

Research Article

Autorotating dispersal units of *Getonia floribunda* Roxb. (Combretaceae): morphology, aerodynamics and geometrical significance

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Dispersal units that continuously rotate while falling purely due to aerodynamic forces are called autorotating dispersal units. Single- to multi-winged forms of autorotating dispersal units occur in nature. The dispersal unit of *Getonia floribunda* Roxb. (Combretaceae) is an example of a multi-winged whirling diaspore that performs efficient autorotation in the air during wind dispersal. The present study aims to investigate the diaspore morphology, geometry, underlying principles, and reasons for the specificity of its autorotation during the dispersal and to find the morphological variations and geometrical significance. Plants and their diaspores from four locations in northern Kerala, South India, were selected for this study. Detailed macromorphological, micromorphological, developmental, anatomical, aerodynamic, and experimental studies were performed on the collected diaspores. The results show that fruit diaspores with distinct spatial configuration of persistent cyclically arranged tepals (perianth whorl) and distribution of the centre of mass along the middle vertical axis are the reasons for vertical autorotation or helicopter motion. Wing modification and paper model experiments prove that the wings have an intrinsically predetermined geometrical right-side leading-edge curvature, which is the reason for its distinct anticlockwise direction during autorotation. A significant variation in morphological parameters of these diaspores was observed across locations. Still-airdrop tests and further statistical analysis show that wing fold angle developed due to the distinct spatial configuration of the wings exhibited a significant, predictable relationship with descent rate and terminal velocity in this diaspore across locations. Thus, wing geometry has an impact on flight in these diaspores and demonstrates the relationship between the shape and fitness of natural flight organs.

Keywords: anemochory, autorotation, *Calycotris floribunda*, descent rate, helicopter fruits, whirling diaspores.



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Introduction

The greatest possibility for plants to colonise new environments and overcome the limits of the survival of progeny close to conspecific adults is through dispersal (Smith et al. 2015). This is believed to be beneficial because it allows for more effective screening of the environment for new inhabitable microhabitats and avoids severe mortality of juveniles around the parent plant (Augspurger and Franson 1993). As sessile creatures in general, certain plants produce winged diaspores as dispersal units to expand their dispersal distance. The aerodynamics of these diaspores enable them to prolong their flight time and range of establishment (Azuma and Yasuda 1989). Various morphological and functional adaptations are seen in winged diaspores to slow down the descent, allowing them to spend more time aloft (Thomson and Neal 1989). For instance, when the diaspores separate from the tree, they exhibit aerodynamic behaviours such as gliding, rocking, and spinning or autorotation (Minami and Azuma 2003) in the air to slow their rate of descent and allow the wind to carry them away (Tennakone 2017). Implementing these aerodynamic potentials demands stable and efficient geometric configurations that direct the flow of the surrounding air (Rabault et al. 2019). The environment, sensing ability of their tissues, and their morphology interact in a complicated and dynamic way to achieve this (Mazzolai et al. 2022). Because of these adaptations, winged diaspores have drawn particular interest among other diaspores that utilise wind dispersal methods. The concept of borrowing ideas from the aerodynamics of winged diaspores has numerous applications in space mission designing, aviation, aeroballistics, aerial photography, robotics, and sports domains (Pandolfi and Izzo 2013).

Among the various aerodynamics in winged diaspores, autorotation is one of the most efficient mechanisms that minimise descent rate by creating a lifting force due to the autorotational flight as they fall against gravity to enhance their dispersal distance under lateral winds (Azuma 1992, Arranz et al. 2018). Autorotation is the continuous rotation of an object that is sustained exclusively by the effect of aerodynamic forces (Rao et al. 2014). Soon after the diaspore starts to descend from the tree, the rotary wing spins specifically in a clockwise or anticlockwise direction (Tennakone 2017). It begins to drop with an acceleration due to gravity, but soon a leading-edge vortex created by its autorotation results in a lifting force against the force of gravity and reduces the rate of fall until it reaches an equilibrium state of steady descent rate, or terminal velocity (Lentink et al. 2009, Lee et al. 2014). Aerodynamics of autorotating winged diaspores has already piqued the interest of the scientific community (Norberg 1973, Green 1980, Azuma and Yasuda 1989, Rosen and Seter 1991, Seter and Rosen 1992, Yasuda and Azuma 1997), due to the broad range of applications in creative concepts. The ideas of *Samarai*, a rotating mono-wing nano-air vehicle (NAV) designed at Lockheed Martin Advanced Technology Laboratories based on maple seeds (Fregene and Bolden 2010), the robotic samara developed by

Ulrich et al. (2010), designing of a single-blade autorotating vehicle by Andreas Kellas (2007) (Rao et al. 2014), samara type decelerator based on maple seed (Kline and Koenig 1984), samara autorotating wings based on maple samara (Win et al. 2019), three dimensional electronic microflyers by Kim et al. (2021) and tethered autogyro system based on *Acer* samaras (McConnell 2022) are some of the notable examples. As a result, they offer numerous noteworthy examples of solid design and specialised functionality as well as a diversity of motivating perspectives on design innovation (Pandolfi and Izzo 2013).

In most of the studies undertaken on the autorotation in winged diaspores, samaras or diaspores with single flat wings (Greene and Johnson 1990, 1993, Seter and Rosen 1992, Varshney et al. 2011, Camposano et al. 2015, Chen et al. 2021, Niu et al. 2022) were considered, and overlooked the fact that many autorotating winged diaspores have multi- or helicopter (Augspurger 1986) and heteromorphic wings (Rabault et al. 2019, Gan et al. 2022). A complete understanding of aerodynamics in multi-winged or helicopter diaspores remains elusive (Rabault et al. 2019). The most investigated category in multi-winged diaspores is vertical autorotation in double-winged fruits of the Dipterocarpaceae family (Smith et al. 2015, Tennakone 2017, Rabault et al. 2019, Eadkong et al. 2020). Many other plant families, including Combretaceae, Verbenaceae, Hernandiaceae, Rubiaceae (Van Staden 1990), and Polygonaceae (Ladera and Pineda 2009), which produce multi-winged or helicopter diaspores with characteristic morphology, did not receive adequate attention in the studies. Only in a small subset of helicopter diaspores have descent rates and terminal descent velocities been documented. For instance, Ladera and Pineda explored the vertical and rotating motion of a tri-winged seed in 2009. They experimented to confirm their theoretical predictions about the angular speed of revolving seeds (Eadkong et al. 2020). According to the current understanding, no studies have been done to describe how the morphology and wing forms of multi-winged (more than three wings) whirling diaspores affect their terminal velocity, rotational frequency, and rate of fall. Persistent perianth whorls in the flower develop and act as wings during dispersal in most multi-winged whirling diaspores. However, it is yet unclear how the growth, shape, number, and geometry of the perianth whorls of diaspores relate to flight performance (Rabault et al. 2019). The main elements that influence the autorotation and descent rate in these spinning helicopter diaspores are still not understood.

The dispersal unit of *Getonia floribunda* Roxb. (Combretaceae) is one such example of a multi-winged whirling diaspore that performs striking specific autorotation in the air during wind dispersal. Five cyclically winged (rarely with six wings) fruits are the dispersal units in this plant, which assist in performing distinct anti-clockwise autorotation in its vertical axis during dispersal. The plant is a large woody climber (Supporting information) commonly known as *Pullaanni*, *Varavalli*, *Poorappoovu*, *Jadappoo*, or *Narayanpoo* in regional Malayalam language and *Paper flower climber* in English. The genus *Getonia* Roxb. is monotypic and is native

to Peninsula Malaysia, China, and India (POWO 2024). There was a nomenclature conflict between the generic names *Getonia* and *Calycopteris* Lam., a synonym of this taxon. Before the end of 2000, the name *Calycopteris floribunda* (Roxb.) Lam. ex Poir. was accepted; however, Mabberly (2008) drew attention to the fact that *Getonia* had precedence over *Calycopteris* (Patil 2020). Patil resolved the nomenclature ambiguities in 2020 by stating unequivocally that *Getonia* is the correct name as per the code (Turland et al. 2018). *G. floribunda* produces flowers and fruits from January to May. Dense hairy branches and leaves, leafy bracts, cream or greenish-yellow coloured flowers in dense axillary racemes, presence of perianth tube with 5 lobes (tepals), diplostemonous epiphyllous stamens, unilocular inferior ovary with 3 pendulous ovules and drupe fruits are the distinguishing features of this plant (Supporting information).

Despite the astonishing autorotation of diaspores of this plant, there are no previous studies on this topic, and nobody has unravelled its specificity in the direction of rotation. Understanding how they work is, therefore, a fascinating issue that represents an avenue not only for scientific advancements but also for rethinking the design of technologies that may better interact with our ecosystems (Mazzolai et al. 2022). In this context, this study aims to unveil the following: 1) how did the morphology and geometry develop in the diaspores of *G. floribunda*?, 2) what is the underlying principle and reasons for the specificity in the direction of rotation of this diaspore?, 3) is there any significant variation in morphological parameters in this diaspore across locations?, and 4) what are the factors affecting the descent rate and autorotation in this diaspore across locations?

Material and methods

Studies on morphology, development and anatomy

Plants and dispersal units from four different locations (location I: 11°86'50.8"N–75°50'89.6"S; location II: 11°86'50.8"N–75°25'67.8"S; location III: 11°90'55.1"N–75°50'46"S; location IV: 11°13'27"N–75°88'97.1"S) in northern Kerala, South India were used for this study. Careful observations of the developmental stages from bud to fruit were carried out at 5–10-day intervals and captured using an EOS760D (Canon, Japan) digital camera. Developing stages were collected for detailed morphological and anatomical studies. Detailed morphological and micromorphological studies were carried out and captured with an M205 stereo microscope (Leica LAS X, Germany) equipped with a 12 MP microscope camera (Flexacam C3, Leica microsystems) and MSZ-TR stereomicroscope (Magnus, India) equipped with a Magcam DC-5 (Magnus, India) camera. To investigate the detailed micromorphology of the wings, FE-SEM (Octane Plus, ZEISS Gemini SEM 300) analysis was carried out. Changes in the internal structure of the wings and the development of the unique geometry were studied by taking freehand sections of the wings at different developmental stages. The sections were stained with 0.5% toluidine blue

and observed under a Vision-2000 (Labomed, India) stereo-microscope. Observations of developmental stages, dispersal behaviour, and diaspore collections were carried out from January to April in the years 2022 and 2023. The voucher specimens (CU 178095, CU 178096, CU 178097, CU 178098) were deposited in the Calicut University herbarium (CALI).

Physical measurements

Ten mature fruits from each location were randomly selected for the experimental studies. The weight of each fruit was measured using an analytical weighing balance with a readability of 0.1 mg (± 0.0001 g) (Shimadzu, Kyoto, Japan), and the position of the centre of mass was determined, followed by Tennakone (2017). Due to the small size of the fruit, the diaspores were balanced on a horizontally placed moderately thin twin (instead of a horizontal edge). The length and breadth of each wing were measured manually, and the surface area was measured by tracing the outline of each wing on graph paper and counting the squares coming inside the outline. Wing fold angle and geometry were measured as explained by Gan et al. (2022) by using Image J software (ver. 1.54). Wing fold angle is measured as the angle formed by each wing tip with a horizontal line passing through the origin of the wings which is shown in Fig. 1B. Wing loading (mg mm^{-2}) was calculated by dividing the weight of the diaspore by wing area (sum of the area of the five wings). Here, we used wing loading rather than the traditional square root of wing loading as explained by Augspurger (1986).

