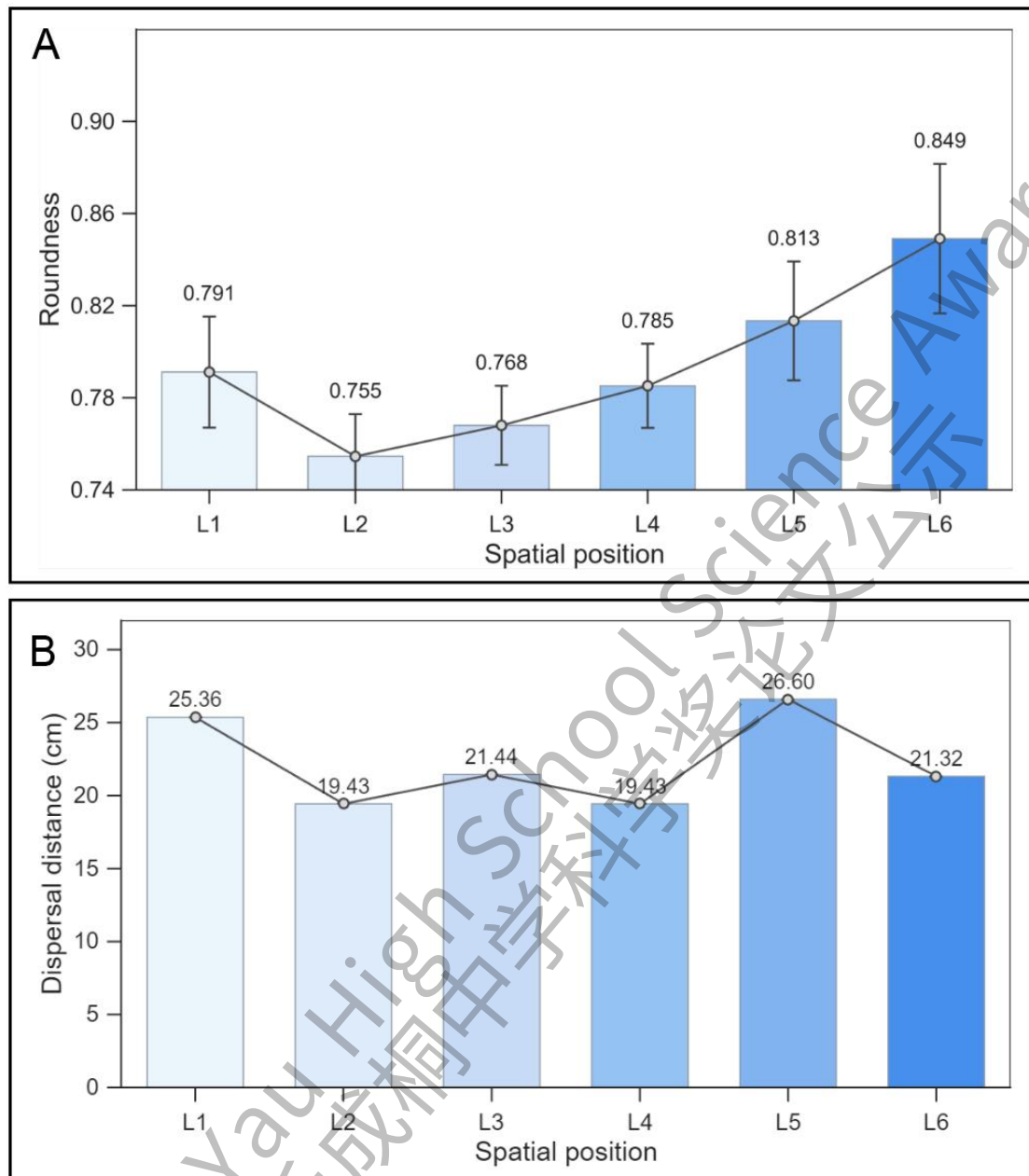


Figure 9. (A) Relationship between seed roundness and attachment layer position. (B) Relationship between mean seed dispersal distance and attachment layer position.

3.2 Relationship between Roundness, Flight Pattern, and Dispersal Distance

As noted earlier, the roundness of seeds within a seed pod exhibits an approximately monotonically increasing trend from the outside to the inside. Based on these previous results, we first sought to investigate the

macroscopic trend between roundness and diffusion distance. We plotted a relationship curve with the average roundness of seeds at each layer on the x-axis and the average horizontal dispersal distance on the y-axis (Figure 10A). We observed that roundness and average dispersal distance exhibit a monotonically increasing trend, which led us to speculate that roundness may influence seed dispersal distribution in some way.

However, roundness itself may not be a physical variable that directly determines the dispersal distance. We hypothesize that the influence of roundness on dispersal distance is most likely achieved by regulating the seed's flight pattern in the air.

To verify this hypothesis, we first observed the flight behavior of the seeds during their descent and summarized our findings. Based on our observations, we found that the flight behavior of flame tree seeds can be categorized into two typical patterns: (1) the chaotic pattern (Figure 10B), in which the seeds exhibit erratic tumbling, swaying, or trembling during descent, with frequent changes in direction and a lack of stable spatial orientation; (2) Gliding mode (Figure 10C), in which the seed maintains a stable attitude angle and glides downward along an approximately straight or low-angle curved trajectory, with a continuous and stable horizontal velocity component. (See the attached video.)

