RHEEDEA
Journal of the Indian Association for Angiosperm Taxonomy

RESEARCH ARTICLE

Vol. 32(3): 145-174 (2022)
ISSN: 0971-2313 (Print edition)
ISSN: 2582-2438 (Online edition)
https://dx.doi.org/10.22244/rheedea.2022.32.03.01

Morphological diversity of winged diaspores of woody angiosperms in South India and their significance in dispersal

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Abstract: Dispersal units, technically seeds, fruits and infructescences equipped with wings for their long-distance dispersal are called winged diaspores. The diversity of flowering plants in South India is noteworthy, and they create a wide range of diaspore morphologies, as evident in their dispersal methods. The present study was carried out to prepare a list of woody angiosperms (both native and introduced) in South India, producing winged diaspores and to analyse their morphological variations, wing formation, and their significance in dispersal. Information from field studies and available literature resulted in a list of 186 species (of which 40 are introduced) which produce winged diaspores, distributed among 26 families in South India. The wings in these diaspores develop from the integument, ovary, perianth whorls or bracts. With a variety of morphology and flight behaviours, they are generally adapted to dispersal by wind, with the exception of a few that are adapted to dispersal by water. The study shows that wings of the diaspores are significant to their survival and distribution.

Keywords: Anemochory, Hydrochory, Morphogenesis, Wind dispersal, Winged fruits, Winged seeds.

Introduction

South India is rich in its flowering plant diversity, and hence diversity in diaspore morphology too, resulting in varied types of dispersal mechanisms. Diaspore is a broad term for dispersal units, which can be fruits, seeds, or other structures (Thomson & Neal, 1989) that are transported away from the parent plant to establish the progeny as an independent seedling (Augspurger, 1988). Diaspore dispersal is vital for plants since it is the most prevalent, and, aside from pollination, probably the only, mobile stage of most terrestrial sexually reproducing plant species during their lives (Harper *et al.*, 1970; Snell *et al.*, 2019). This is crucial for spatial distribution, gene flow, population expansion, and hence a species' survival, as well as preserving species coexistence and variety, and so community structure (Nathan & Muller-Landau, 2000; Levine & Murrell, 2003; Saatkamp *et al.*, 2019). One of the modifications identified in diaspores for accomplishing these functions is the formation of wings.

As in birds, the key responsibility of wings of plants is to allow gliding in the air. According to their environmental requirements, diaspore wings are built to allow a slow rate of descent to float as long as possible in the air current (Minami & Azuma, 2003). Winged diaspores can be produced in bulk quantities (Burnham & Carranco, 2004) and readily dispersed by wind (Anemochory) with the help of varying descent patterns, such as gliding, straying or rocking and spinning or autorotation (Minami & Azuma, 2003). Because of these distinct aerodynamic behaviours, winged diaspores have attracted much interest among scientists over past decades. Studies have been conducted by various investigators (Norberg, 1973; Azuma & Yasuda, 1989; Green & Johnson, 1990; Rosen & Seter, 1991; Yasuda & Azuma, 1997; Varshney *et al.*, 2011; Eadkong *et al.*, 2020) in attempts to

Received: 16.08.2022; *Revised & Accepted*: 11.09.2022
Published Online: 30.09.2022

understand the reasons behind these aerodynamic behaviours because these natural phenomena inspire new ideas and creative thoughts. Such investigations are quite rare in South India. In 1950, Razi presented a list of diverse active and passive dispersal mechanisms in plants of Mysore (South India), which included 68 genera of plants that produce winged diaspores.

The size and shape of diaspores varies depending on the species, but a majority of them have the same physical structure: a thin, leaf-like wing with a thicker leading edge; and a nut (or seed body) on one side of the wing (Arranz *et al*., 2018). The wings are developed from structures such as ovary (as outgrowths), hypanthium, perianth components, and/or bracts (Manchester & O'Leary, 2010). These structures undergo different ways of transformation and results in changes in morphology and aerodynamics during dispersal. In the case of winged diaspores, morphology is the primary determining element of aerodynamic behaviour and dispersal. Despite this significance, little attention has been paid to investigate the morphogenesis of the wings. Characters such as aerodynamic behaviour, diaspore configuration, number of wings, venation patterns, wing ontogeny and nature of diaspore (fruit/seed) have been used to classify winged diaspores (Augspurger, 1986, 1988; Minami & Azuma, 2003; Manchester & O'Leary, 2010). However, these categorizations have often ignored the process of wing development in diaspores.

It is worth noting that the dissemination of winged diaspores can range from tens of metres to kilometres (Nathan, 2006), on account of the occurrence of secondary dispersal in some instances. Primary dispersal is the initial release of diaspores from the plant into the air, and secondary dispersal occurs when diaspores reach the ground and are moved further by wind, gravity, animals, or water flow (Kaproth & McGraw, 2008; Gärtner *et al*., 2011; Zhu *et al*., 2019). This primary and secondary dispersal in different media confirmed that diaspore wings can perform other modes of dispersal in addition to wind dispersal. For example if the primary dispersal agent is wind, then then the diaspore landed in water bodies (secondary dispersal agent) it could float due to the wing's buoyancy. Wings are the sole devices for water dispersal (hydrochory) in some species; for example, the winged diaspore of *Dolichandrone spathacea* (L.f.) K.Schum. has been proposed to be solely adapted to dispersal in water (Sprague, 1919). This different mode of dispersal of winged diaspores was also observed by Razi (1950). Thus, winged diaspores are a fascinating area to research, and such investigations can stimulate creative ideas and innovation.

One of the main determinants of the aerodynamic behaviour during dispersal is wing morphology which also influences the diaspore's mass, dispersal potential, and species regeneration potential. Even though, there is no adequate source for comparative data on winged diaspore-bearing species, nor is there a comprehensive list around the world (Manchester & O'Leary, 2010). Mirle and Burnham (1999) presented a key for use in identifying asymmetrically winged samaras from the western hemisphere. They recorded species bearing asymmetrically winged fruits in 39 genera from 11 families. In central Europe, a database named DIASPORUS was created based on diaspore dispersal (Bonn *et al*., 2000), in which terminal velocity from a specified release height of more than 500 species are provided, based on literature surveys and measurements. The terminal velocity values of a further 300 species have been measured by Thompson *et al*. (1999). Thus, extending this database will help to assess the (wind) dispersal potentials of many species (Tackenberg *et al*., 2003). The South Indian vegetation is an excellent system for studying diaspore dispersal. However, until now, diaspores of only a limited number of taxa have been studied in detail and their significance in dispersal has not been evaluated. The present study was carried out to prepare a list of woody angiosperms (both native and introduced) in South India that produce winged diaspores and to analyse their morphological variations, wing ontogeny and their significance in dispersal.