Experimental studies

Still air drop test

For studying the entire trajectory, descent rate, flipping or transition time, rotating time, and terminal velocity of *G. floribunda* fruits, the video recording method of the still-airdrop test explained by Seter and Rosen (1992) was followed. Initial trial tests indicate that these diaspores travel a small distance, approximately 25 cm, to start autorotation and to attain terminal velocity before reaching 1 m after being released from rest. In addition to this, due to the smaller size of the diaspore, a 2 m release height was selected for the experiment so that they could be observed more readily. The experimental setup, as Seter and Rosen (1992) described, consisted of an LED light source, a digital camera with 18–135 mm zoom lens (Canon EOS 760 D, Japan), and a 2 m high white screen with a 2 m labelled metric scale placed on the left side, and a digital timer fixed on the right side of the screen arranged in a closed room to avoid distortion of airflow. The height of the camera in the tripod was adjusted to 1 m, and the distance between the camera and the screen was 1.5 m. Ten selected dispersal units from four selected locations were dropped down vertically from a height of 2 m above the floor, and their entire falling process was recorded in the digital camera. For each diaspore, this experiment was repeated thrice, and the average value was taken for further analysis. With the help of the digital timer and metric scale

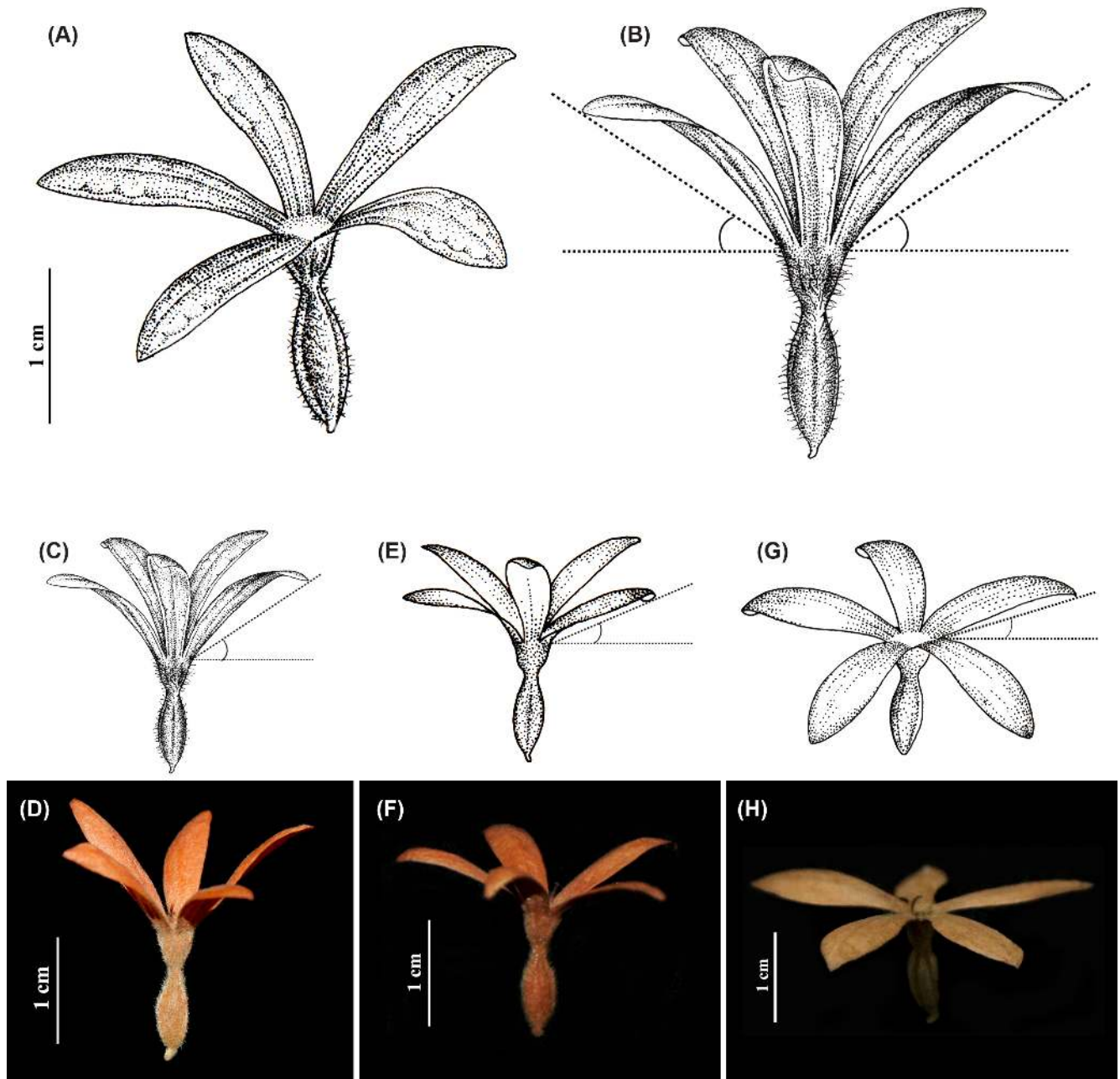


Figure 1. (A) Illustration of the diaspore of *Getonia floribunda* Roxb., (B) fruit of *Getonia floribunda* in vertical orientation showing the measurement of wing fold angle, (C–H) morphology of fruits with variations in the wing fold angles.

attached to the screen, it was possible to track the flipping and rotating movements and time of vertical positioning clearly by playing the recorded video at a slow pace. By this method, the time taken to reach the ground, descent rate (it is the distance travelled per second), flipping time or time taken to change initial orientation, and rotating time of each diaspore were recorded. According to Augspurger (1986), the diaspore takes a few seconds after release before it starts moving aerodynamically and before it achieves its terminal velocity (it is the continuous fall rate in autorotation). Therefore, the rate of descent is not exactly equivalent to the terminal

velocity. Here, the initial free-falling or orientation-changing time is very small due to the small size of the diaspore; hence, the terminal velocity was measured according to the method explained by Nathan et al. (1996) by using the metric scale placed on the left side of the screen by freezing the video starting from the moment of release.

Paper model experiment

For investigating the direction or sense and mechanism of specific (anti-clockwise here) rotation performed by the diaspores, morphological alterations to the wings by removing

the natural inclination of the wings (Fig. 2A and B) and experiments with paper models imitating the natural diaspores that are capable of rotation during fall were conducted (Tennakone 2017). Based on the curvature or inclination of the wings, 3 types of paper models were used for the experiment. In the model I wings, inclination was similar to the natural diaspore, i.e. toward the right side when the diaspore is held facing us (Fig. 2C and D) (the right side and left side of each wing in a diaspore is shown in Fig. 2A); in model II wings, inclination was opposite to that of the natural diaspore, i.e. towards the left side (Fig. 2E and F); and model III has no inclination in the wings, i.e. straight flat wings (Fig. 2G and H). These three models were constructed in two ways; one type with similar weight and size of natural diaspores, and the second type (Fig. 2) with double the weight and size of natural diaspores, and the falling experiment in still air was conducted several times to confirm the results.

Data analysis

One-way ANOVA of morphological parameters such as weight, area, length, width, wing fold angle, and wing loading across samples of four locations were performed to find any significant inter-location difference in morphological parameters. If it is significant, then Tukey's honest significant difference (HSD) post-hoc test was performed to find which group pairs have statistically significant differences. To investigate the relative influence of the morphological parameters on autorotation, bivariate correlation followed by multiple linear regression analysis was conducted. The multicollinearity of independent variables was assessed through the variance inflation factor (VIF) and the eigenvalues of the regression matrix. Samples from each location were analysed independently. Regression analyses were performed with SPSS ver. 20 (IBM) and other statistical analyses with plots were performed using R, ver. 4.5.1 (www.r-project.org). The analyses in R, we used the packages 'ggplot2' for data visualization (Wickham 2016), 'dplyr' for data manipulation (Wickham et al. 2025), 'patchwork' for combining multiple plots (Pedersen 2025) and 'ggpubr' for publication-ready plots (Kassambara 2023).

Results

Development of the diaspore

The entire fruit of *Getonia floribunda* acts as a dispersal unit or diaspore. In terms of structure, this fruit is homologous to the flowers since it is a modified structure of the entire flower after fertilisation. From the fertilized flower to the fruit, the pistil must undergo many changes, including the transformation of the ovule into a seed, but the shape of the pistil or ovary in *Getonia floribunda* changes relatively little compared to the sepals. *G. floribunda* requires approximately one to two months from flower opening and fertilisation to modification of the entire flower into a mature dispersal unit. Generally, the flowering of this plant begins in January, and its dispersal of fruits occurs in March, and it may last up to April. A gradual transition from buds to flowers and ultimately to fruits was observed (Fig. 3). Flowers are borne in the dense

axillary racemes, and their anthesis begins from base to apex. In the bud stage, each flower has a leaf-like bract at its base (Supporting information). This leafy bract protects the entire bud at its early stages of flowering. After fruit development, this will fall off. Flower buds are characterised by a prominent middle constriction and lower slightly curved ovary region covered with dense hairs (Fig. 4E) and upper valvately closed perianth lobes or tepals (Fig. 3A and B). After 10 to 15 days of bud initiation, it reaches its maximum size and begins to open the perianth whorls (Fig. 3C and D). When the flower is fully opened, the perianth whorls or tepals are seen entirely curved downward by touching their apex into the middle-constricted portion of the flower (Fig. 3D). These perianth whorls are linear elliptic or obovate with acute apex, a spongy texture, light greenish, and both surfaces densely covered with hairs (Supporting information). Stamens are visible above the perianth tube only at this time. Following fertilisation of the opened flower, dehiscent anthers fall off within a period of two to three days, leaving only filament in the mouth of the perianth tube. At this time, the curved tepals also began to expand and bend upward (Fig. 3E and F). The ovary began to develop into fruit during this stage, with pronounced ridges and grooves developing on its outer surface. After 10 to 15 days, the wings of this flower take on a specific geometry and configuration as a result of structural modification through the expansion of cells, curving of wings, and differentiation of dorsal and ventral surfaces (Fig. 3G and H). Later, when the fruit gradually lost water content and reduced weight, it took the shape of a dispersing diaspore. Fruits are brownish at this point, and all the bracts and leaves have detached (Fig. 3I and J). Finally, densely packed panicles with dry brownish fruits remain; this is an adaptation for easy dispersal in strong winds (Fig. 3I). The overall change that takes place during this diaspore development is the transformation of tepal morphology and configuration (Fig. 3).

Morphology and configuration of the diaspore

The diaspore in *Getonia floribunda* is a fruit with five persistent perianth lobes or tepals arranged in a cyclical pattern above the perianth tube (Fig. 4A and B). Rarely, six or seven wings are also observed in dispersing fruits. The length of the diaspore is 1.3–2.0 cm (length of the long axis), the width is 2–3 cm (maximum diameter of the long axis), and the projected area of the wings varies according to the configuration or fold angle of the wings (Supporting information). Fig. 1 shows technical illustrations of *G. floribunda* fruit in a vertical position, with its five curved wings inclined at a specific angle with respect to the vertical symmetry axis of the diaspore. The diaspore is almost spatially triangular, three-dimensional in configuration due to the distinct symmetrical arrangement of the wings at the apex of the fruit in its vertical axis (Fig. 4C). The base of the diaspore is the fruit, which is 6–8 × 2–3 mm (length of the long axis multiplied by the maximum diameter of the cross section), narrowly elliptical with a point tipped at the basal region and narrowly constricted at the upper region, and its outer surface is covered with prominent ridges and furrows covered with numerous hairs (Fig. 4F). Wings are persistent, modified tepals placed above the perianth tube. The