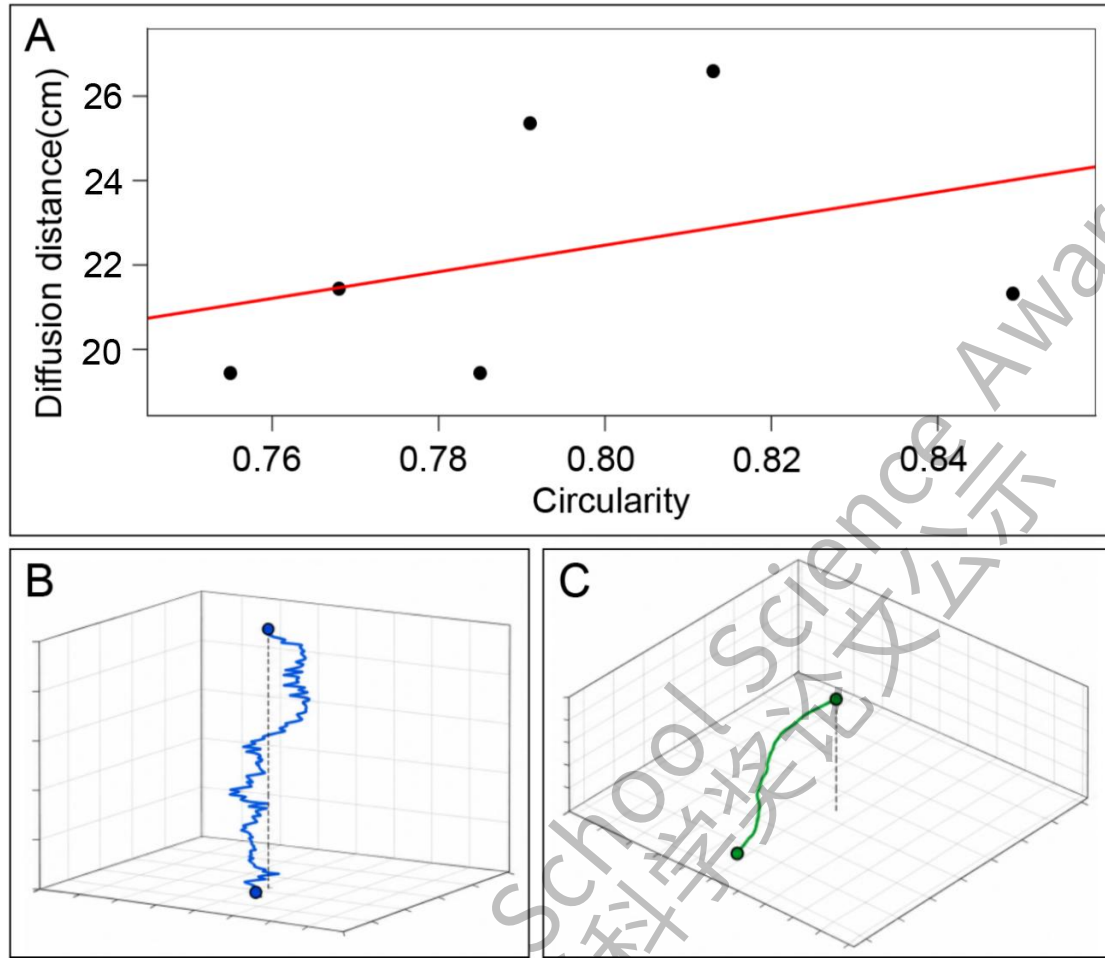


Figure 10. (A) Relationship between circularity and horizontal dispersal distance. (B) Typical disordered-state flight trajectory. (C) Typical gliding-state flight trajectory.

Next, we conducted a grain-by-grain classification and statistical analysis of the flight modes of seeds from layers L1–L6 during free fall (Table 1).

Table 1 Distribution of the two flight modes for seeds at different levels (visual classification)

	L1 (C=0.791)	L2 (C=0.755)	L3 (C=0.768)	L4 (C=0.785)	L5 (C=0.813)	L6 (C=0.849)
Unordered	6	9	7	9	8	8
Gliding	3	0	2	1	1	2

To quantitatively assess the effect of roundness on flight modes, we set the average roundness of disordered seeds to a , and the average

roundness of gliding-state seeds as b . We construct an overdetermined system of linear equations using the average roundness of the two flight modes as the unknown column vector (a, b) , the frequencies of the two flight modes for seeds in each layer as the coefficient matrix, and the roundness of seeds in each layer as the constant-term column vector. By solving for the optimal approximate solution using the least squares method, we can obtain the average roundness corresponding to each flight mode (Equation 2).

$$\begin{pmatrix} 0.66 & 0.33 \\ 1 & 0 \\ 0.77 & 0.22 \\ 0.9 & 0.1 \\ 0.88 & 0.11 \\ 0.8 & 0.2 \end{pmatrix} \cdot \begin{pmatrix} a \\ b \end{pmatrix} = \begin{pmatrix} 0.791 \\ 0.755 \\ 0.768 \\ 0.785 \\ 0.813 \\ 0.849 \end{pmatrix}$$

Equation (2): Overdetermined linear system relating roundness to flight modes

The results show that the average roundness of seeds in the disordered state is $a = 0.78$, while that of seeds in the gliding state is $b = 0.89$. In other words, the more circular a seed is, the more its flight behavior tends to shift from disordered to gliding, whereas seeds that are closer to a square shape are more likely to remain in a disordered state.