Materials and Methods

The list of woody South Indian angiosperms with winged diaspores was compiled based on an exhaustive survey of works of Hooker (1872–1897), Gamble and Fischer (1915-1936), Fyson *et al*. (1932), Bor (1953), Saldanha and Nicolson (1976), Matthew (1981-1983), Manilal and Sivarajan (1982), Nair and Henry (1983), Saldanha (1984, 1996), Henry *et al*. (1987), Chandrabose and Nair (1987), Manilal (1988), Ramachandran and Nair (1988), Sharma *et al*. (1993), Sharma and Balakrishnan (1993), Sharma and Sanjappa (1993), Mohanan and Henry (1994), Hajra *et al*. (1995, 1997), Sahni (1998), Singh *et al*. (2000), Chacko *et al*. (2002), Sasidharan (2004), Daniel (2005), Balakrishnan *et al*. (2012) and other taxonomic literature (Razi, 1950; Naidu & Kumar, 2015; Murthy *et al*., 2020). Diaspore morphology of the taxa included in this list was verified by field surveys and by the study of images of herbarium specimens available at Calicut University Herbarium (CALI) (http://caliherbarium.org/) and Kew Herbarium (K)(http://apps.kew.org/herbcat/navigator.do) and with images and information from the linked sources named Flowering Plants in Kerala (http://keralaplants.in/search-flowering-plants-of-kerala.aspx); Flora of Peninsular India (http://flora-peninsula-indica.ces.iisc.ac.in/, http://flora-peninsula-indica.ces.iisc.ac.in/karnataka /gallery.php), India Biodiversity Portal (https://indiabiodiversity.org/) and eFlora of India–Database of plants of the Indian subcontinent (https://efloraindia.bsi.gov.in/eFlora/eFloraHomePage.action). Only those taxa that produce diaspores with wings and in which the wings play a significant role in their dispersal, are included in the list. Plants with microscopic or very small wings (such as species of *Casuarina* L., *Mitragyna* Korth., *Uncaria* Schreb., *Neonauclea* Merr.), and herbaceous taxa that possess winged diaspores are excluded. Few taxa that produce winged fruits, but disperse their seeds individually through ballistic mechanisms (*e.g.*, species of *Begonia* L.), and some other taxa that produce winged dehiscent capsules are excluded as they did not fall within the scope of the present investigation on the mechanism of dispersal. A few other taxa were also omitted due to the lack of sufficient information of the morphology of their diaspores. The geographic distribution status of the taxa is based on Sasidharan (2004) and online databases, such as the Plants of the World Online (POWO) (https://powo.science.kew.org/) and World Checklist of Selected Plant Families (http://apps.kew.org/wcsp/home.do). The families follow the APG system (APG IV, 2016). The names are updated using Plants of the World Online (POWO) (https://powo.science.kew.org/).

The plants from which the diaspores were collected during field explorations for the present study were identified using pertinent literature and by comparisons with images of voucher specimens available at CALI and K. Detailed morphological and micromorphological studies of diaspores were done with CSM2 (Labomed, India), M80 (Leica, Germany), and MSZ-TR (Magnus, India) stereomicroscopes. Photographs of the diaspores were taken using EOS M50 Mark II and EOS 760D (Canon, Japan) digital cameras and Magcam-DC5 microscope digital camera (Magnus, India).

The morphogenesis of diaspore wings was studied by collecting diaspores of selected species (*Swietenia macrophylla* G.King., *Ailanthus triphysus* (Dennst.) Alston., *Dioscorea wallichii* Hook.f., *Hiptage benghalensis* (L.) Kurz., *Pterocarpus marsupium* Roxb., *Neuropeltis malabarica* Ooststr., *Getonia floribunda* Roxb., and *Symphorema involucratum* Roxb.) under different categories at various stages of development. The morphological significance of wings in diaspores for dispersal was studied by observing their flight behaviour during dispersal in the field and indoor conditions and by comparing it with previous works on the aerodynamic classification of winged diaspores. For explaining the development of the characteristic morphologies in winged diaspores and its significance in dispersal, primary categorization based on the ontogeny and morphogenesis of the wings were carried out. In order to explain the aerodynamic behaviour of the diaspores during wind dispersal, Augspurger's (1986) terms and Minami and Azuma's (2003) categories were followed.

Results

A total of 186 woody flowering plants in South India belonging to 26 families were recorded as producing winged diaspores (Appendix 1), out of which 40 were introduced species. The table shows the type of dispersal unit, its category based on the ontogenetic development of wings, distribution and conservation status of each taxon. Out of the 186 species, 44.09% are climbers, 52.69% trees and 3.22% shrubs. Fifty-one species (27.42%) are endemic, and three of them are critically endangered. The winged dispersal units of the recorded plants belong to 3 categories: fruits, seeds and infructescences. The wings are variously developed from the ovary wall, integuments, perianth whorls or bracts. Based on their ontogeny and wing development pattern, the diaspores are categorized as follows:

1. ovary wall-derived
2. integument-derived
3. perianth-derived
4. bract-derived

1. Wing development from the ovary wall

In these taxa with winged fruits, the ovary wall differentiates into clearly defined wings for flight. The ovary wall begins to expand in a specific direction after fertilisation and takes on distinct forms that vary depending on their developmental pattern. Based on the direction of the growth of the ovary wall and final diaspore morphology, there are five basic types of growth patterns that are noted:

i) Unidirectional growth: Cells on one side of the ovary wall divide continuously in a unidirectional pattern. In most cases the opposite side of the ovary attachment (opposite of stalk) grows continually and produces wings. The morphology and number of these wings may vary, due to the syncarpous condition of the ovary in some species (*e.g.*, species of *Acer* L.). Most of the species in Appendix 2 possess one wing with (*e.g.*, species of *Acer*) or without (*e.g.*, species of *Ventilago* Gaertn.) a thick leading edge at one side of the wing. The major mass of the fruit (location of seed in this case) is ending on one end of the wing (Fig. 1a–f). Thus, whatever the number of wings, diaspores of all species of this type perform autorotation or spinning around their vertical axis during dispersal (Fig. 3c).

ii) Bidirectional growth: Here, opposite sides of the ovary wall (in most cases, ovary attachment region with stalk and its opposite side) grow more than the other two sides and result in an elongated, flattened structure (wing) with a seed in the middle. After fertilisation, taxa with superior ovary begin to grow more in the ovary attachment to the stalk/pedicel side and its opposite side (Fig. 5f), consequently the seed-bearing area is shifted to the middle region of the diaspore, and the fruit is known as samara (Fig. 1i–l); sometimes more than one seed develops in samara-like (samaroid) fruits (Fig. 1h, Appendix 2) (Manchester & O'Leary, 2010). In the samara of *Ailanthus triphysus* (Fig. 1l) for example, the fruits develop from the superior syncarpous ovary, and two or three mature in one flower. During wing development, the style disintegrates and the regions above and below the style origin begin to grow, resulting in fruit elongation in the longitudinal plane with the seed in the centre (Fig. 5f). Along with the completion of wing growth, the diaspore develops a curvature on the ends of the wings and has the maximum weight in the central region. This result in rotation on two axes simultaneously during dispersal, one is rolling around its longitudinal axis and the second one around one end of the diaspore in a spiral path (Fig. 4f & g). High wind velocities can cause the skipping of the spiral rotation, resulting in only self-rolling along the direction of wind.

iii) 3-directional growth: Here, three sides of the ovary wall grow in three directions in an equal or unequal manner, resulting in diaspores with three wings with a trigonal configuration. It is similar to the diaspores with unidirectional growth in that the majority of the fruit mass (location of the seed in this case) is located at one end of the wings, for example as in diaspores of *Hiptage benghalensis* (Fig. 1g). In this case, the ovary is tricarpellary syncarpous, and produces schizocarpic fruits where each carpel shows three directional wing developments, resulting in a diaspore with one large and two small wings (Fig. 6a). As the spatial configuration of this diaspore is similar to that of unidirectionally developing ones, it has similar flying behaviour during dispersal. They spin tightly around a vertical axis with the three asymmetric wings in a clockwise or counter-clockwise rotation (Fig. 3g).