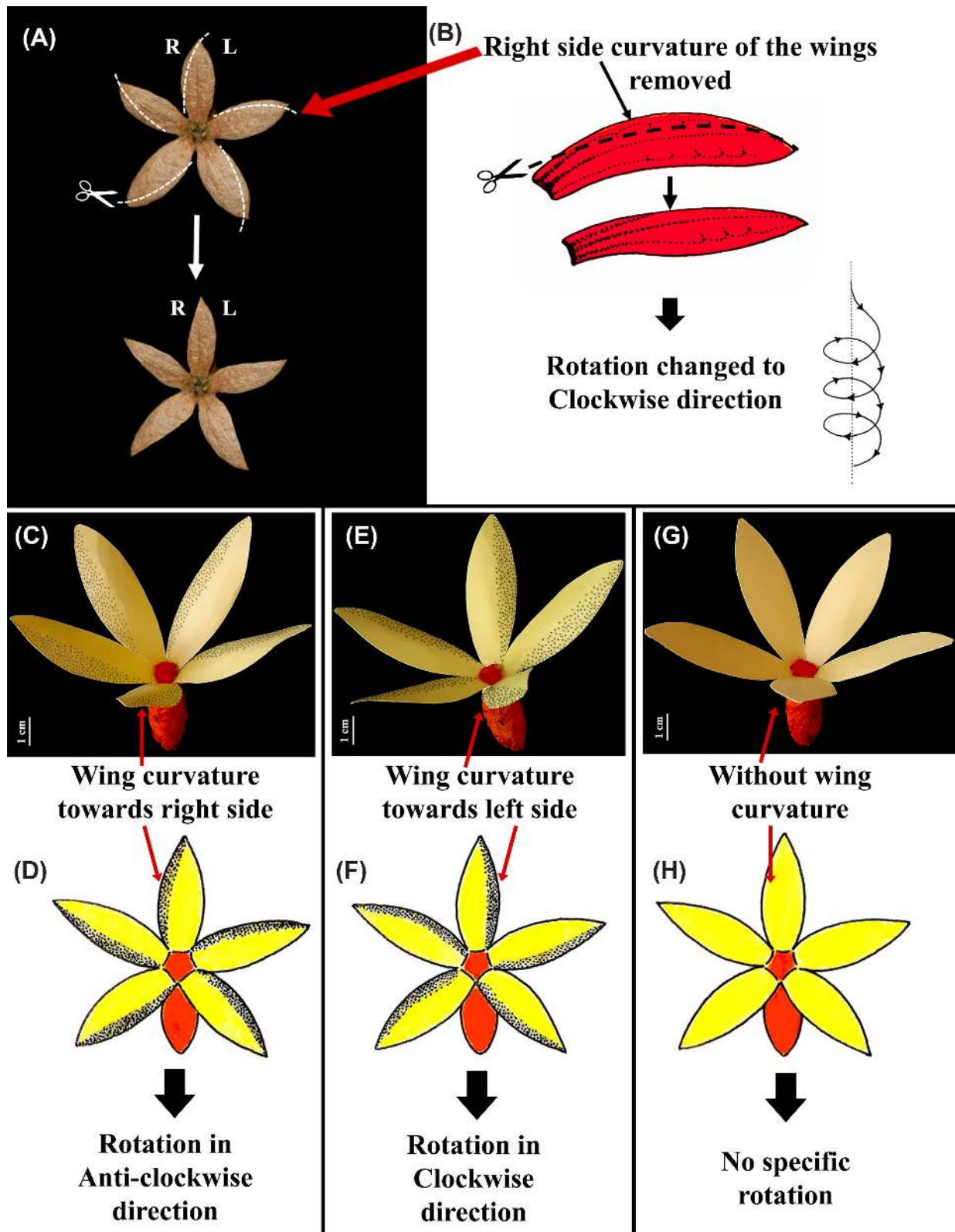


Figure 2. Result of experimental studies in *Getonia floribunda* Roxb. diaspore. (A) and (B) Result of wing modification experiment, (C–H) result of paper model experiments (R = right; L = left).

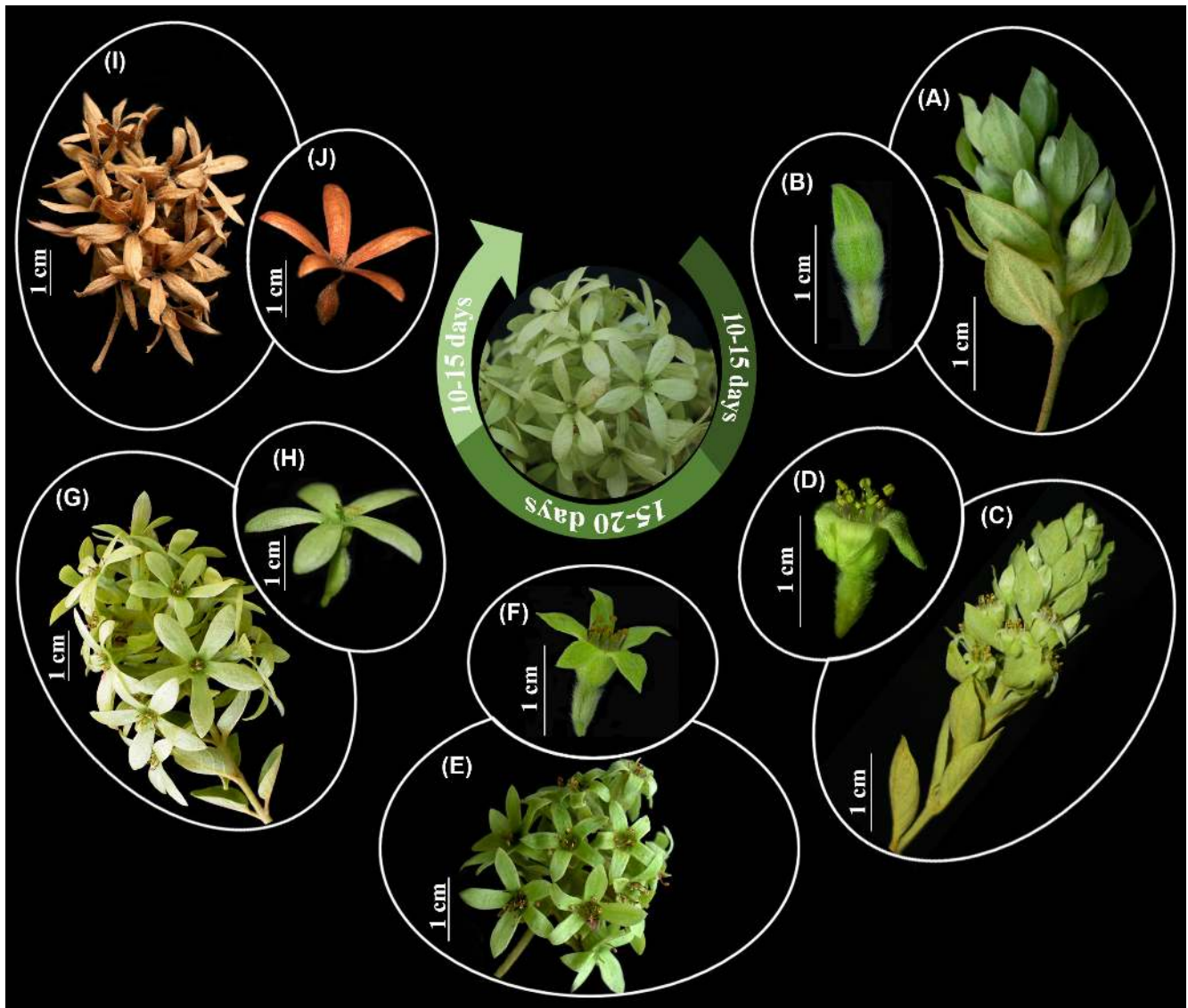


Figure 3. Development of the fruit of *Getonia floribunda* Roxb. (A), (C), (E), (G), (I) Transformation of buds to fruits in an inflorescence branch, (B) (D) (F) (H), (J) transformation of a single bud to fruit. Figure D and G reproduced with permission from Drisya et al., 2022 Copyright © 2022, Rheedea.

perianth tube is the small campanulate region that serves as the connecting link between fruit and wings in the diaspore and is 2–3 mm in length and 2–3 mm in width, with villous ridges and furrows. There is a prominent constriction present in the area where the perianth tube is attached to the fruit (Fig. 4A).

Wings are linear-obovate, linear-elliptic, or oblanceolate with 1.0–1.7 mm length and 2–6 mm width at the region below the apex and 2.0–2.5 mm width at the basal portion (Fig. 4G). The tip of the wing is broad and tapering to an acute apex (Fig. 4G), with an outward horizontal tip curvature (Fig. 4A). These wings are light brownish in mature fruits, with prominent dorsiventral differentiation; the dorsal surface is smooth and convex (Fig. 4B and 5D), and the

ventral surface is concave with ridges of veins (Fig. 5E). The orientation of each wing on a diaspore varies, leading to variation in the wing fold angle of each wing with respect to its horizontal plane (Fig. 1C–H). Hence, the geometry of diaspores is mostly determined by the variations in the fold angle of the wings. Supporting information illustrates the notable range of wing fold angles observed in these diaspores. Fig. 1 displays the wing orientations that are most frequently observed in *G. floribunda* diaspores. In addition to this, when the diaspore is held towards us, we can see that each wing terminal region is slightly inclined to the right side (i.e. the leading-edge inclination of each wing) (Fig. 4H–J). Thus, the diaspores differ in terms of the fold angle/configuration, mass, length, width, and area of the wings.

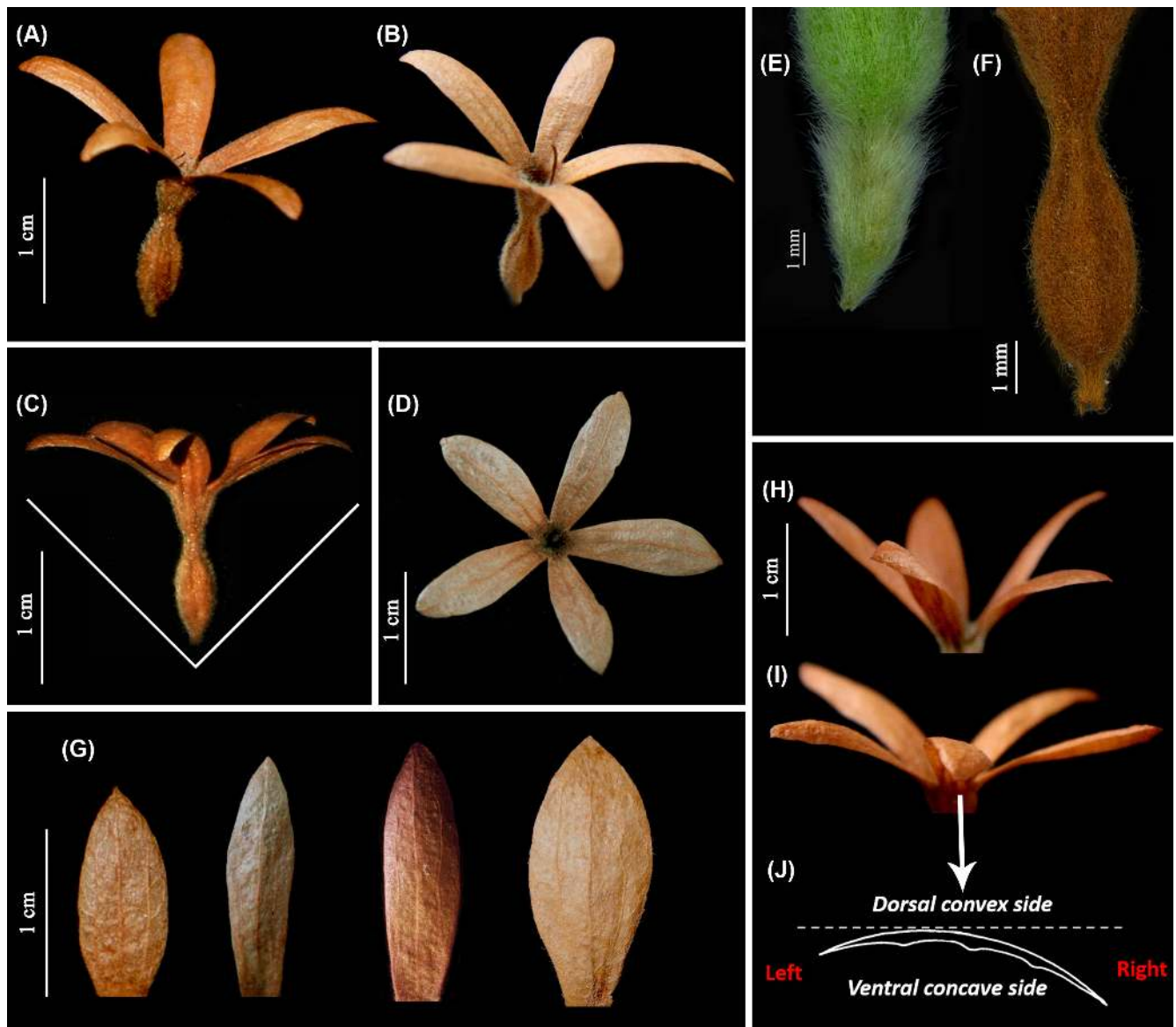


Figure 4. *Getonia floribunda* Roxb. fruit. (A) and (B) Morphology of fruit, (C) spatial trigonal configuration of the fruit, (D) arrangement of wing tepals in fruit, (E) basal ovary region during the early stages of flower development, (F) basal fruit region of the diaspore at mature stages showing narrow constriction and prominent ridges and furrows, (G) diversity in the morphology of the wings, (H) and (I) picture showing the inclination of the tip of the wings towards one side, (J) drawing showing the breadthwise inclined orientation of the tips of wings towards one side (right side here). Figure A reproduced with permission from Drisya et al., 2022 Copyright © 2022, Rheedea.