Furthermore, we analyzed the impact of the two flight modes on diffusion distance. Let the average diffusion distance for seeds in the disordered state be c , and the average diffusion distance for seeds in the gliding state be d . We construct an overdetermined system of linear

equations using the average dispersion distances of the two flight modes as the unknown column vector (c, d) , the frequencies of the two flight modes for seeds in each layer as the coefficient matrix, and the average dispersal distances of seeds in each layer at a height of 1 m as the constant term column vector, to solve for the average dispersion distance corresponding to each flight mode (Equation 3).

$$\begin{pmatrix} 0.66 & 0.33 \\ 1 & 0 \\ 0.77 & 0.22 \\ 0.9 & 0.1 \\ 0.88 & 0.11 \\ 0.8 & 0.2 \end{pmatrix} \cdot \begin{pmatrix} c \\ d \end{pmatrix} = \begin{pmatrix} 25.36 \\ 19.43 \\ 21.44 \\ 19.43 \\ 26.60 \\ 21.32 \end{pmatrix}$$

Equation (3): Overdetermined linear system relating average dispersion distance to flight modes

The solution results are as follows: the average dispersion distance for seeds in the disordered state is $c = 20.19$ cm, and the average dispersion distance for seeds in the gliding state is $d = 33.71$ cm. The average dispersion distance for seeds in the gliding state is significantly greater than that for seeds in the disordered state.

Based on the above analysis, we identified a causal chain linking seed morphology to diffusion distance: roundness $\rightarrow$ flight mode $\rightarrow$ diffusion distance. Different levels of roundness in seeds can alter the type of flight mode; rounder seeds tend to glide, while squarer seeds tend to tumble erratically, thereby affecting their horizontal diffusion

efficiency. It is worth noting that the gliding mode exhibits the highest dispersal efficiency among all flight modes and the most aggressive dispersal strategy, yet its frequency of occurrence within the population is relatively low; although the erratic mode has the lowest dispersal efficiency and the most conservative dispersal distance, it accounts for the overwhelming majority of seed frequencies. This seed dispersal strategy—featuring a large number of conservative seeds paired with a small number of aggressive ones—may be the key to the flame tree population's ability to expand both efficiently and robustly.

3.3 Programmable Control of Artificial Seed Replication and Dispersal Distribution

Having previously identified the causal chain “roundness → flight mode → dispersal distance,” we sought to verify whether this chain holds true for artificially manufactured seeds and whether the dispersal distribution of artificial seeds can be programmatically controlled based on this pattern. However, the above conclusions are all based on analyses of natural seeds, and the asymmetry of the seed coat in natural seeds remains a potential confounding factor that cannot be ruled out.

Furthermore, since the asymmetry of natural seeds is a complex factor that is difficult to describe accurately, we calculated the average contour of 56 seeds and ultimately obtained a contour with a roundness value of $C = 0.82$ (Figure 11A). We used this average contour as the reference

contour for the artificial seeds. By longitudinally stretching or compressing this reference contour, we obtained the disordered-state contour with a roundness value of $C = 0.78$ (Figure 11A) and the gliding-state contour with a roundness value of $C = 0.89$ (Figure 11A). We also measured the average surface density of the seed coat of natural seeds to be $0.4 \text{ mg} / \text{mm}^2$ and that of the seed disc to be $7.6 \text{ mg} / \text{mm}^2$. Therefore, we used an ultrathin PI (polyimide) film with a similar surface density as the seed coat material for the artificial seeds. Additionally, when printing the seed discs for the artificial seeds, we adjusted the thickness of the PLA printed by the 3D printer to match the surface density of the real seed discs. Ultimately, through a combined approach of 3D printing and laser cutting, we fabricated artificial seeds with different roundness values (Figure 11B), specifically a disordered state with roundness $C = 0.78$ and a gliding state with roundness $C = 0.89$.

After fabricating the artificial seeds, we sought to verify whether it is possible to select flight modes on demand by independently controlling seed roundness, thereby achieving artificial programming of their dispersal distribution.

We first released the two types of artificial seeds under identical conditions (height of 1.0 m, windless indoor environment) and observed their flight patterns during descent. The results fully matched our design

expectations: the disordered artificial seeds exhibited chaotic tumbling trajectories, while the gliding artificial seeds descended steadily along an approximately straight path. (See the attached video.)