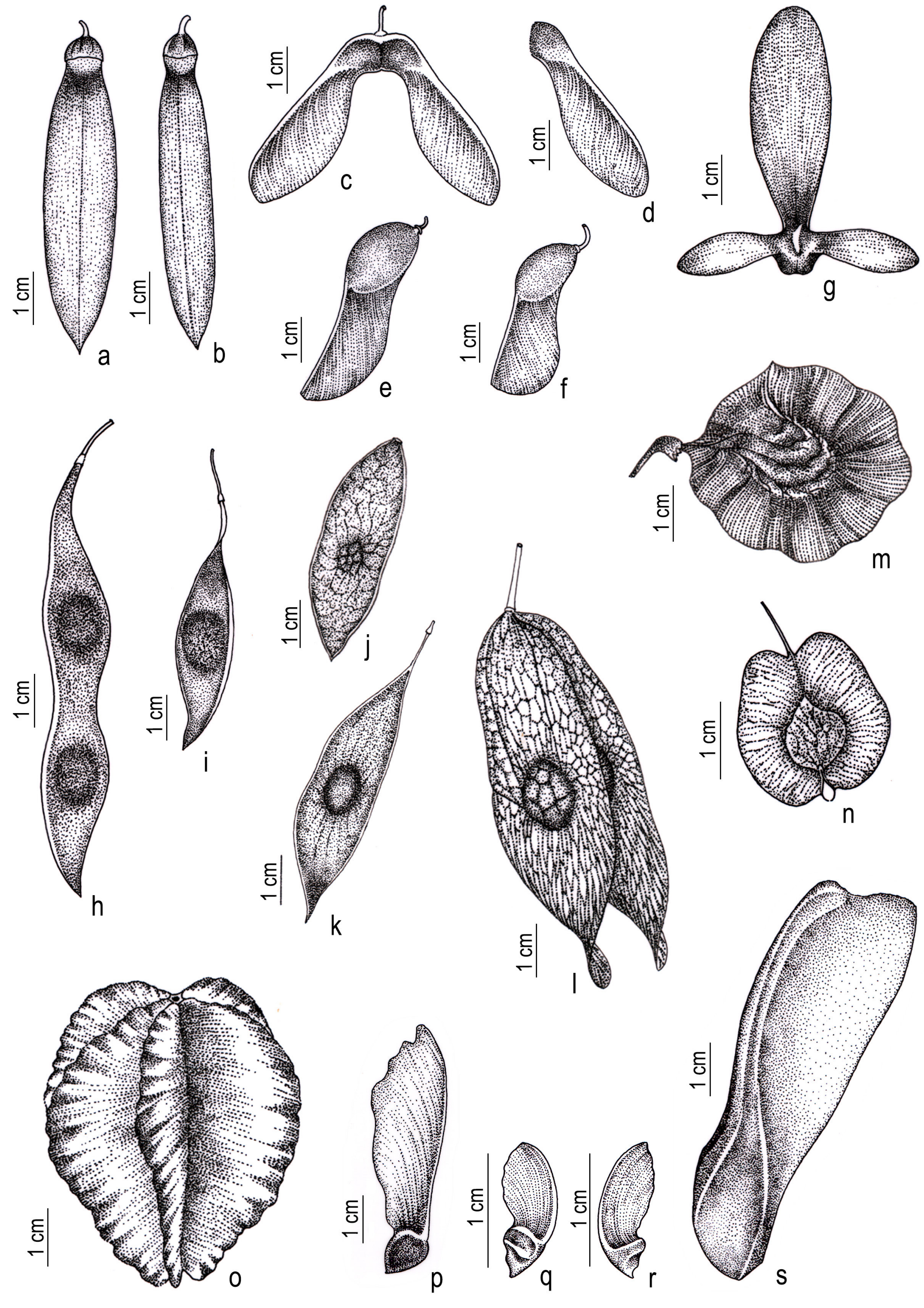

Fig. 1. Morphology of diaspores based on pattern of wing development: **a**-**f.** Wing develops unidirectionally in fruit diaspores: **a** & **b.** *Ventilago denticulata* Willd.; **c** & **d.** *Acer oblongum* Wall. ex DC.; **e** & **f.** *Pterolobium hexapetalum* (Roth) Santapau & Wagh.; **g.** Wings develop by 3-directional growth in fruit diaspore of *Hiptage benghalensis* (L.) Kurz.; **h**-**l.** Wing develops by bidirectional growth in fruit diaspore: **h** & **i.** Samara and samaroid type in *Brachypterum scandens* (Roxb.) Miq.; **j.** *Dalbergia horrida* (Dennst.) Mabb.; **k.** *D. lanceolaria* L.f.; **l.** *Ailanthus triphysus* (Dennst.) Alston; **m** & **n.** Wing develops by elliptical surrounding growth in fruits: **m.** *Pterocarpus marsupium* Roxb.; **n.** *Holoptelea integrifolia* (Roxb.) Planch.; **o.** Wings develop by multi-directional growth in fruits of *Terminalia elliptica* Willd.; **p**-**s.** Wing develops unidirectionally in seed diaspores: **p.** *Pterospermum diversifolium* Bl.; **q** & **r.** *Lagerstroemia speciosa* (L.) Pers.; **s.** *Swietenia macrophylla* G.King (drawn by Drisya V.V.).

iv) Multidirectional growth: In this type, the ovary wall begins to expand in multiple directions at the same time, resulting in a central seed-bearing area surrounded by three or more wings (Fig. 1o), the so-called "fin-winged" morphology of Manchester and O'Leary (2010). The entire surface of the ovary takes part in wing formation. Therefore, depending upon the species, diaspores possess three, four or five separate wings (Appendix 2). They tumble in the air due to the diaspore's symmetrical shape, but not on a consistent axis. The morphology and tumbling motion of this category can be seen in *Terminalia elliptica* Willd. (Fig. 3f).

v) Elliptical surrounding growth: Plants with flattened or laterally compressed ovaries show this type of wing development. The compressed ovary wall begins to expand evenly all around the edge, resulting in a flattened diaspore with a core seed region surrounded by a broad wing almost all around the central part (Fig. 1m–n). The diaspore has developed a flattened, somewhat circular or elliptical shape prior to dispersal. They exhibit gliding and undulating motions during dispersal. The wing development in *Pterocarpus marsupium* is shown in Fig. 6b, and the flight behaviour in *Holoptelea integrifolia* (Roxb.) Planch. during dispersal is shown in Fig. 4e. The wings of fruits of the two grow similarly, though the style and stalk of the pistil are also involved in wing development in the latter (Fig. 1n).

2. Wing development from integuments

After fertilisation, the ovule of an angiosperm develops into seeds, and the ovary into a fruit. During this process, the integuments of the ovules transform into the seed testa, but in winged seed diaspores, they are modified into wings. The integuments start to enlarge in a particular direction and as a result, different morphologies are attained. According to the final diaspore wing configuration, four types of integument growth patterns are observed in South Indian plants.

i) Unidirectional growth: The development in this type is similar to the unidirectional growth of the ovary, in that only one side of the integument tissue participates in wing formation, which may be the apical region (ovule attachment region with placenta) as in *Swietenia* Jacq. spp. or the basal region (free end of ovule) as in *Pterospermum* Schreb. spp. (Fig. 1p–s). If the apical region participates in wing formation, the funicle (a component of the ovule which attaches it to the placenta) is also involved (*e.g.*, *Swietenia* spp.). Wing expansion in one direction ends in a thin part on one side of the wing and a thick leading edge on the other. The number of wings is always one, and it develops inside the fruits to facilitate wind dispersal upon dehiscence. These winged seeds are autogyros, autorotating or spinning on their vertical axis during dispersal. The aerodynamics and development of the diaspores of *Swietenia macrophylla* are illustrated in Figs. 3c and 5e respectively.

ii) Bidirectional growth: Here, two opposite sides of the integument take part in wing formation and result in an elongated, slightly flattened diaspore, with a central seed. Generally, two opposite ends of the integument near the funicle of the ovule take part in wing formation. These wings might be smooth, membranous, and hyaline (as in *Tecoma* Juss. spp.) or thick, rigid and curved (as in species of *Stereospermum* Cham.) (Fig. 2a & b). Elongated or flattened dehiscent pods produce these types of winged seeds, and the morphology and spatial configuration of the wings are dictated by the orientation of pods. Among South Indian taxa, this type of diaspore is mainly produced by members of the family Bignoniaceae (Appendix 2). They execute autorotation (in the vertical axis) (Fig. 4i, k & l) or a rolling motion (in the longitudinal axis) in a semi-spiral or straight path (Fig. 4j) during dispersal due to their lightweight, elongated shape, and distinct positioning of the centre of mass (cotyledonary region) in the middle of the diaspore. The diaspores of *Stereospermum tetragonum* DC. have a trigonal spatial configuration due to two horizontal wings with a distinct curvature and a wedge-shaped cotyledonary region (centre of mass) in between these wings (Fig. 2b).