Microscopic morphology of the diaspore

The whole surface of the diaspores of *Getonia floribunda* shows micromorphological peculiarities. Unicellular villous hairs are seen on the outer surface of the fruit, the perianth tube, and both the surfaces of the wings. These are moderately dense, long, soft, often curly, and more or less erect but not necessarily straight. It is straight and densely packed at the flowering stage. However, during the fruiting stage, the water content in the hairs decreases, and they turn to become curly-villous. The fruit and perianth tube regions are more villous than the wings (Fig. 5A–C). Wings have conspicuous reticulate veins as well as dorsal convex and ventral concave

surfaces. The dorsal surface of the wings is characterised by distantly located long surface-appressed hairs with bulbous bases compared to the ventral surface (Fig. 5E and F). The ventral surface is distinguished by prominent ridges of three veins with densely packed curly unicellular hairs and numerous large peltate multicellular glandular hairs in the intervein region (Fig. 5H–K). These unicellular and glandular peltate hairs are also present on the lower surface of the leaves of this plant. In dry, dehiscent fruits, all hairs are dry, curled, and exhibit a consistent pattern of surface striations. Peltate glandular hairs were observed shedding their contents and bulginess to form a cup shape in mature, dehiscent fruits.

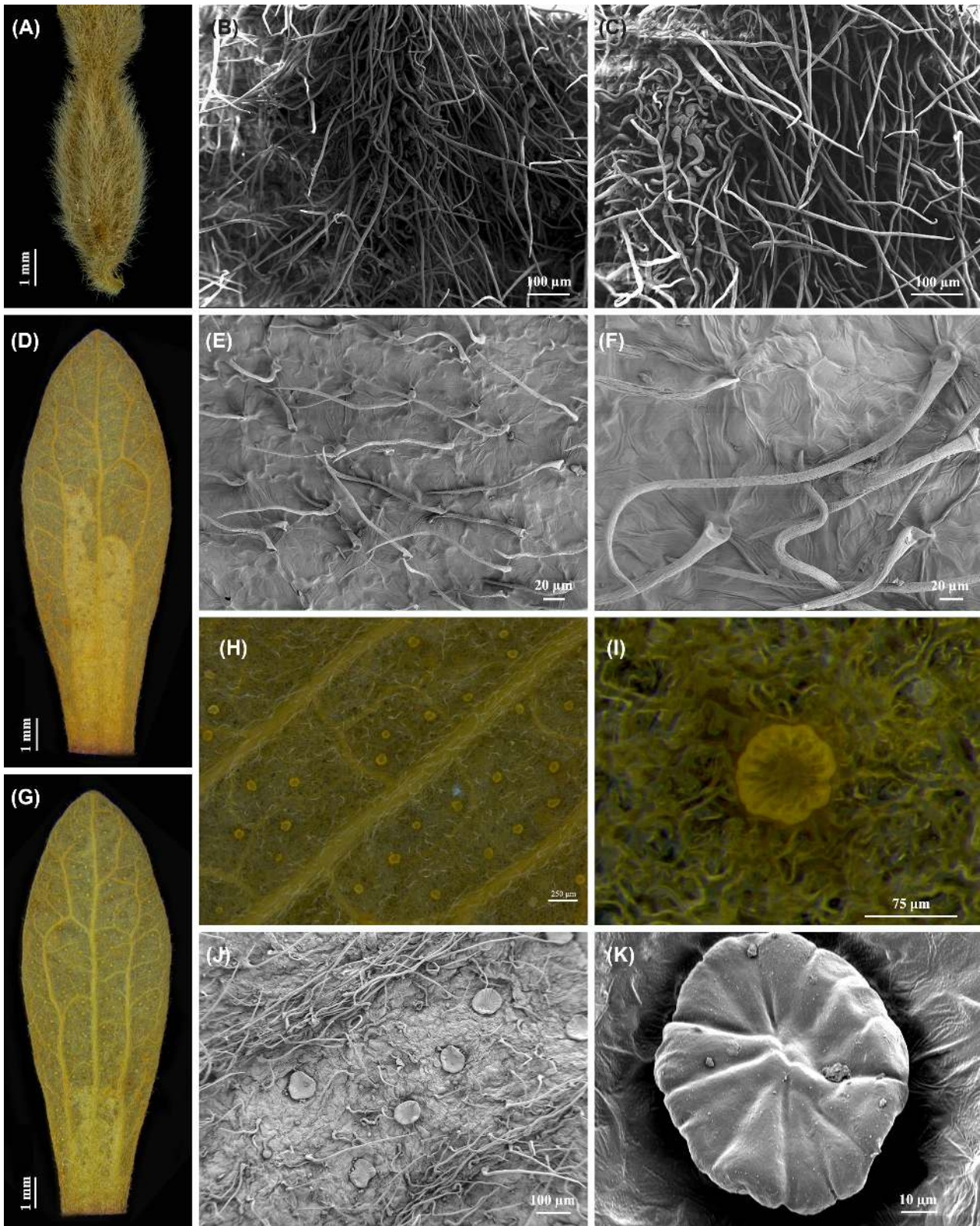


Figure 5. Microstructure of *Getonia floribunda* Roxb. diaspore. (A) Ovary part showing hairs, (B) and (C) hairy texture of the ovary region, (D) dorsal view of the wing tepal, (E) and (F) hairy texture of the dorsal region of the tepal, (G) ventral view of the wing tepal, (H) and (I) microscopic view of the ventral region of the tepal, (J) and (K) unicellular and peltate glandular hairs of the ventral region of the tepal. Images A, D, G, H, and I show the results observed under an optical microscope; images B, C, E, F, J, and K show the results observed under a scanning electron microscope.

The outline of the wing in cross-section varies in different stages of development (Fig. 6). When compared to mature ones, the dorsal and ventral surface distinction of the wing is relatively minimal at younger stages. At the time of dispersal, tepal breadth is high and thickness is less than that in the early phases. The upper and lower epidermises are uniseriate in cross-section of the wing, with large and small cells interspersed, and are covered by thin cuticles and many unicellular hairs. Moving from either the epidermis to the centre, three distant vascular bundles and irregularly shaped, thin-walled, tubular chlorenchyma that resembles spongy parenchyma cells of leaves are observed (Fig. 6A–F). Intervein chlorenchyma cells are very closely packed in immature wings (Fig. 6C), but in mature wings, these cells are loosely packed due to wing growth and the creation of vast air spaces in between them, which also lead to non-specific orientations of these cells (Fig. 6I–M). As a result, the area of wings increased, and the thickness of the interven region relative to the vascular region decreased. As wings mature, the chlorenchyma tissue shrinks to minimise weight by losing its cell inclusions and water content. Consequently, the ventral portion of mature wings has three prominent ridges of veins (Fig. 6F). This is one of the major transformations developed in the wings to achieve a specific geometry or configuration for flight.

Each wing has three vascular bundles, which are symmetrically structured by a primary vascular bundle in the centre and two lateral minor vascular bundles on either side of the middle one (Fig. 6C and F). The arrangement of veins in the wing serves as the structural backbone, providing rigidity and support. The middle vascular bundle is made up of xylem and phloem tissues embedded in sclerenchyma fibres, externally covered (lining both epidermises) by uniformly arranged parenchyma cells without intercellular spaces (Fig. 6H–J). Therefore, the vascular region is denser than the interven regions. Lateral vascular regions are smaller than the middle, which also comprises vascular tissues covered by sclerenchyma fibres (Fig. 6K and L). There are some parallelly arranged transfusion tissues or transport canals that occur in the interven region. The lower epidermis of the wing is highlighted by unicellular hairs and multicellular, cup-shaped, peltate glandular hairs (Fig. 6N and O).

Falling behaviour of diaspore

During dispersal, diaspores of *Getonia floribunda* perform anticlockwise autorotation in their vertical axis passing through its centre of mass (Fig. 7A). A diagram illustrating the vertical trajectory of diaspore is shown in Fig. 7. From the field observations and experimental studies, two distinct phases were observed during autorotation: the initial change of orientation or transition phase known as falling and flipping (Eadkong et al. 2020) (Fig. 7B and C), and then the continuous autorotation in its vertical axis, i.e. the autorotating phase (Fig. 7B and C). In any circumstances, only an anticlockwise direction of rotation was observed in all diaspores of *G. floribunda*. In the field conditions, the high velocity of horizontal wind changes its straight vertical line path into an inclined path without changing its direction of

autorotation (Fig. 7C). Therefore, the distance of dispersal of diaspore depends upon the release height (height of parent plant), wind velocity, and velocity of autorotation.

The falling and flipping phase in *G. floribunda* diaspore is relatively short, due to the comparatively small size and symmetrical shape of the diaspore (Fig. 7B and C). In natural conditions, due to the sessile nature of the flower, the base of the fruit is connected to the peduncle. As a result, the circularly arranged curved wings were pointing freely outward from the inflorescence branch; this configuration allows the diaspores to disrupt the airflow and move easily away, along with the horizontal wind. Consequently, at the time of first release, the wings of the diaspores face downward, but it quickly reverses its posture by facing the fruit region downward and its wings upward. Compared to the autorotating phase, this transition period in *G. floribunda* diaspores is much shorter (Supporting information). Following this phase of transition, the diaspore quickly begins to fall rapidly due to gravity. However, because of the action of aerodynamic forces on wings, as the autorotation phase starts, a lift force develops, which counteracts the gravity pull, and the net force acting on the diaspore becomes zero. This will lead to the movement of the diaspore with a constant speed soon after starting autorotation, i.e. the fruits attain a terminal velocity. After attaining terminal velocity, the descent rate of the diaspore is comparatively less than the initial rotating time. This is advantageous for the diaspores to carry far along the wind. Hence, the descent rate of the diaspore depends upon the falling and flipping phase, the start of autorotation, and how fast the diaspores attain terminal velocity.

Mechanism of autorotation

After falling and flipping, the diaspore starts to autorotate in its vertical axis in an anticlockwise direction. This autorotation of diaspore is the result of three forces, namely, the gravity force, the drag force, and the lift force. During a fall, the force of gravity (F_G) acts in a downward direction. The asymmetry of wings causes an equivalent and opposite air force acting vertically upward, F_N . It is the result of lift forces (F_L) and drag forces (F_D) acting on the wings. F_L is the force perpendicular to the wingspan and creates lift. F_D is the drag/reaction force acting opposite to the curvature of the wing; it creates rotation of the wing (Fig. 8A).

During fall, due to the weight of the diaspore, the reaction force (F_D) created is on the curved phase of the wing as shown in Fig. 8B. The right-side inclined configuration of the wing pushes the air more downward, so there is an equivalent and opposite reaction force acting on the curved side of the wings (Newton's third law of motion); it is called a reaction force. Due to the cyclical-wing nature, the same reaction force acts in the opposite direction in the wings of the other side. This produces a couple of forces, and due to this, the fruit starts to rotate within the axis of rotation passing through its centre of mass in the anticlockwise direction (Fig. 8A).