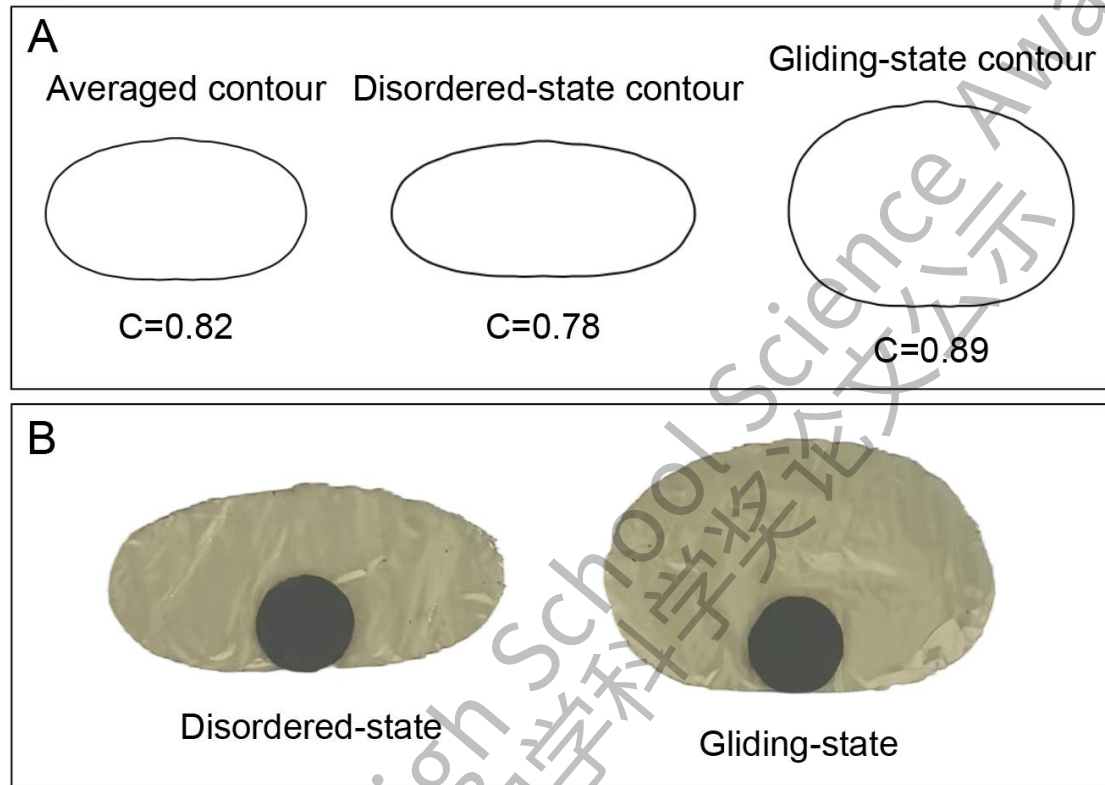


Figure 11. (A) Contours of the artificial seed membrane (left: averaged contour; middle: disordered-state contour; right: gliding-state contour). (B) Artificial seeds (left: disordered state; right: gliding state).

Furthermore, we conducted scattering experiments with the two types of seeds under standard indoor, windless conditions at five heights: 0.6 m, 0.9 m, 1.2 m, 1.5 m, and 1.8 m. In each experiment, 60 seeds were scattered, and the Weibull distribution was used to describe the probability distribution of the landing points for both types of seeds.

Let the radial distance be r ; then, the standard form of the Weibull distribution density function is:

$$f(r | H) = \frac{k}{\lambda(H)} \cdot \left(\frac{r}{\lambda(H)} \right)^{k-1} \cdot \exp \left[- \left(\frac{r}{\lambda(H)} \right)^k \right], \quad r \geq 0$$

H : Drop height (in meters).

$\lambda(H)$: Scale parameter, which increases linearly with height.

k : Shape parameter, a constant.

The Weibull distribution for the disordered state obtained by fitting the experimental results is shown in (Figure 12A):

$$f_1(r | H) = \frac{1.78}{\lambda_1(H)} \cdot \left(\frac{r}{\lambda_1(H)} \right)^{0.78} \cdot \exp \left[- \left(\frac{r}{\lambda_1(H)} \right)^{1.78} \right]$$

$$\lambda_1(H) = 9.30H + 7.36$$

The Weibull distribution for the gliding regime, obtained by fitting the experimental results, is shown in (Figure 12B):

$$f_2(r | H) = \frac{1.90}{\lambda_2(H)} \cdot \left(\frac{r}{\lambda_2(H)} \right)^{0.90} \cdot \exp \left[- \left(\frac{r}{\lambda_2(H)} \right)^{1.90} \right]$$

$$\lambda_2(H) = 11.43H + 40.69$$

To verify the predictive capability of the above Weibull distribution models in a mixed deployment scenario of “ $\lambda(H)$,” we designed an experiment: We mixed the two types of artificial seeds—disordered and gliding—in a 2:1 ratio (60 disordered seeds and 30 gliding seeds, for a total of 90 artificial seeds), released them all at once from a height of 1.0 m, and recorded the spatial distribution of all landing points. At the same

time, we used the Weibull distribution parameters independently fitted for each type of artificial seed, linearly superimposed them according to the weights of the mixture, and calculated the predicted probability density distribution for the mixed population. We compared the scatter plots of the experimental and predicted landing points (Figure 12C) as well as the frequency distributions of the radial distributions (Figure 12D). As can be seen, the probability density distribution of the predicted curve closely matches that of the experimental scatter plot. The shape of the mixed distribution is not a simple replication of a single mode but exhibits a bimodal characteristic, with the short-range main peak contributed by the disordered seeds and the tail peak contributed by the gliding seeds. The model successfully predicted the specific details of this mixed distribution.