iii) Multidirectional growth: : In this type, the whole surfaces of the integument participate in wing creation and begin to expand evenly in all directions surrounding the globular cotyledons, resulting in a diaspore with three or more equal wings with a symmetrical shape (Fig. 2g–i). Among the South Indian taxa, only species of *Moringa* Adans. produce this type of diaspore, with three symmetrical wings. It behaves aerodynamically like a tumbling fruit diaspore, performing tumbling motions during dispersal. Seed tumblers have thin membranous wings and are lighter than tumbling fruits; therefore, they disperse farther than fruit tumblers.

iv) Elliptical surrounding growth: This type of diaspore development is similar to that of orbicular ovary growth in fruit diaspores. Taxa with flattened or compressed ovules in the ovary undergo this type of development (Fig. 5g–k). The circular margins of compressed ovules develop more or less evenly in the beginning, forming a round or semi-circular flattened diaspore with a central cotyledon region encircled by a broad, membranous, thin, transparent wing around. In South India, these diaspores are produced mainly by members of Bignoniaceae and Dioscoreaceae (Appendix 2). A complete circular wing around the cotyledon is observed in Dioscoreaceae (Fig. 2d & e), while in Bignoniaceae unequal elliptical surrounding growth is observed. Thus, the cotyledon can be seen on one side of the wing (Fig. 2c & f). These types of seeds are developed inside the dehiscent capsule and glide in a straight or spiral manner (Fig. 4c & d) during dispersal.

3. Wing development from perianth

In most cases, calyx is the part of the perianth whorl that is involved in wing formation of diaspores. In wind-dispersed diaspores, persistent perianth whorls act as wings or undergo some morphological changes and develop into wings (Appendix 2).

i) Persistent perianth whorls further develop into large wings: Tepals or sepals in some species persist and undergo development after fertilisation of the ovule and form large wings for fruit dispersal. These modifications enable adequate rotation of the diaspores during dispersal. Two or three accrescent sepals or tepals of a flower (*e.g.*, species of *Hopea* Roxb.) or entire calyx (*e.g.*, species of *Shorea* Roxb. ex C.F.Gaertn., *Ancistrocladus heyneanus* Wall. ex J.Graham) of a flower take part in wing formation. Hence, the number of wings may vary between species, but their spatial configurations are similar (Fig. 2 k–m). This type of wing development can be seen in both unisexual (*Gyrocarpus americanus* Jacq.) and bisexual (Dipterocarpaceae members) flowers.

ii) Persistent perianth whorls as such act as wings: In this type, no further development in the perianth segments occurs, and the fully grown sepal at the time of fertilization as such acts as a wing during diaspore dissemination. Among South Indian species, this type of diaspore is seen only in *Getonia floribunda* (Fig. 2j). This flower has only one non-essential whorl (tepal), which is greenish and fleshy during flowering, but brownish, dry and attains a specific spatial configuration for a distinct direction of rotation during fruit dispersal (Fig. 6g & h).

Both types of wing development from perianth whorls result in a similar autogyration of the diaspore, *i.e.*, the major mass (fruit in this case) is located at one end of the wings, so they perform autorotation tightly around the fruit end of the diaspore in the vertical axis (Fig. 3h–k).

4. Wing development from bracts

In some flowering plants, persistent bracts develop as wings for diaspore dispersal. Two types of bracts that develop into wings in South Indian plants are observed: floral bracts and involucral bracts. They show different flight behaviours.

i) Wing developed from floral bract: The woody climber *Neuropeltis malabarica* is the only species in this category recorded in South India. In this plant, the floral bracts developed into a broadly elliptical, flat, membranous wing attached to the fruit (Fig. 2n). These bracts are small, *c.* 5 mm long, densely tomentose and minutely mucronate in flower. After anthesis, these immediately start to grow in an orbicular manner into a 3–3.5 cm long flat, membranous, reticulately veined, enlarged wing (Fig. 6c–e). After the complete development of the wing, fruits are seen on one side of the bract. At the time of dispersal, it becomes greyish in colour and its fleshy texture changes into a thin papery, light-weight structure for easy movement in the