During the wing modification experiment, the removal of the right-side wing-tip curvature (leading edge of the diaspore) resulted in a change in its natural anticlockwise

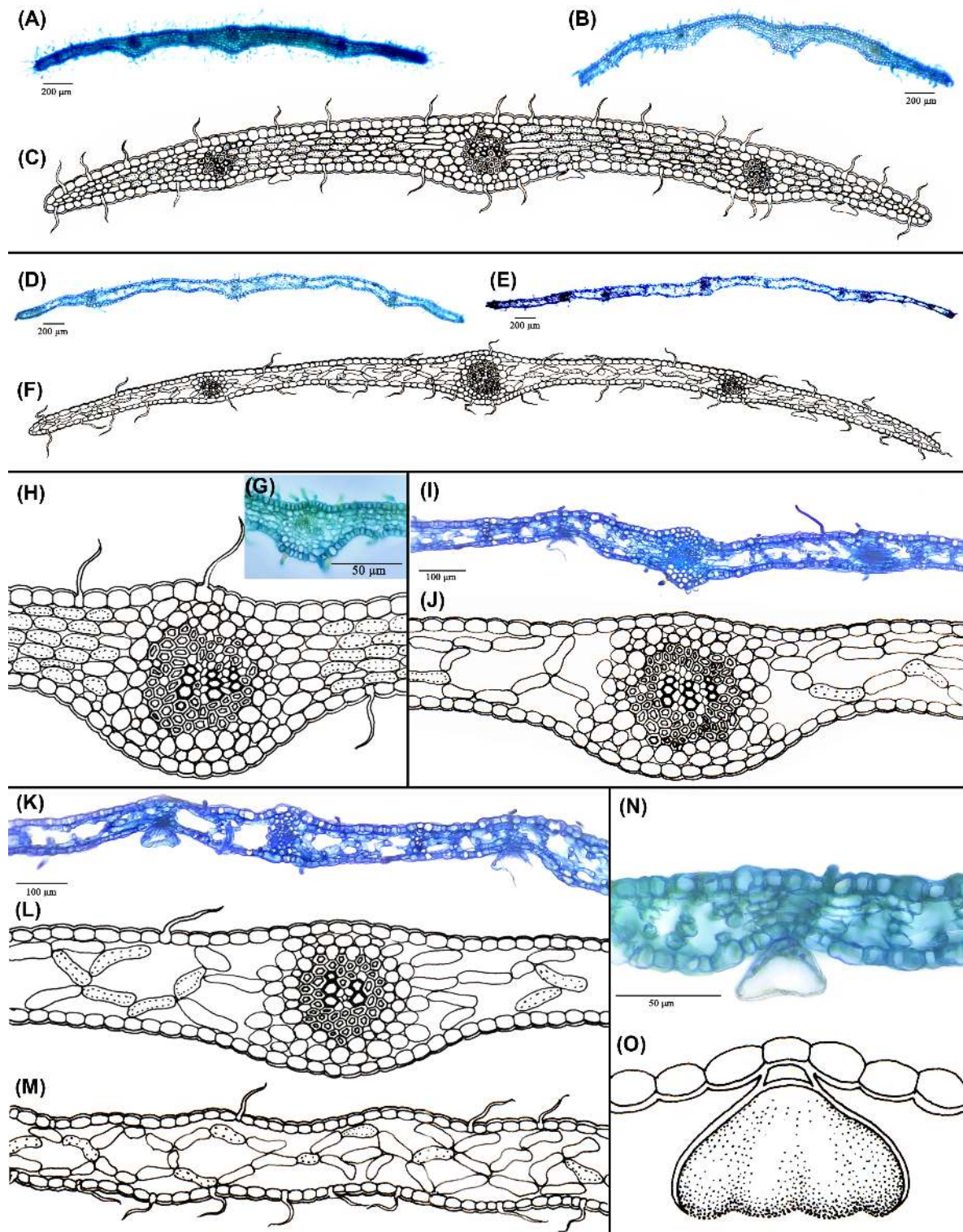


Figure 6. Anatomy of wings in *Getonia floribunda* Roxb. diaspores. (A) and (B) Cross-section of wing at early stages of development, (C) enlarged cellular drawing of images A and B, (D) and (E) C.S. of wing at mature stages, (F) enlarged cellular drawing of images D and E, (G) C.S. of wing showing central vascular region and closely packed intervein chlorenchyma cells, (H) enlarged drawing of the image G, (I) C.S. of wing showing central vascular region and loosely packed intervein chlorenchyma cells with vast air spaces in between them, (J) enlarged drawing of the image I, (K) C.S. of intervein and lateral vein region of mature wings, (L) enlarged drawing of lateral vein region of mature wings, (M) enlarged drawing of inter vein region of mature wings, (N) C.S. of peltate gland of wing, (O) enlarged drawing of image N.

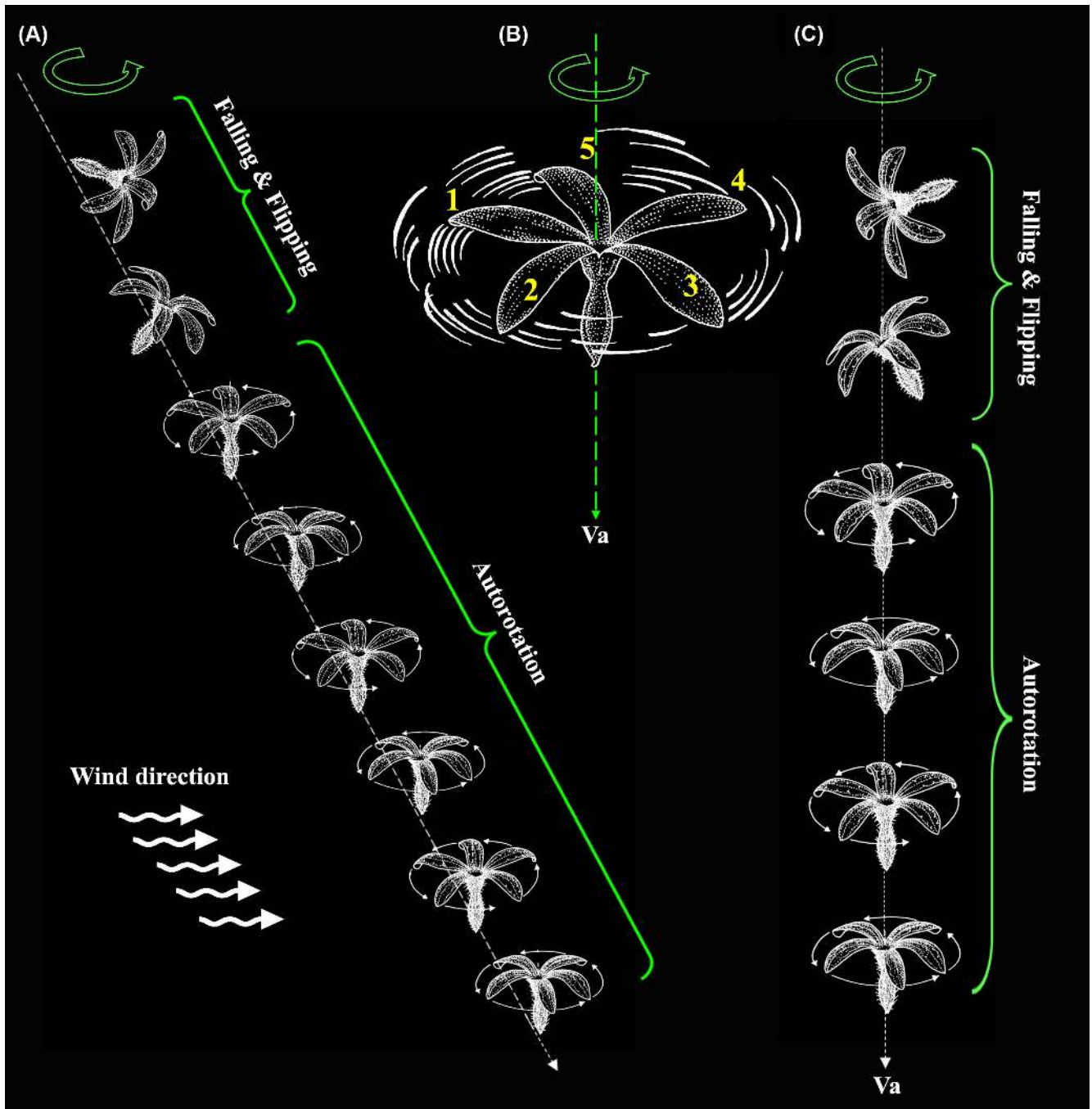


Figure 7. Autorotation in *Getonia floribunda* Roxb. fruits. (A) Autorotation of diaspore in disturbed air, (B) vertical anticlockwise direction of rotation in diaspore, (C) autorotation of diaspore in still air (V_a = vertical axis). Figure C reproduced with permission from Drisya et al., 2022 Copyright © 2022, Rheedea.

direction of rotation to a clockwise direction (Fig. 2A and B). A trailing edge to leading edge transformation was observed. The paper model constructed with wing curvature opposite to the natural diaspore, i.e. curvature towards the left side (at the trailing edge), also resulted in a clockwise direction of rotation (Fig. 2E and F). Therefore, in *G. floribunda* diaspores, a right-side or leading-edge curved configuration of

the wing tips is the determining factor of its specific anti-clockwise direction of rotation during dispersal.

The initial falling and flipping phase of the diaspore is primarily due to its roughly spatial triangular geometry and distribution of the centre of mass along the central-vertical axis of the diaspore. The configuration of the wings and texture of the diaspore are other factors that help to change the

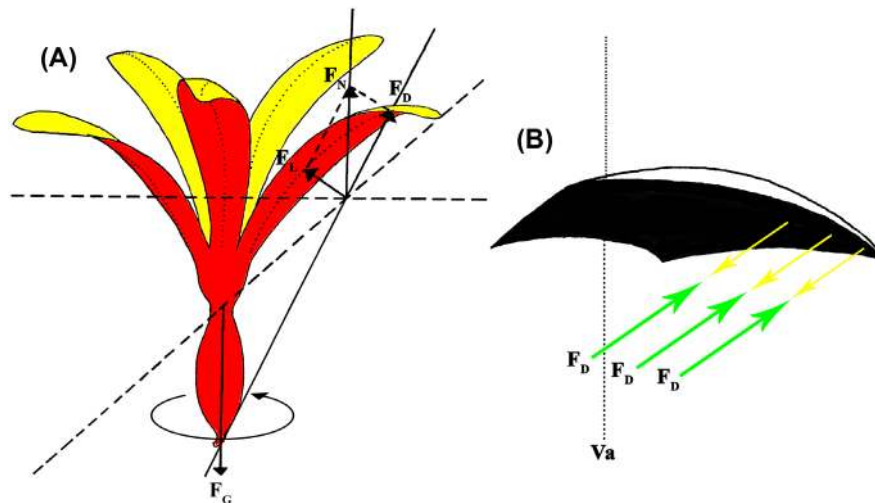


Figure 8. Mechanism of autorotation in *Getonia floribunda* Roxb. diaspore. (A) Diagram showing forces acting on the diaspore during falling, (B) cross-section diagram of a single wing showing reaction force acting on the curved side for anti-clockwise rotation (F_G = gravity force; F_D = drag force; F_L = lift force; F_N = net force [$F_D + F_L$]; Va = vertical axis).

orientation during falling. The smooth, convex upper surface of the wings facilitates an easy flow of air over the surface, and this leads to a decreased air pressure on the surface. The lower side of the wing has a concave surface with ridges of veins and a hairy texture, which leads to a disturbance in airflow, and this creates higher air pressure on the lower surface than on the upper surface of the wing. This air pressure difference between the upper and lower surfaces of the wings, and the centre of mass distribution along the middle vertical axis of the diaspore with a pointed, elongated, semi-perpendicularly arranged fruit region of the diaspore leads to a change of orientation during the fall.