The above experiments constitute a complete closed-loop validation: starting from the morphology of natural seeds, we discovered the influence of roundness on the dispersal distribution; using this as a design basis, we manufactured two types of artificial seeds via 3D printing that differed only in their geometric features, successfully replicating the two flight modes—disordered and gliding—and their corresponding dispersal distributions; we subsequently established a quantitative prediction model based on the Weibull distribution and validated its ability to predict the dispersion distribution of mixed populations in combined seeding

experiments. These results hold significant importance on both theoretical and practical levels. Theoretically, they demonstrate that the causal chain “geometric features $\rightarrow$ flight mode $\rightarrow$ dispersion distance” is complete. On the applied level, it demonstrates that by designing passive flying devices with specific geometric features and releasing them in a mixed distribution according to the desired proportions, we can pre-calculate and precisely control the landing point distribution of large-scale releases—ranging from short-range dense coverage (with a high proportion of disordered-type devices) to directional long-range delivery (with a high proportion of gliding-type devices), as well as any combination of mixed modes. This provides computable, programmable, biomimetic design solutions for application scenarios such as the deployment of large-scale distributed sensor networks, precision agriculture seeding, and environmental monitoring.

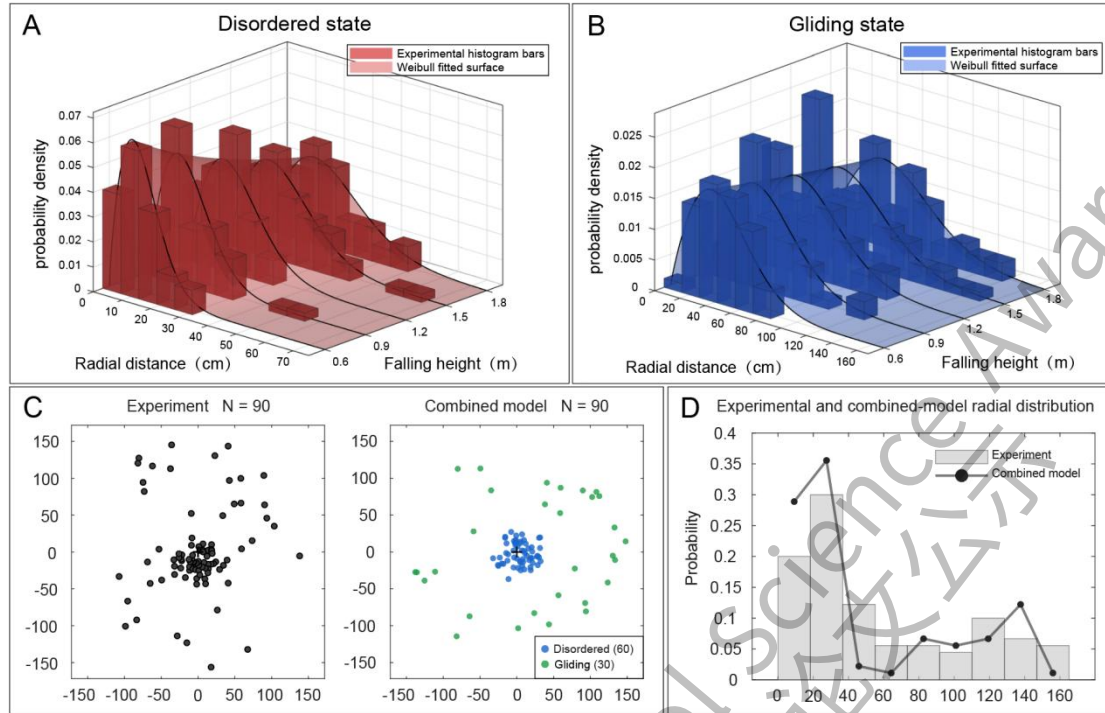


Figure 12. (A) Weibull distribution fitting of artificial seeds in the disordered state. (B) Weibull distribution fitting of artificial seeds in the gliding state. (C) Comparison between predicted and experimental landing positions in mixed-drop experiments. (D) Comparison of predicted and experimental frequencies in mixed-drop tests.

4. Discussion and Outlook

4.1 Aerodynamic Mechanism of How Roundness Controls Flight

Mode

Through systematic scattering experiments and verification using replicated artificial seeds, this study uncovered a causal chain: “roundness $\rightarrow$ flight mode $\rightarrow$ dispersion distance.” However, the specific physical mechanism by which roundness—a planar geometric parameter—influences the flight modes of seeds in flight still requires explanation from an aerodynamic perspective.