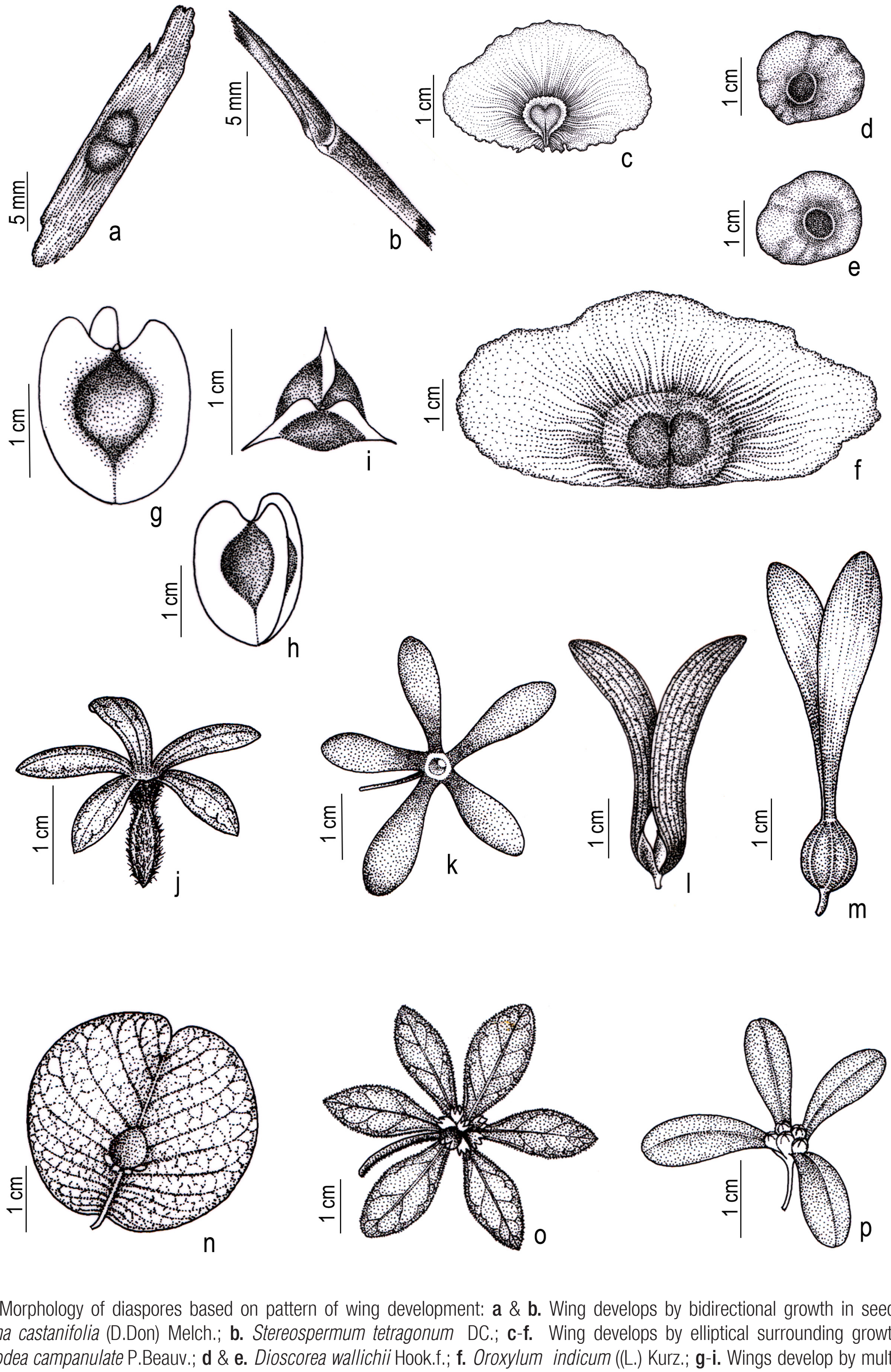

Fig. 2. Morphology of diaspores based on pattern of wing development: **a** & **b.** Wing develops by bidirectional growth in seed diaspores: **a.** *Tecoma castanifolia* (D.Don) Melch.; **b.** *Stereospermum tetragonum* DC.; **c**-**f.** Wing develops by elliptical surrounding growth in seeds: **c.** *Spathodea campanulate* P.Beauv.; **d** & **e.** *Dioscorea wallichii* Hook.f.; **f.** *Oroxylum indicum* ((L.) Kurz.; **g**-**i.** Wings develop by multi-directional growth in seed diaspores of *Moringa oleifera* Lam.; **j.** Persistent perianth whorls as such act as wings in *Getonia floribunda* Roxb. fruit; **k**-**m.** Perianth whorls develop into wings: **k.** *Ancistrocladus heyneanus* Wall. ex J.Graham; **l.** *Hopea ponga (*Dennst.) Mabb.; **m.** *Gyrocarpus americanus* Jacq.; **n.** Floral bract develops into wings in *Neuropeltis malabarica* Ooststr.; **o** & **p.** Involucral bracts act as wings: **o.** *Symphorema involucratum* Roxb.; **p.** *Congea tomentosa* Roxb. (drawn by Drisya V.V.).

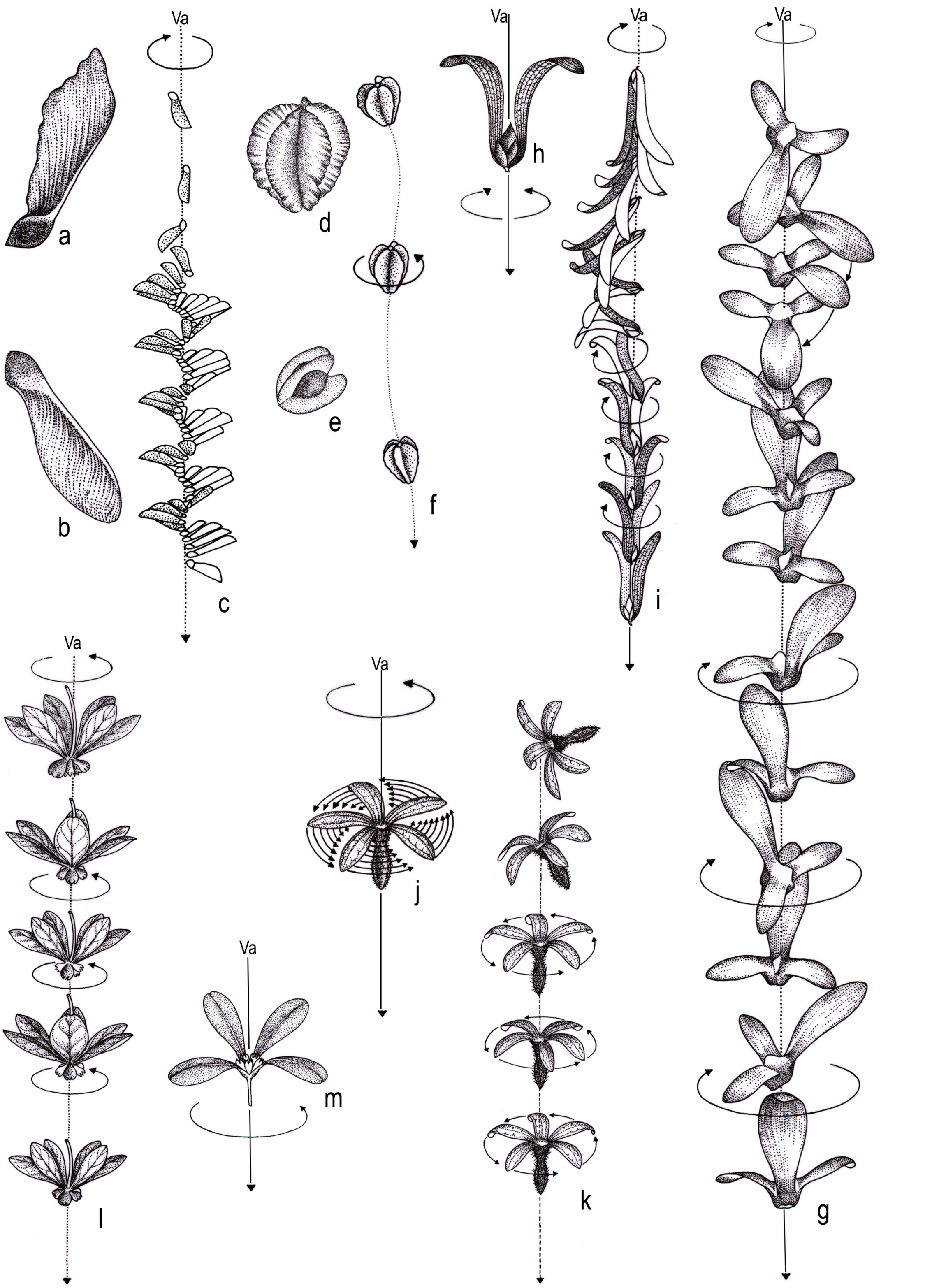

Fig. 3. Flight behaviour of winged diaspores: **a** & **b.** Wing develops by unidirectional growth in seed and fruit diaspores; **c.** Pattern of autorotation in **a** & **b** in vertical axis; **d** & **e.** Wings develop by multi-directional growth in fruit and seed diaspores; **f.** Pattern of tumbling motion of **d** & **e**; **g.** Autorotation in diaspores with wings developed by 3-directional growth in *Hiptage benghalensis* (L.) Kurz.; **h** & **i.** Vertical autorotation in *Hopea ponga* (Dennst.) Mabb.; **j** & **k.** Vertical autorotation in *Getonia floribunda* Roxb.; **l** & **m.** Pattern of vertical autorotation in infructescences: **l.** *Symphorema involucratum* Roxb.; **m.** *Congea tomentosa* Roxb. (Va-Vertical axis) (drawn by Drisya V.V.).

air. During dispersal, they perform gliding movements in a straight or spiral path in the air (Fig. 4a & b).

ii) Wing development from involucral bracts: The persistent involucral bracts, coupled with 3–7 fruits, act as dispersal units for wind dissemination in some species. Typically, 3–6 bracts are arranged symmetrically around the peduncled capitate cyme inflorescence. It gives the diaspore a trigonal structure and a discrete axis for rotation (Fig. 2o & p). These involucral bracts are fully developed before anthesis (Fig. 6f). South Indian taxa that produce this type of dispersal unit are listed in Appendix 2. The number of involucral bracts varies in different genera: six bracts around the peduncled capitate cymes in *Symphorema* Roxb. and *Sphenodesme* Jack, and 3 or 4 bracts in *Congea* Roxb. When the diaspores are ready for dispersal, the involucre becomes rigid, thin, and membranous, with the major mass (fruits in this case) located at one end of the wings, giving the diaspores a trigonal shape. They autorotate or spin around its vertical axis passing through the middle of the inflorescence in a particular direction. The rotating positions of diaspores may change depending on wing configuration and fruit location, as shown in Fig. 3l & m.