Factors affecting autorotation

Diaspores from different plants as well as from the same plant, show considerable variations in weight, area of wings, length, width, wing fold angle, and wing loading (Supporting information). Measurements of morphological parameters such as weight of diaspore, area of wings, length of wings, width of wings, wing fold angle and wing loading, and measurements of autorotation, including descent rate, terminal velocity, flipping and rotating time of diaspores of plants of four locations are shown in Supporting information. ANOVA resulted a statistically significant differences in weight ($F=87.73$, $p < 0.001$), area of wings ($F=102.7$, $p < 0.001$), length of wings ($F=71.06$, $p < 0.001$), width of wings ($F=81.41$, $p < 0.001$), wing fold angle ($F=7.343$, $p < 0.001$) and wing loading ($F=5.963$, $p < 0.01$) of *G. floribunda* diaspores across four locations. Then the Tukey's post-hoc test revealed significant pairwise differences in weight and area of wings between all locations ($p < 0.001$) except locations III and II (Supporting information); a significant pairwise differences in length of wings between locations II and I, III and I, IV and II, IV and III ($p < 0.001$) (Supporting information); significant pairwise differences in width of wings between locations III and I, IV and I, IV and II, IV and III ($p < 0.001$)

(Supporting information); significant pairwise differences in wing fold angle between locations III and I, IV and II, IV and III ($p < 0.05$) (Supporting information); and a significant pairwise differences in wing loading between locations III and I, III and II, IV and III ($p < 0.05$) (Supporting information) respectively. As a consequence, the descent rate and terminal velocity vary in diaspores, following these factors.

According to the bivariate correlation analysis of morphological measures on descent rate, in location I (< 0.05 level) and location III (< 0.01 level), only the wing fold angle shows a significant positive correlation with descent rate, while in location II (wing fold angle at < 0.01 level and wing loading at < 0.05 level) and location IV (wing fold angle and wing loading at < 0.01 level) samples, the wing fold angle and wing loading exhibit significant positive correlation. Therefore, multiple linear regression analysis was performed to investigate the effects of morphological parameters on descent rate and terminal velocity. After removing variables with high multicollinearity by checking the variance inflation factor, wing fold angle and wing loading were selected as independent variables in the analysis model. From the t-test results conducted for examining the significance of coefficients of independent variables, we observed that only the wing fold angle has a significant relationship ($p < 0.05$) with the descent rate in samples of all four locations (Table 1, Fig. 9A). The relationship between wing fold angle and descent rate was strongly positive in samples of all four locations ($R^2=0.492, 0.682, 0.828, 0.676$, respectively). At any location, there was no significant relationship between wing loading and descent rate ($p > 0.05$) (Fig. 9B). Similarly, correlation analysis of morphological measures on the terminal velocity of samples from four locations shows that the wing fold angle exhibits a significant ($p < 0.01$) positive correlation with terminal velocity. In addition to this, wing loading ($p < 0.05$) also exhibits a significant positive correlation in location IV. Results of multiple regression analysis also show

Table 1. Multiple regression analysis of wing fold angle and wing loading on the descent rate of four samples of locations (n = 10, p < 0.05).

	Model	Unstandardized coefficients		Standardized Coefficients	t value	p value	Collinearity statistics		Partitioned R ²	F
		B	SE				Tolerance	VIF		
Location I	Constant	0.704	0.126		5.594	0.001				4.578
	Wing fold angle	0.003	0.001	0.699	2.605	0.035	0.860	1.163	0.492	
	Wing loading	0.853	1.884	0.121	0.453	0.664	0.860	1.163	0.028	
Location II	Constant	0.455	0.199		2.291	0.056				15.188
	Wing fold angle	0.013	0.003	0.748	3.874	0.006	0.718	1.393	0.682	
	Wing loading	3.820	3.026	0.244	1.263	0.247	0.718	1.393	0.186	
Location III	Constant	0.800	0.116		6.919	0.000				19.560
	Wing fold angle	0.009	0.001	0.965	5.809	0.001	0.786	1.272	0.828	
	Wing loading	-1.180	1.869	-0.105	-0.631	0.548	0.786	1.272	0.054	
Location IV	Constant	0.708	0.164		4.309	0.004				26.472
	Wing fold angle	0.014	0.004	0.977	3.820	0.007	0.255	3.917	0.676	
	Wing loading	-0.535	3.187	-0.043	-0.168	0.871	0.255	3.917	0.004	

that the wing fold angle of all four locations only shows a significant relationship ($p < 0.05$, $R^2 = 0.612, 0.829, 0.634, 0.880$, respectively) with terminal velocity (Fig. 10A). Hence, according to regression analysis, the wing fold angle shows a more linear positive relationship with descent rate and terminal velocity (Fig. 9A, 10A). The predictive accuracy of the models with descent rate as a dependent variable and wing fold angle as an independent variable are obtained as 49.2 and 67.6%, respectively.

The effect of wing fold angle and wing loading on the flipping and rotation time of samples from four locations showed a nonuniform result. Wing fold angle and wing loading exhibit a negative correlation with rotating time in all locations (Fig. 11). Among these, a significant correlation of

wing fold angle with rotating time (< 0.01) was observed in locations II and III. Wing loading of location II (< 0.05) and location IV (< 0.01) samples exhibits a significant correlation with rotating time. Location I samples do not display a significant correlation between wing fold angle and wing loading with rotation time. In the case of the relationship with flipping time, wing fold angle exhibits a negative correlation in all locations (Fig. 12A), but wing loading shows a positive correlation with flipping time in locations I and III and a negative correlation in locations II and IV (Fig. 12B). This indicates that morphological parameters of *G. floribunda* diaspores are the major determining factors that show a significant relationship with descent rate and terminal velocity and ultimately affect their aerodynamic and dispersal potential.

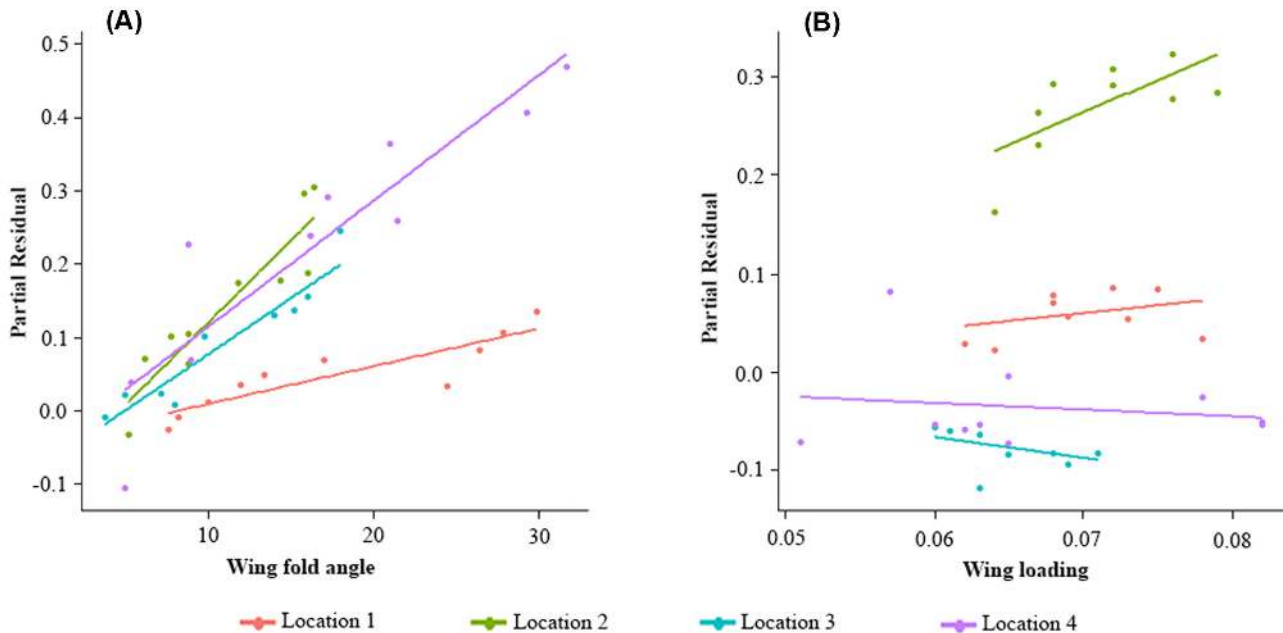


Figure 9. Plots showing the results of regression analysis in the diaspores of *Getonia floribunda* Roxb. (A) Combined partial regression plots of wing fold angle on descent rate across four locations, (B) combined partial regression plots of wing loading on descent rate across four locations.

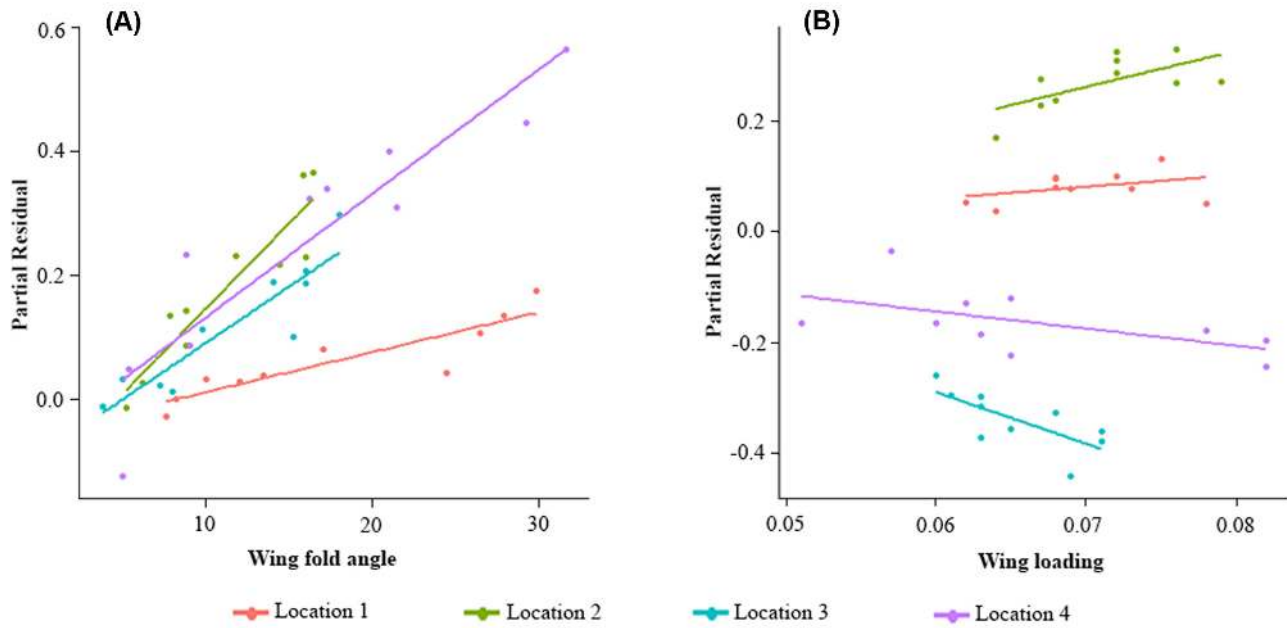


Figure 10. Plots showing the results of regression analysis in the diaspores of *Getonia floribunda* Roxb. (A) Combined partial regression plots of wing fold angle on terminal velocity across four locations, (B) combined partial regression plot of wing loading on terminal velocity across four locations.

Discussion

Overall morphology in winged diaspores determines their aerodynamic behaviour during fall and eventually their dispersal capacity. Specific morphological adaptations in *Getonia floribunda* diaspores facilitate their autorotation during dispersal. The morphology, micromorphology, anatomy, configuration, and curvature of wings and the geometry of the diaspore are adaptations for a specific autorotation.