Based on experimental observations and static stability theory, this paper proposes the following hypothesis: roundness is not a physical variable that directly determines dispersal distance; rather, it influences the distribution of flight modes by regulating the static stability margin between the center of mass and the aerodynamic center, thereby ultimately affecting horizontal dispersal efficiency. Seeds with higher roundness have a greater distance between their center of mass and aerodynamic center, making it easier for them to satisfy the static stability conditions for planing flight and resulting in stable gliding; conversely, seeds with lower roundness have a smaller distance between these centers, leading to insufficient static stability margin. As a result, their flight attitude is difficult to maintain, causing them to tend toward disordered tumbling.

According to classical theories of static stability, when a seed moves through an airflow, the relative position of its aerodynamic center (i.e., the point of action of the resultant aerodynamic force) and its center of mass (i.e., the point of action of gravity) determines whether the seed can automatically return to a balanced attitude after being disturbed. When the center of mass is located ahead of the aerodynamic center—that is, when the distance between them is large—any pitch or roll disturbance will cause the aerodynamic torque to generate a restoring torque, bringing the seed back to its equilibrium attitude. This is precisely the condition for

static stability in flat-plate flight. For nearly circular seeds with high roundness, the contour is uniform in plan view, and the aerodynamic center is closer to the geometric center. Since the lever arm between the center of mass (seed disk) and the aerodynamic center is long, the restoring torque is significant. Consequently, the seed can maintain a stable attitude for an extended period, gliding downward along a trajectory that is approximately straight or a slight arc, with a continuous and stable horizontal velocity component.

Conversely, for nearly square seeds with low roundness, the contour is angular, the aerodynamic center fluctuates sharply with changes in attitude, and the distance between the center of mass and the aerodynamic center is small; the restoring torque is insufficient to offset the destabilizing torque caused by disturbances. The seeds lack sufficient static stability margin in the airflow and are easily triggered by random perturbations to roll, wobble, or flutter, resulting in frequent changes in motion direction and exhibiting disordered behavior. This mechanistic explanation is consistent with the phenomena observed in the experiments: seeds in the gliding state have an average roundness of 0.89, with a shape close to a perfect circle and a long effective lever arm between the center of mass and the aerodynamic center; whereas seeds in the disordered state have an average roundness of 0.78, with a shape

tending toward a square, a shorter lever arm, and insufficient static stability margin.

4.2 Outlook

Although this study has established a quantitative relationship between geometric features and diffusion capacity at the mechanistic level and achieved programmable control of diffusion distribution at the level of artificial seeds, there is still room for further expansion of existing manufacturing schemes and experimental methods. Future work can be carried out in the following three directions.

First, improving the manufacturing methods for artificial seeds. The current composite process—combining PI film with PLA printing and laser cutting—allows for independent control of planar contours and mass distribution; however, there is still room for improvement in terms of interfacial bonding strength between the seed tray and seed film, thickness uniformity, and batch manufacturing efficiency. Future efforts could explore micro- and nanofabrication techniques to achieve higher precision and greater consistency in the mass production of biomimetic seeds, laying the foundation for large-scale applications.

Second, integrating microsensors. Currently, artificial seeds function solely as passive flight bodies to verify how geometric features regulate dispersion patterns. In the future, micro-sensors for temperature, humidity, atmospheric pressure, or acceleration could be integrated into the seed

discs, enabling them to collect environmental parameters in the target area in situ and transmit the data wirelessly while dispersing according to a preset distribution. This would upgrade biomimetic seeds from mere “dispersal units” to “distributed sensing nodes,” offering broad application prospects in environmental monitoring, meteorological observation, and ecological surveys.

Third, the use of drones for dispersal. The dispersal experiments in this study were all conducted indoors under windless conditions, which significantly limited the release height and method. In the future, artificial seeds could be mounted on drone platforms to conduct field release experiments at different altitudes and under various meteorological conditions. This would validate the applicability of the Weibull distribution model in real atmospheric environments and explore the use of drone formations to achieve large-area, programmable, and precise dispersal (Figure 13). Combined with the probability density prediction model established in this study, it is expected to enable end-to-end control—from “on-demand design of geometric features” to “on-demand planning of deployment paths”—providing computable, programmable, bio-inspired solutions for precision agricultural seeding, distributed sensor network deployment, and environmental monitoring.