Discussion

Significance of wings in dispersal

In comparison with plumed diaspores (those having hairs for parachute mechanism, *e.g.*, cypsela fruit) winged diaspores are usually heavier in their mass, and store reserve food for the early stages of plant growth, therefore their long-distance dispersal is not possible without any adaptations for flight (Tennakone, 2017). The wings change their aerodynamic behaviours that help to reduce the rate of descent and increase the distance of dispersal. The flight behaviour of dispersal units varies with their morphology. Minami and Azuma (2003) found that various flight modes of winged seeds and fruits are strongly dependent on their plan form and the location of their centre of gravity. Different growth patterns of wings lead to a change in the centre of gravity in diaspores. Unidirectional growth of the ovary wall or integument produces a single-winged diaspore with a significant mass or centre of gravity at one end of the wing; these diaspores autorotate around the heavier end during dispersal with a distinct sense of direction (Fig. 3c). Wings developed by three-directional growth, and modification of sepals and involucral bracts in to wings, also result in diaspores with the main mass at one end of the wing, but the number of wings varies. Thus, they also autorotate or spin (Figs. 3g–m). Bidirectional expansion of wings results in an elongated diaspore with a significant mass in the centres of wings, causing a rolling along their longitudinal axis and autorotation around one end in a spiral path (Fig. 4f & g). Seed diaspores with wings developed by bidirectional growth exhibit variation in flight behaviours such as rolling in the longitudinal axis and spiral path (Fig. 4j), or autorotation in the vertical axis (Fig. 4i, k & l). The multi-directional expansion of the wings results in a symmetrical diaspore with an even distribution of weight across the wings, hence they only tumble in the wind (Fig. 3f). Elliptical surrounding growth leads to a flattened diaspore with a major mass near the middle of the circular wing; it creates gliding motion with undulation in some during descent (Fig. 4c–e). Wings modified from floral bracts also have a similar configuration of gliding diaspores and perform gliding motion in a spiral or straight path (Fig. 4a & b). Thus, the structure from which the development of wings happens has a significant impact on the final diaspore configuration and their aerodynamic performance.

Considering the significance of wings in dispersal, water dispersal is a possibility that cannot be ruled out. For example, the short, opaque, spongy wings of *Dolichandrone spathacea* are worse adapted for transport over long distances by wind, but better adapted for dispersal by means of water (Sprague, 1919). *Derris trifoliata* Lour., *Heritiera littoralis* Aiton and *Terminalia paniculata* B.Heyne ex Roth

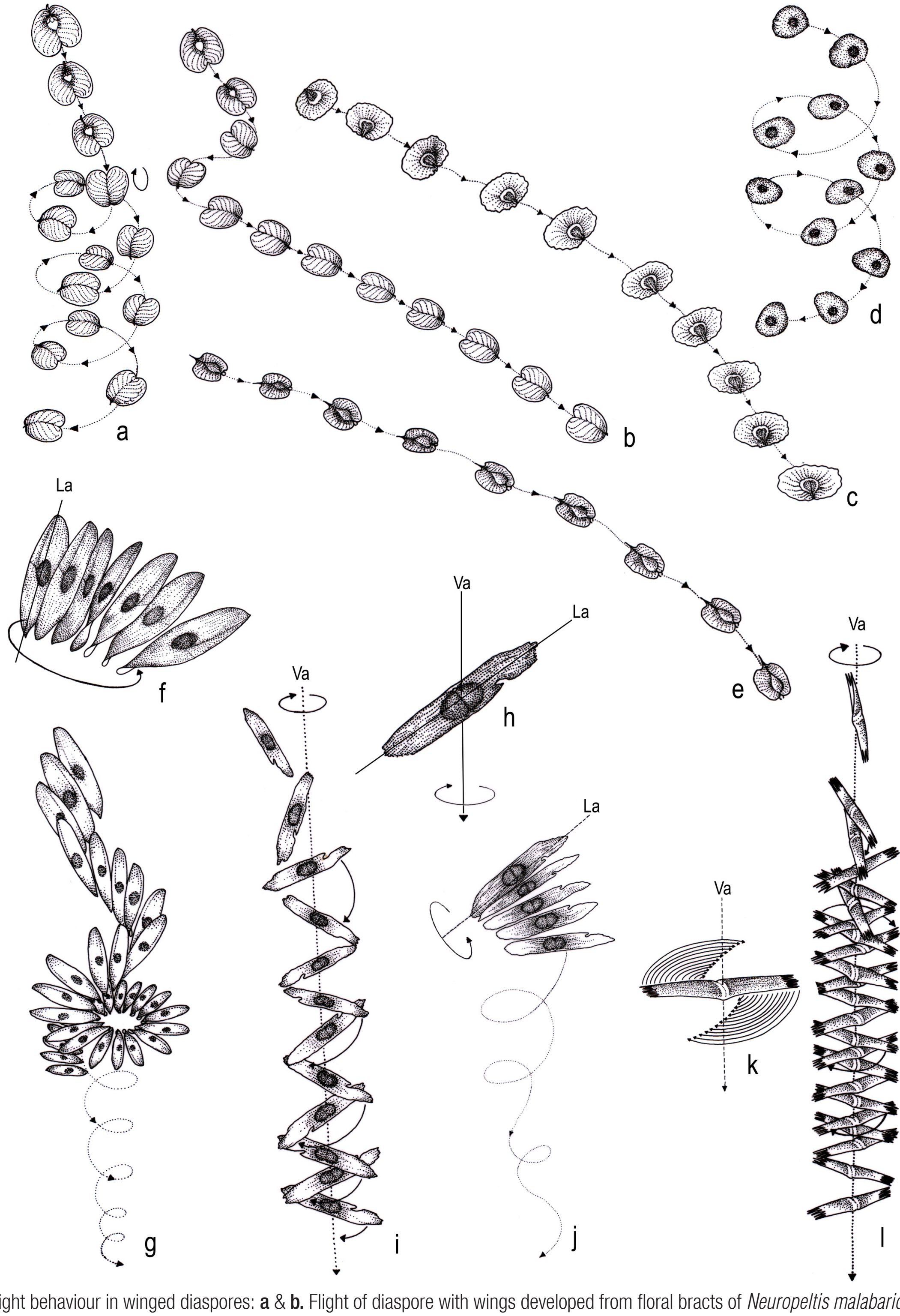

Fig. 4. Flight behaviour in winged diaspores: **a** & **b.** Flight of diaspore with wings developed from floral bracts of *Neuropeltis malabarica* Ooststr.: **a.** Spiral gliding; **b.** Straight gliding; **c** & **d.** Flight of seeds with wings developed by elliptical surrounding growth: **c.** Straight gliding with undulation in *Spathodea campanulata* P.Beauv.; **d.** Spiral gliding in *Dioscorea wallichii* Hook.f; **e.** Gliding with undulation motion in fruit diaspore with wings developed by elliptical surrounding growth in *Holoptelea integrifolia* (Roxb.) Planch.; **f** & **g.** Flight of fruit with wing developed by bidirectional growth in *Ailanthus triphysus* (Dennst.) Alston: **f.** Self-rotation in longitudinal axis (rolling); **g.** Self-rotation with spiral motion; **h**-**l.** Various flight behaviours of seeds with wings developed by bidirectional growth: **h.** Rotation around longitudinal and vertical axes in *Tecoma castanifolia* (D.Don) Melch.; **i.** Vertical axis of rotation of seeds of *T. castanifolia* (D.Don) Melch.; **j.** Rotation around longitudinal axis with spiral motion of seeds of *T. castanifolia* (D.Don) Melch.; **k** & **l.** Clockwise vertical axis autorotation in *Stereospermum tetragonum* DC. (La-Longitudinal axis; Va-Vertical axis) (drawn by Drisya V.V.).

are some examples of South Indian plants that produce winged diaspores for water dispersal. Most of the species use their wings for secondary dispersal in water, which also helps to increase the dispersal distance. Hence, wings of diaspore play an important role in their distribution and survival.