Relationship between qualitative morphological characters and autorotation of diaspores

The biomaterial in plant wings imparts them with mechanical resistance to flying forces during wind dispersal. This is related to macro-to-microscale structural and mechanical features. The vein network within the wings serves as a mechanical ladder, while the material found between the veins serves as the aeronautical surface for the development of flight forces (Ezra et al. 2023). These structural mechanical laws

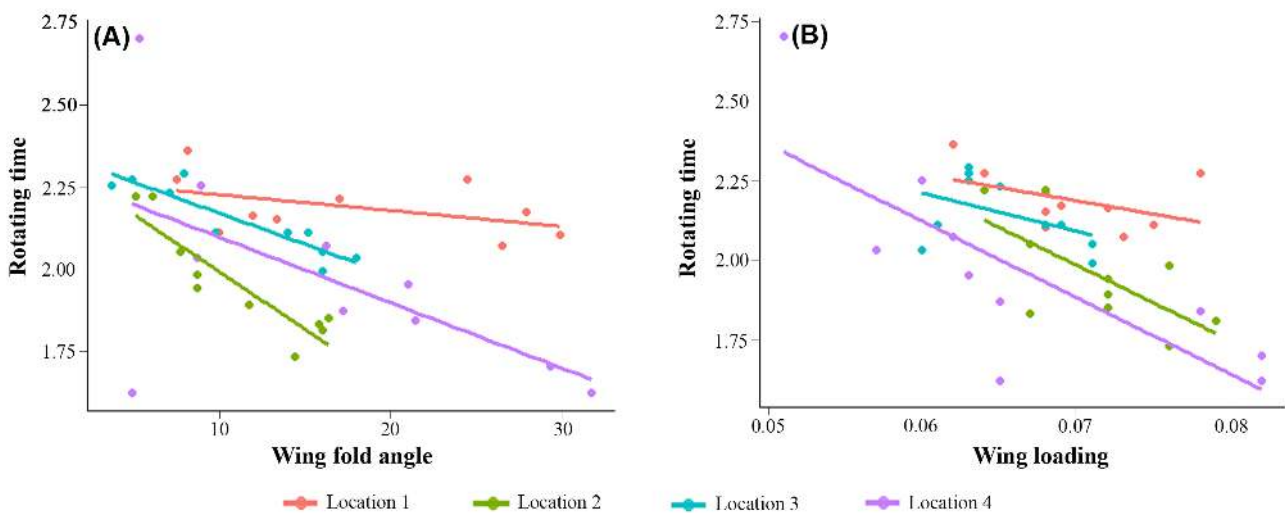


Figure 11. Plots showing the results of correlation analysis in the diaspores of *Getonia floribunda* Roxb. (A) Combined correlation plot of wing fold angle versus rotating time across four locations, (B) combined correlation plot of wing loading versus rotating time across four locations.

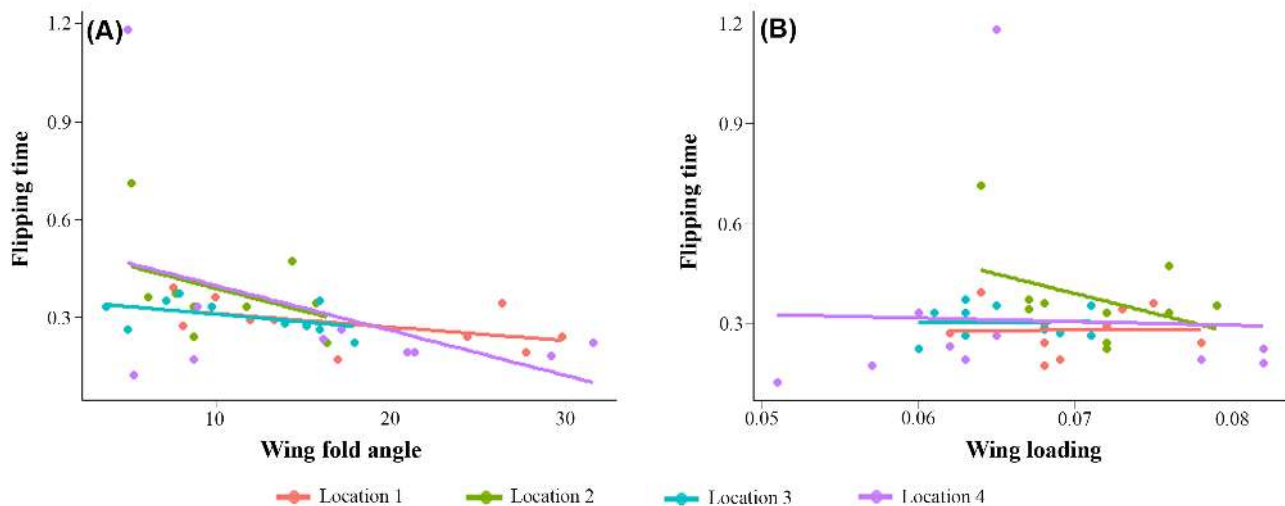


Figure 12. Plots showing the results of correlation analysis in the diaspores of *Getonia floribunda* Roxb. (A) Combined correlation plot of wing fold angle versus flipping time across four locations, (B) combined correlation plot of wing loading versus flipping time across four locations.

governing the wings of plants exhibit novel design ideas that open the door to the creation of small-scale wing components for miniature aviation platforms with specialised mechanical capabilities (Fregene 2012, Floreano and Wood 2015, Kim et al. 2019, Ezra et al. 2023). Similarly, the biomaterial in the wings of *G. floribunda* diaspore primarily imparts the physical shape of the wings; through this, they sustain the aerodynamic loadings for autorotation. Three veins in the wings act as mechanical scaffold and structural framework for binding intervein materials and the building up of aeronautical surfaces. The presence of numerous sclerenchyma fibres in the veins is an adaptation to provide additional mechanical strength to the veins. During developmental stages, numerous air spaces are developed in the intervein region by degrading or displacing the chlorenchyma cells, which is also an adaptation for offering buoyancy in the air. According to the research on autorotating *Tipuana tipu* (Benth.) Kuntze tree samaras, the load-bearing mechanism begins at the global vein texture, which supports the flight forces, comes down into the microtubular arrays, which support the forces within the veins, and culminates at the cell walls, which support the forces within the microtubules (Ezra et al. 2023). In the case of diaspores of *G. floribunda*, we currently have little information about microscopic cellular changes during the transformation of the perianth whorl to the wing. For a better understanding of the load-bearing mechanism, hierarchical structural characteristics down to the micrometre scale with the use of electron microscopy and computed tomography study (Ezra et al. 2023) are needed. This will help to learn more about how structural mechanisms emerged in these spinning fruits, which could lead to the development of novel microengineering design concepts for sophisticated aerofoils.

The presence of villous hairs on the outer surface of the fruit and wings of the diaspore is an adaptation to increase the drag force for a slow descent since the airflow around the

object could be altered by a change in surface (Thomson and Neal 1989). Hairy nature makes the surface rough, which disrupts airflow and increases drag in the opposite direction of the moving surface. Swimmers and cyclists removing their body hair and using smoother bodysuits are some of the live examples of the drag effect of surface hairs and rough textures. Smoother ‘skin’ and more compression forces on a swimmer’s body provide at least 10% less drag than hairy skin; hence, many swimmers in the 2008 Beijing Olympics wore (Speedo) bodysuits: it might have made a difference in breaking many world records (Moebs et al. 2016). It is interesting to note that winged diaspores need to increase the drag force to reduce the descent rate. *G. floribunda* diaspores have more villous hairs in the lower region of the fruit because it is the region where the centre of gravity is affected; to reduce this effect of gravity force, they need to roughen the surface. The less hairy character of the top convex side of the wings is another micromorphological adaptation to increase the lift by decreasing air pressure on the upper surface of the wings more than that on the lower surface. Comparatively hairier ventral surfaces with prominent striations of veins and peltate sessile glands also help to increase air drag and pressure in the ventral surface of the wings. SEM analysis of the diaspore hairs of *G. floribunda* reveals that during the time of dispersal, the outer surface of the hairs was not smooth but instead had parallel striations (Fig. 5F). These striations contribute to increased lift forces. Perhaps they serve both as vortex producers and confiners (Tennakone 2017).

Quantitative analysis of morphological features and their role in autorotation

The ideal three-dimensional, triangular, five-winged arrangement of diaspore provides a more stable design that supports the vertical axis of rotation, similar to the motion observed in the fruits of Dipterocarpaceae. Five wings are arranged

symmetrically at the apex of the fruits, which makes it easier to change positions during the initial fall and quickly attain terminal velocity. However, Tennakone (2017) asserts that an increase in the number of wings in *Dipterocarpus*, which resembles multi-winged helicopter fruits also provide stability, but it is not favourable for their efficient dispersal through autorotation. Due to this, as part of selection, a cut down in the number of wings was observed in *Dipterocarpus* for slow descending (Tennakone 2017). However, diaspores in *G. floribunda* are much smaller than the whirling fruits of Dipterocarpaceae, and their weight has a positive correlation with the area of their wings. Another explanation for its stable spinning is that the wings are attached above the fruits rather than at the base of the fruit, as in *Dipterocarpus*. Thus, a reduction in the number of wings in *G. floribunda* diaspores delays the initial flipping of position and the start of autorotation. Five wings in this diaspore increase the moment of inertia and decrease the angular velocity and terminal velocity, which helps in long-distance transport through the wind. A natural selection towards the most suitable number of wings according to their morphology is observed here. The position of the centre of gravity is yet another important factor that determines the axis of autorotation in spinning diaspores. In *G. floribunda*, the exact position of the centre of gravity varies in each diaspore, but it always lies in the vertical axis of the diaspore. Due to this alignment of the centre of gravity along the vertical axis and its triangular configuration as in the fruits of the Dipterocarpaceae family, stable vertical autorotation happens. This alignment of the centre of gravity in the vertical axis also contributes to the initial transition of position or flipping as well.

The development of the characteristic wing morphology in *G. floribunda* is a key feature for developing aerodynamic forces and performing autorotation. Gravity primarily affects the seed portion of autorotating diaspores, while aerodynamic lift and drag forces, as well as inertial forces, develop on the wing portion (Minami and Azuma 2003, Lentink et al. 2009). The development of a narrow basal region and a much wider terminal region with distinct curvature is designed for the specific autorotation in *G. floribunda*. Generally, wing-tip vortices increase with the increase in tip breadth (Sipe and Linnerooth 1995). In turn, to lessen the impact of the wing-tip vortices, ideal wings taper when they get closer to the tip (Norberg 1973), and the tips of the wings of *G. floribunda* similarly exhibit this tapering to a pointed apex. In addition to these, variations in the curvature are the most relevant morphology of wings in this diaspore, which is adapted to do specific roles for autorotation. Breadthwise curvature of each wing resulted in upper convex and lower concave surface delimitation, which gives every wing an asymmetric nature and is called cambered wings in aeronautics (Mueller and DeLaurier 2003). Such a cambered profile is efficient for creating an air pressure difference between two surfaces and lift at a zero angle of attack (McArthur 2008). This cambered wing is configured above the fruits in a manner where its terminal region bends horizontally outward and downward. This is rational from an aerodynamic perspective because the

air loading is concentrated near the tip, and the heavy tip decreases the coning angle in flight and thus increases the effective disc area by reducing the fold angle, and the blade root then helps to provide a large drag area through which the horizontal force distribution is extended widely (Azuma and Yasuda 1989).

Curvature or inclination of the wing terminal region more towards one side (it is towards the right side when the diaspore is held facing us) is another adaptation in *G. floribunda* diaspore, which determines the direction of rotation. This inclination or curvature determines the leading and trailing edge of the wings and the specificity in the direction of rotation in the diaspore. Tennakone (2017) stated that right-handedness or left-handedness in rotation can be attained either naturally by one sense of rotation being chosen as a result of the aerodynamics resulting from the design of the seed or intrinsically by the seed itself possessing a geometrical right-left asymmetry providing support to one sense of motion. Results of experiments with the removal of wing-tip curvature and paper fruit simulated experiments indicate that diaspores of *G. floribunda* come under the second category explained by Tennakone, which has a one-sided inclination that imparts their wings a geometric right-left asymmetry. Following Newton's third law of motion, this predetermined right-side curved configuration merely supports the anti-clockwise direction of wing movement. The horizontally downward and one-sided inclination of the wing tips facilitates an increase in the angle of attack on each wing and an increase in lift.