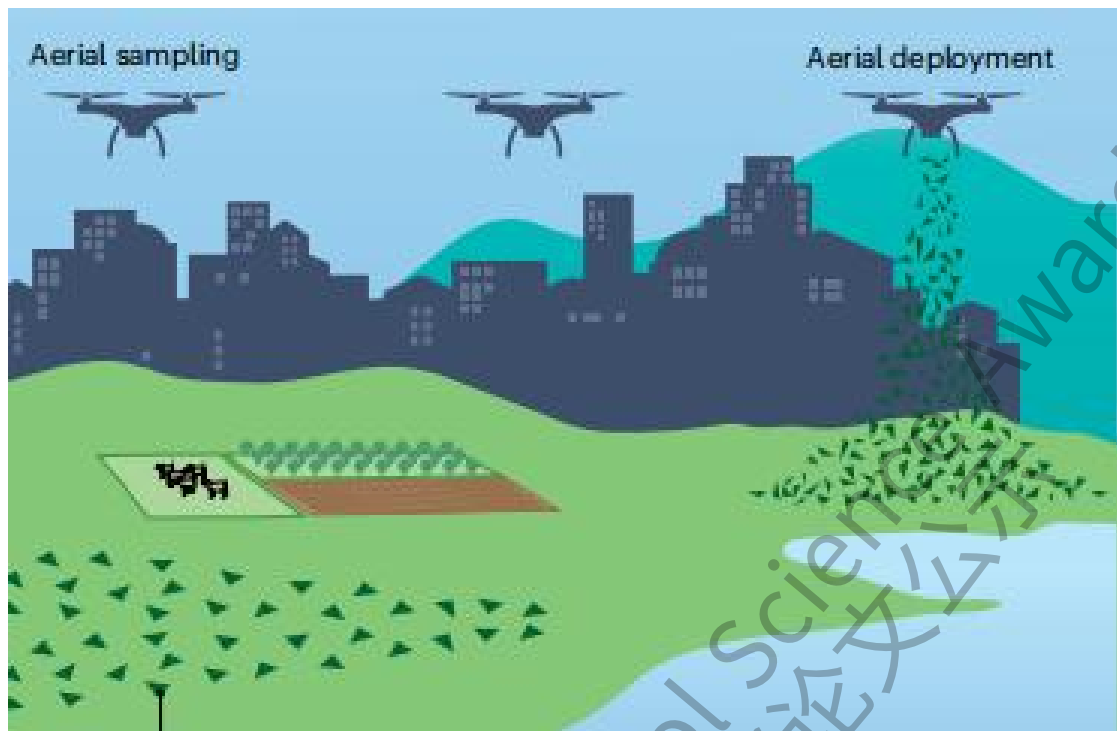


Figure 13. Large-scale swarm deployment scenario of bioinspired passive micro air vehicles^[21]

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Acknowledgments

During the course of this research, I used DeepSeek V4 and GPT-5.6 Sol as auxiliary tools, primarily for literature searches, logical checking, consultation on challenging questions, and code development.

Their use spanned the entire research process, with the primary use occurring during key stages such as literature review, research design, data analysis, and academic writing. The frequency of use varied according to specific needs. I generally used these tools when encountering difficulties in literature retrieval, logical organization, technical questions, or code debugging, rather than using them continuously or at a fixed frequency.

Specifically, during the literature search stage, I used the aforementioned tools to efficiently identify relevant literature, obtain information on the research background and recent developments in the field, and supplement and verify my research ideas. For logical checking, I used them to help organize the structure of my arguments, identify potential flaws in reasoning, and improve the rigor of the research framework. When encountering challenging questions, I used them as consultation tools to ask questions and discuss specific concepts, methods, or technical details, thereby broadening my perspectives and deepening my understanding. In the area of code development, I used them to assist

in generating, debugging, and optimizing the code required for the research, thereby improving implementation efficiency.

It should be emphasized that all AI-generated content was independently evaluated, verified, and revised by me. I take full responsibility for the final research results.

I first noticed the flame tree in a park near my home. In late summer, a large number of seeds were scattered beneath the tree, and their distribution on the ground did not appear entirely random. Out of curiosity, I picked up a few seeds to examine them closely and discovered distinct morphological differences between them. After reviewing the literature, I learned that inside the fruit pods, flame tree seeds undergo a morphological change, gradually becoming rounder from the outside in. Puzzled by this, I carefully peeled back the layers of a whole fruit pod myself and began to wonder: Could these morphological differences alter the seeds' dispersal patterns? This curiosity, born from everyday life, marked the beginning of this research.

As I complete this thesis, I would like to express my sincerest gratitude to all the teachers, family members, and academic institutions that have supported me.

First and foremost, I would like to extend my heartfelt gratitude to my advisor, Professor Wu Jianing of the School of Advanced Manufacturing at Sun Yat-sen University. I first met Professor Wu at a junior high

school science research lecture. Driven by a keen interest in his research, I took the initiative to reach out to him on multiple occasions. During one such conversation, I shared my field observations of flame tree seeds, and Professor Wu inspired me by asking, ““Could we study flame tree seeds and apply biomimicry to them?”” It was precisely this question that transformed an ordinary everyday observation into a research topic worthy of exploration. Professor Wu placed great emphasis on strengthening my fundamental research skills. From thesis formatting standards and scientific illustration to the use of image processing software, this series of training helped me gradually develop the ability to conduct research independently. I was primarily responsible for sample collection, experimental procedures, data analysis, and paper writing for this project, while Professor Wu provided crucial guidance on research methodology, overall structure, and academic standards. I am deeply grateful to Professor Wu for his selfless and dedicated mentorship, which allowed me to fully experience the authentic scientific research process.

I would also like to express my sincere gratitude to YuHe Hong, my senior. Throughout the research process, he provided me with tremendous support and assistance. He was always willing to discuss new ideas with me and help me evaluate the feasibility of my concepts. During the sample preservation phase, some pods became moldy due to moisture, and when I proposed using a drying oven to treat the samples, he

approved the idea. He explained how to operate the drying oven and provided practical advice on temperature and duration, ensuring that the precious samples were preserved intact. When setting up experimental apparatus and selecting artificial seed materials, he worked with me to analyze the properties of different materials, offered extensive practical advice, and guided me in turning each idea into a testable experiment, helping me maintain my passion for research throughout the process of trial and error.