Dispersal-affecting characteristics of diaspores

The main purpose of winged diaspores is to reduce the rate of descent and therefore increase the distance of dissemination from the parent plant without the assistance of other creatures. Wings have undergone a number of structural modifications for this purpose. The nature of diaspore (fruit/seed), wing ontogeny, number of wings and their configuration, venation types and aerodynamic behaviour are important characteristics of diaspores that influence the process of dispersal. Among the diaspores studied, fruit diaspores are more numerous than seed diaspores. Out of the 186 taxa in South India that produce winged diaspores, 93 have fruit diaspores, 88 seeds, and 5 are infructescence diaspores. In terms of fulfilling their function, seed diaspores travel faster and easier than fruit diaspores. Because of the extra ovary tissues and/or use of tissues with a higher density rather than having higher moisture content, fruit diaspores have slightly higher mass compared to seed diaspores (Augspurger, 1988). Thus, winged seeds are usually lighter than winged fruits and are more efficient in wind dispersal (Augspurger, 1988). Similarly, wing venation and texture are other factors that affect the wing mass and dispersal potential of a diaspore. Wing venation is more prominent in fruit diaspores than in seeds. Seed wings can instead have striation patterns of fibres. According to Manchester and O'Leary (2010), the venation pattern varies depending on the derivation of the tissues which form the wings. They found that wings developed from the ovary and/or fruit wall tend to have a simpler vein pattern than wings developed from perianth or bracts. This is equally applicable for the species studied here, where wings formed from bracts and perianth whorls exhibit notable elaborated venation patterns. During dispersal, the veins help maintain rigidity and a specific spatial configuration of the wings during dispersal. Most of the autorotating diaspores in Appendix 2 have wings developed from the ovary wall, bracts and perianth whorls possess hair-like vestitures or rough textures of the wings that help to create pressure difference for assisting the flight. This also helps to reduce the retention of water on the wings. These act as lift-reducing spoilers, just like those on aeroplane wings.

The most significant factor influencing diaspore dispersal over long distances is their aerodynamic behaviour. Augspurger (1986) classified winged diaspores into seven categories based on their morphology and aerodynamic behaviour. Based on the analysis of aerodynamic behaviour of the winged diaspores in South Indian plants, six types were identified; namely, autogyros, rolling autogyros, helicopters, tumblers, undulators/gliders, and non-classified. On the basis of this classification, all fruit and seed diaspores with wings developed by unidirectional growth are autogyros. Diaspores with wings developed by tri-directional growth, and from perianth whorls and involucral bracts are helicopter types, because they are similar to autogyro fruits with added wings. Diaspores with wings developed by multidirectional growth are tumblers, and those with wings developed by elliptical surrounding growth and by floral bract modifications are undulators/gliders. Diaspores with wings developed by bidirectional growth are rolling autogyros, except for some seeds with wings developed by bidirectional growth that show diverse flight behaviours of the same and between diaspores during dissemination, and are hence placed in the non-classified category. The geometry of wings and the spatial configuration of diaspores determines this aerodynamic behaviour. Most of the autogyros and rolling autogyros diaspores of South Indian species rotate in a particular direction. However, in the diaspores of some species, there is

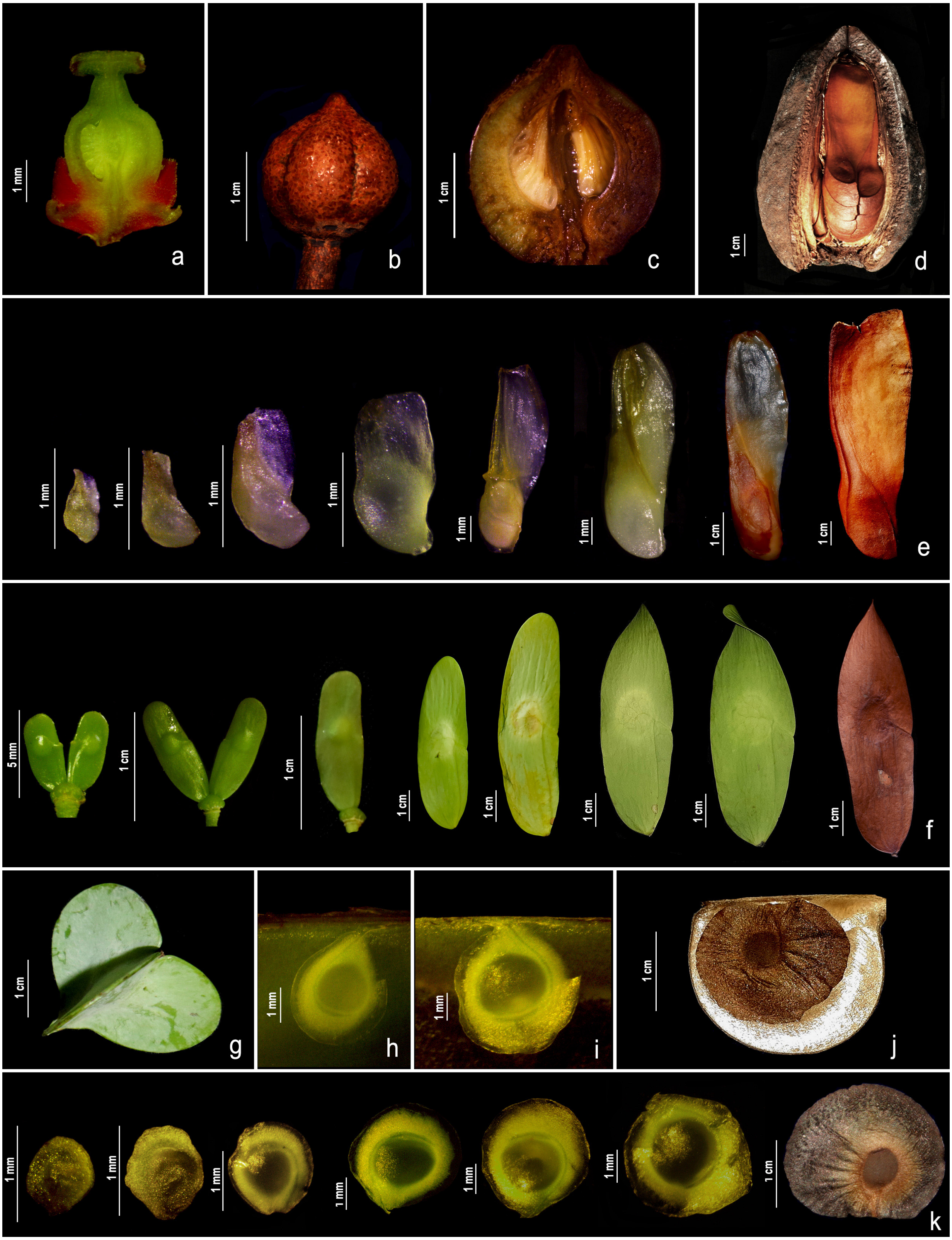

Fig. 5. Development of wings in diaspores: **a**-**e.** *Swietenia macrophylla* King: **a.** L.S. of ovary showing ovule arrangement; **b.** Young fruit; **c.** L.S. of developing fruit showing development of seeds in locules; **d.** Mature fruit showing arrangement of completely developed winged seeds; **e.** Stages of wing development in seeds by unidirectional growth; **f.** Stages of wing development of fruits of *Ailanthus triphysus* (Dennst.) Alston by bidirectional growth; **g**-**k.** *Dioscorea wallichii* Hook.f.: **g.** Winged fruit; **h**-**j.** Attachment of seed in ovary at different stages of development; **k.** Stages of wing development in seed by elliptical surrounding growth (images by Drisya V.V.).