Wing fold angle developed due to the configuration or orientation of wings above the fruits, determine the rotational velocity and descent rate. Due to the five-winged nature, each wing shows variations in fold angle. This variation in fold angle could be the consequence of the congested panicle arrangement of the diaspores in the parent plant during the developmental stages. This variation in the fold angle of the wings due to their configuration alters the wing-span area, which is an important parameter in determining the rate of autorotation and descent. Since wing fold angle and initial flipping time are negatively correlated, increasing the wing fold angle results in a reduction in flipping time (Fig. 12A). However, flipping time does not exhibit a significant relationship with the descent rate (Fig. 13A), because the descent rate is dependent on the terminal velocity and the angular velocity of the remaining autorotation. In *G. floribunda* diaspores, a negative relationship between wing fold angle and rotation time is seen (Fig. 11A). The reason is that diaspores with a greater wing fold angle rotate faster, which increases terminal velocity and, in turn, speeds up the rate of descent than diaspores with a lesser wing fold angle. This impact of the wing fold angle on rotation time is the reason for the negative relationship between flipping time and descent rate.

The results of ANOVA confirm that there is a significant difference in morphological parameters between the diaspores of *Getonia floribunda* in the four locations studied. Although, the experimental studies in the samples of these locations uniformly show that morphological measures have

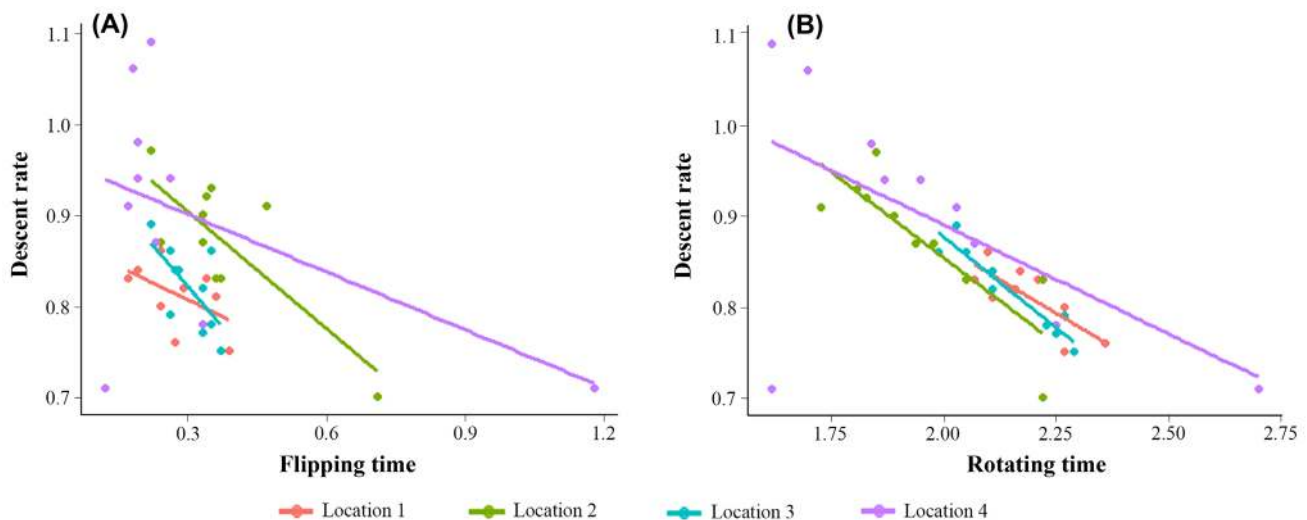


Figure 13. Plots showing the results of correlation analysis in the diaspores of *Getonia floribunda* Roxb. (A) Combined correlation plot of flipping time versus descent rate across four locations, (B) combined correlation plot of rotating time versus descent rate across four locations.

a high impact on its descent rate and autorotation. This shows that diaspores of *G. floribunda* exhibit an ecological variation in morphological parameters, but their rate of rotation depends upon the same variable. That means, the wing fold angle showed a significant relationship with descent rate and terminal velocity than other parameters (Fig. 9A and 10A) in the samples of the four location. While Augspurger's (1986) study on the effect of morphological variables on the rates of descent of six aerodynamic groups found that in all, the rate of descent of diaspores was significantly correlated with wing loading, regardless of the species or aerodynamic group. In a study, Green (1980) also found that for seven species of temperate trees, the rate of descent of diaspore is highly correlated with its wing loading. But in contrast to other aerodynamic groups, the helicopter group in Augspurger's (1986) analysis exhibited a lesser coefficient of determination of wing loading on the rate of descent. Likewise, this study shows that, in *G. floribunda* diaspores, the prediction capacity of regression models is quite low with wing loading. Wing loading for the samples of all four locations shows a positive correlation with the descent rate, but it is not significant ($p > 0.05$) to predict the regression model. According to Azuma and Yasuda (1989), the geometrical characteristics of rotating seeds, such as the span and area of the wing, the mass of the seed, the configuration of the aerofoils, the location of the centre of mass and the centre of moment, as well as the radius of gyration or moment of inertia, determine the rate of descent, spinning rate of autorotation, pitch angle, and coning angle. In the present study on the diaspores of *G. floribunda*, all the morphological variables considered show a positive or negative correlation with descent rate, but only the wing fold angle (i.e. the aerofoil configuration mentioned above) shows more significant predictive power for the regression model than other variables.

Wing loading is a valuable indication of prospective aerodynamic behaviour, but it might not reflect in all the effects

that morphological features may have on flight because it does not explicitly take diaspore mass distribution or form into account (Sipe and Linnerooth 1995). The only morphological variable that Augspurger (1986) studied was the impact of wing loading on the rate of descent, and he also noted that additional research is required to ascertain the aerodynamics of the various groups and to discover which morphological characteristics most accurately predict the rate of descent. It is challenging to compare different species based solely on wing-loading measurements since each morphological group has its own aerodynamic properties (Tomson and Neal 1989). Study of the wing loading and vertical settling time of diaspores of *Hopea ponga* by Muralikrishna and Chandrashekar (1997) resulted in no direct correlation between these two factors. Planchuelo et al. (2016) realised that wing loading would produce more precise predictions of dispersal potential in the flat diaspore than in the three-dimensional diaspore. As a result, morphological variables that can depict the three-dimensional nature of diaspores are required to give more importance to improving the prediction capacity of their dispersal potential. However, Sipe and Linnerooth (1995) and Norberg (1973) have noted that, for single-winged diaspores, planform shape is more crucial than wing loading for producing lift. Diaspores with the same wing loading can have vastly different dispersal abilities due to the effect of the three-dimensional configuration on the descent velocity. The study on the rolling samara of *Ailanthus altissima* showed that the height of the side and perimeter of the samara, which are linked to their three-dimensional arrangement, are significant variables for determining their descent velocity (Planchuelo et al. 2016). Therefore, the more significant characteristic to be taken into account when studying autorotating diaspores is their three-dimensional orientation. The diaspores of *G. floribunda* have unique three-dimensional geometry, which is determined by the way the wings are configured or folded. Consequently, when

examining wing fold angle in conjunction with wing loading to determine the effect on descent rate in diaspores of *G. floribunda*, it is clear that more than wing loading, wing fold angle has substantial predictive potential for descent rate. Augspurger (1986) defined wing loading as weight (mass $\times$ acceleration) divided by area, and using his method, here we assessed the total surface area of all helicopter wings, similarly to what he had done. Wings of *G. floribunda* diaspore are arranged cyclically above the fruits in an upward-curved three-dimensional configuration. This configuration or fold angle of each wing within and between diaspores varies. As a result, variations in wing configuration and fold angle cause changes in the drag and lift forces that occur during rotation. When the wing fold angles of *G. floribunda* increase, as indicated in the figure 1C and D, drag or air resistance for rotation lowers as a result of the span area of the wings being reduced, and vice versa. Hence, each wing lobe area in these cyclically winged fruits does not affect its span area due to the symmetrical arrangement of wings above the fruits and the distribution of weight in the middle of the diaspore in a semi-perpendicular manner. The wing configuration, or fold angle, as well as occasionally the length of the wings, determines this span area. Because of the variations in the wing configuration or fold angle above the fruits, diaspores with similar wing areas display varying span areas. Due to the different wing fold angles, the distance between the wingtip and vertical rotation axis differs; this leads to variations in the moment of inertia of wings and hence the angular velocity of rotation. When the distance between the wing tips and the vertical rotation axis rises, the wing fold angle decreases, resulting in an increase in the rotational moment of inertia and a drop in angular velocity and terminal velocity. This causes variations in the action of drag and lift forces, as well as the descent rate. Therefore, by applying the recommendations of Planchuelo et al. (2016), the examination of wing fold angles, which reflect the three-dimensional geometry in *G. floribunda* diaspore, gives a more significant result on descent rate than wing loading. These suggest that, in multi-winged autorotating diaspores like *G. floribunda*, consideration of three-dimensional geometry is of greater importance than wing loading. The feature of morphology that most accurately predicts the rate of descent differs for each aerodynamic group.

Also, Augspurger in his study (1986) noted that it will be difficult to identify the exact area of the diaspore to be measured to calculate the square root of wing loading. This study also revealed that, measuring individual wing areas for wing loading calculations is not relevant for multi-winged helicopter fruits like *G. floribunda*, while it is more significant for flat, single-winged spinning diaspores. Because, in single-winged diaspores, the area of one wing determines the span area for rotation, and the angle of rotation is defined by the area of the wing. Thus, the relationship between the area of the wings and their span is straightforward in this case. As the geometry of multi-winged autorotating diaspores is more three-dimensional, we need to consider the

span area produced by their three-dimensional arrangement of wings regardless of the wing area. Therefore, considering the wing fold angle, here shows a significant relationship with the descent rate. Rabault et al. (2019) discovered an ideal wing fold angle that produces maximal flying time while minimising descent velocity in double-winged whirling fruits. Hence, they highlight that wing curvature can aid as an efficient mechanism for wind dispersal of the whirling fruits. Diaspores of *G. floribunda* also require an ideal wing fold angle to provide the longest possible flight time. More experimental and theoretical studies are needed to find this optimum fold angle of wings in *G. floribunda* because plants adapt the form of diaspores to best suit their environment for survival. Studying more about them provides insight into many possible bio-mimicking opportunities that benefit the society. The geometry of *G. floribunda* diaspores can be useful to design aerial payloads and wind turbine blades like diaspores of *Petrea volubilis* inspired horizontal axis wind turbine (HAWT) invented by Gaitan-Aroca et al. (2020).

Based on the morphological variables, we can predict only the dispersal potential in *G. floribunda* diaspores. In field conditions, the dispersal potential shows variation according to the prevailing environmental conditions. For example, horizontal wind velocity, height of dispersal, and features of dispersing medium such as air density and humidity may alter the flipping time and autorotation behaviour, which in turn affects the dispersal potential and ultimately, the distance of dispersal. The aerodynamic characteristics and flight time vary according to the strength of the force acting on them. Additionally, after falling on the surface of the earth, the winged diaspores may undergo secondary dispersal, which further alters the dispersal distance. Hence, a complete prediction of dispersal distance in natural conditions is a challenging task in the case of winged diaspores.

Conclusion

Getonia floribunda is an interesting multi-winged whirling diaspore, with many morphological and geometrical adaptations for performing a vertical anticlockwise direction of autorotation during wind dispersal. Fruit diaspores with persistent, cyclically arranged tepals or perianth whorls act as wings, with distinct spatial configuration and distribution of the centre of gravity along the middle vertical axis being the reasons for its vertical autorotation. There is an intrinsically predetermined geometrical right-side leading-edge curvature on the wings, which is the reason for its distinct anticlockwise direction during autorotation. A significant inter-location variation in morphological parameters was observed in this diaspore, although, irrespective of this variation, in four locations, wing fold angle developed due to the variation in the spatial configuration of the wings exhibited a significant predictable relationship with descent rate and terminal velocity due to the variation in the angular velocity of rotation. More research is required to find the optimum

fold angle of wings which reduces the descent rate of this whirling diaspore. Further studies with the use of computational fluid dynamics (CFD), wind tunnel experiments, and particle image velocimetry (PIV) are required to understand more about the aerodynamics of this diaspore and model simulations for providing updated ideas for incorporating with our evolving environments. Thus, wing geometry has an impact on flight and demonstrates the relationship between the shape and fitness of natural flight organs. These findings could pave the way for the development of new biologically inspired flying materials.

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.k98sf7mm3> (Drisya et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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