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often begins with a simple question and, through continuous exploration and practice, gradually delves deeper.

2026 S.-T. Yau High School Science Award
仅用于2026丘成桐中学科学奖论文公示

Personal CV:

Name:

Meihui Ding

Education:

The Middle School Attached To SunYat-sen University(8/2022-6/2025)

International Department, The Affiliate High School of

SCNU(8/2025-present)

Position and Award:

The Middle School Attached To SunYat-sen University:

- Merit Student (2022)
- Merit Student (2023)

International Department, The Affiliate High School of SCNU

- Merit Student (2025)

Introduction to my mentor:

Jianing Wu, Ph.D.

Professor & Associate Dean, School of Advanced Manufacturing, Sun Yat-sen University

National Natural Science Foundation of China Excellent Young Scientists Fund Recipient

ACADEMIC APPOINTMENTS

Professor & Associate Dean, School of Advanced Manufacturing, Sun Yat-sen University

2026 – Present

Associate Professor & Associate Dean, School of Advanced Manufacturing, Sun Yat-sen University

2022 – 2026

Associate Professor, School of Aeronautics and Astronautics, Sun Yat-sen University

2018 – 2022

Postdoctoral Researcher, Georgia Institute of Technology, USA

2015 – 2018

EDUCATION

Ph.D. in Mechanical Engineering, Tsinghua University, Beijing, China

2009 – 2015

B.S. in Mechanical Engineering, Beijing Jiaotong University, Beijing, China

2005 – 2009

RESEARCH INTERESTS

- **Biophysical Intelligence:** Biophysical Intelligence: quantitative observation and characterization of species-specific biological behaviors; mechanisms of biological locomotion control
- **Interfacial Mechanics:** Interfacial Mechanics: microfluidics; soft matter physics
- **Bioinspired Manufacturing:** Bioinspired Manufacturing: bioinspired micro/nano devices; bioinspired soft robots

SELECTED PUBLICATIONS

Z. Huang, S. Wu, Q. Wu, T. Mai, J. Zhao, B. Wang, J. Wu, "Tongue microstructure physically constrains division of labor in bumblebee foraging." Proceedings of the National Academy of Sciences 123.3 (2026): e2527391123.

J. Wei, M. Wu, Y. Dai, P. Cao, H. Yang, Z. Chen, J. Yang, Z. Wu, S. Gorb, J. Wu, "Ultrathin seed wing with heterogeneous structures for highly efficient dispersal of African tulip tree." National Science Review (2026): nwag132.

Y. Zhao, J. Zhu, J. Zhang, S. Zhang, M. Shao, Z. Chai, Y. Liu, J. Wu, Z. Wu, J. Zhang, "Enhancing Grasping Diversity with a Pinch-Suction and Soft-Rigid Hybrid Multimodal Gripper." IEEE Transactions on Robotics (2025).

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W. Zhang, W. Jiang, C. Zhang, X. Qin, H. Zheng, W. Xu, M. Cui, B. Wang, J. Wu, Z. Wang, "Honeybee comb-inspired stiffness gradient-amplified catapult for solid particle repellency." *Nature Nanotechnology* 19.2 (2024): 219–225.

RESEARCH FUNDING

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- **NSFC Youth Program (2019 – 2022)** — Bioinspired microstructures of nectar-feeding insect mouthparts and coordinated appendage control (PI, ¥280K)

PATENTS (SELECTED)

- External pipeline cleaning platform (Patent No. 202410401580.9, China)
- Reliability evaluation method for dynamic-based locking-release mechanisms (Patent No. 202411372735.7, China)
- Bistable energy-absorbing device based on tensegrity structures (Patent No. 202410853558.8, China)

TEACHING

- Theory of Machines (Undergraduate)
- Comprehensive Experiments in Mechanical Engineering II (Undergraduate)
- Fundamentals of Machine Design (Undergraduate; University First-Class Undergraduate Course, 2022)
- Mechanical Innovative Design (Undergraduate)
- Academic Integrity and Scientific Writing (Graduate)

AWARDS & HONORS

- Beijing Municipal Science and Technology Award, Second Prize (ranked 3rd of 4), 2025
- Outstanding Graduate Supervisor (one of 20 university-wide), Sun Yat-sen University, 2025
- Second Prize for Excellent Teaching Achievements, Guangdong Society of Academic Degrees and Postgraduate Education, 2025
- Winner, 11th Teaching Competition for Faculty (Engineering Group), Sun Yat-sen University, 2023
- Outstanding Advisor, World University Student CubeSat Challenge (China Finals), 2022
- Outstanding Advisor Award, Contemporary Undergraduate Mathematical Contest in Modeling (Guangdong), 2022

- “Yixian Scholar” (Excellent), Sun Yat-sen University
- Talent of the “Hundred Talents Program,” Sun Yat-sen University

PROFESSIONAL SERVICE

- Committee Member, Young Scientists Committee, International Society of Bionic Engineering (ISBE)
- Member, Chinese Society for Vibration Engineering (CSVE)
- Young Editorial Board Member, SmartBot
- Young Editorial Board Member, Soft Science

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