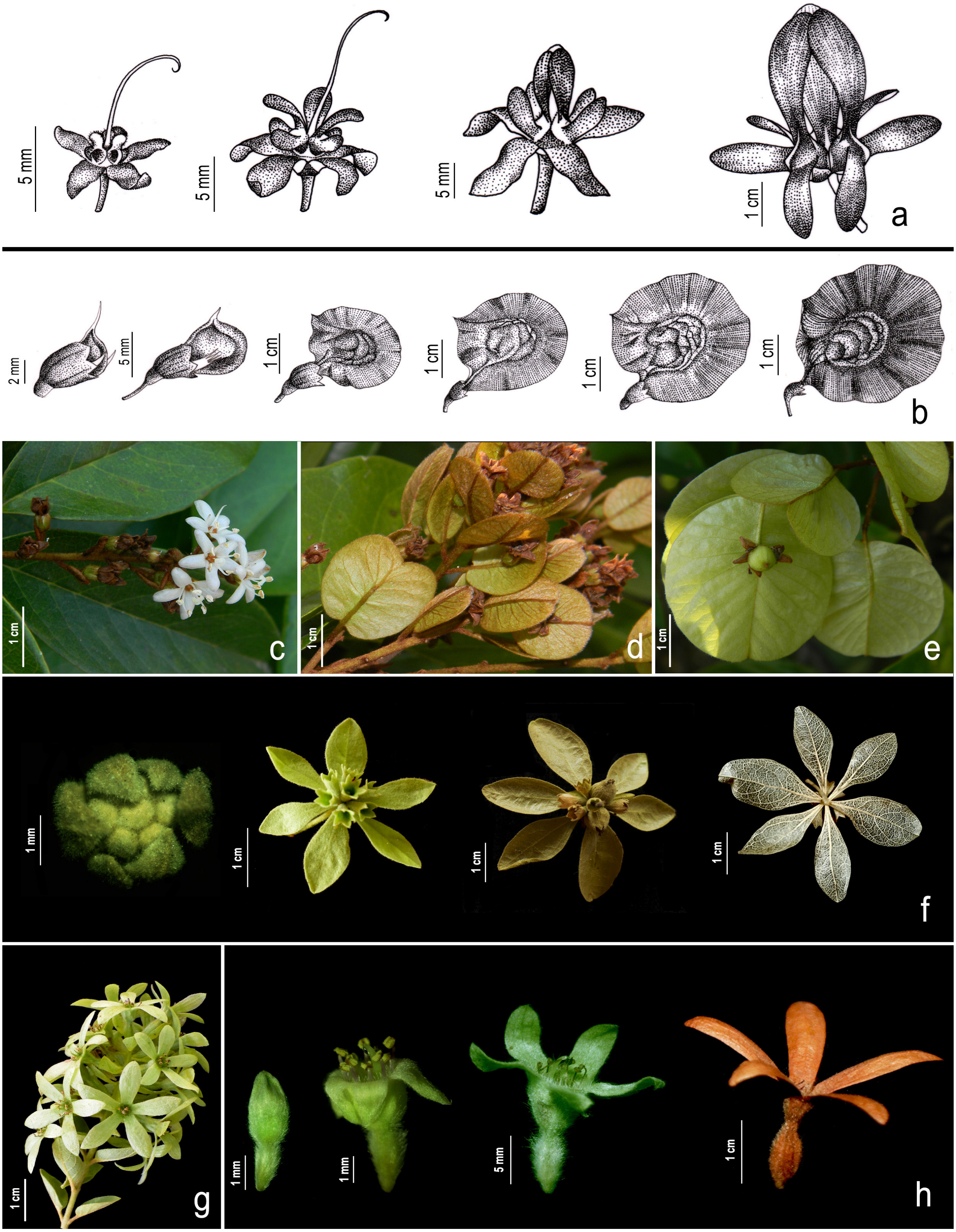

Fig. 6. Development of wings in diaspores: **a.** Different stages of wing development in *Hiptage benghalensis* (L.) Kurz by 3-directional growth; **b.** Different stages of wing development by elliptical surrounding growth in *Pterocarpus marsupium* Roxb.; **c**-**e.** Development of floral bracts to wings in *Neuropeltis malabarica* Ooststr.; **f.** Transformation of involucral bracts into wings in *Symphorema involucratum* Roxb.; **g** & **h.** *Getonia floribunda* Roxb.: **g.** flowering twig; **h.** Different stages of transformation of perianth whorl to wings (**a** & **b** drawn by Drisya V.V.; images **c**-**e** by Pramod C.; **f**-**h** by Drisya V.V.).

no distinct sense for rotation. According to Tennakone (2017), the sense of rotation is achieved either spontaneously or intrinsically based on the geometrical right-left asymmetry of the wings. The dispersal potential of winged diaspores also depends upon the height of their release into the air. Increase in the release height also increases the horizontal displacement of diaspores that further depend upon the canopy density and nature of surrounding vegetation. In addition to this, the parent plants exhibit some adaptations such as shedding of leaves for easy release of their diaspores to the wind (for *e.g.*, *Dioscorea wallichii*, *Symphorema involucratum*), and increase in the wing size of diaspore for elongation of the flight time and thus potential distance of dispersal in a closed canopy (*e.g.*, *Ailanthus triphysus*).

Conclusion

Woody angiosperms of South India exhibit a wide range of winged diaspores. They are either fruits, seeds or infructescences with distinct wings developed from the ovary, integument, perianth whorls or bracts. They are primarily adapted to the wind dispersal and perform diverse flight behaviours such as autorotation, gliding, straying, or tumbling movements in the air, except for a few winged diaspores, which are mainly adapted to water dispersal instead of flight. It is intriguing and thought-provoking to see plants that stand immobile in nature show such motions of their propagules. These natural phenomena still need to be studied carefully by integrating botany, physics and mathematics, as they are important for maintaining the plant biodiversity of the earth. Critical analysis of the underlying principles of autorotation may also lead to innovative ideas in engineering.

Acknowledgements

The authors are grateful to the Principal, Govt. Brennen College, Dharmadam, Thalassery, and Head, Department of Botany, University of Calicut for facilities; the Department of Science and Technology (DST), Government of India, for granting funds under the Fund for Improvement of S & T Infrastructure (FIST) programme (SR/FST/LSI-532/2012). The authors are also thankful to the anonymous reviewers for the critical comments on the earlier version of this article. The first author is thankful to the Kannur University for the financial assistance in the form of a Junior Research Fellowship.

Literature Cited

APG IV 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society* 181: 1–20. https://doi.org/10.1111/boj.12385

ARRANZ G., MORICHE M., UHLMANN M., FLORES O. & M. GARCÍA-VILLALBA 2018. Kinematics and dynamics of the auto-rotation of a model winged seed. *Bioinspiration & Biomimetics* 13(3). https://doi.org/10.1088/1748-3190/aab144

AUGSPURGER C.K. 1986. Morphology and dispersal potential of wind-dispersed diaspores of neotropical trees. *American Journal of Botany* 73(3): 353–363. https://doi.org/10.1002/j.1537-2197.1986.tb12048.x

AUGSPURGER C.K. 1988. Mass allocation, moisture content, and dispersal capacity of wind-dispersed tropical diaspores. *New Phytologist* 108(3): 357–368. https://doi.org/10.1111/j.1469-8137.1988.tb04174.x

AZUMA A. & K. YASUDA 1989. Flight performance of rotary seeds. *Journal of Theoretical Biology* 138(1): 23–53. https://doi.org/10.1016/S0022-5193(89)80176-6

BALAKRISHNAN N.P., CHAKRABARTY T., SANJAPPA M., LAKSHMINARASIMHAN P. & P. SINGH 2012. *Flora of India*. Volume 23. Botanical Survey of India, Kolkata.

BONN S., POSCHLOD P. & O. TACKENBERG 2000. "Diasporus" - a database for diaspore dispersal - concept and applications in case studies for risk assessment. *Zeitschrift für Ökologie und Naturschutz* 9(1/2): 85–97.

BOR N.L. 1953. *Manual of Indian forest botany*. Geoffrey Cumberlege, Oxford University Press, Bombay.

BURNHAM R.J. & N.L. CARRANCO 2004. Miocene winged fruits of *Loxopterygium* (Anacardiaceae) from the Ecuadorian Andes. *American Journal of Botany* 91(11): 1767–1773. https://doi.org/10.3732/ajb.91.11.1767

CHACKO K.C., PANDALAI R.C., SEETHALAKSHMI K.K., MOHANAN C., MATHEW G. & N. SASIDHARAN 2002. *Manual of seeds of forest trees, bamboos and rattans*. Kerala Forest Research Institute, Thrissur.

CHANDRABOSE M. & N.C. NAIR 1987. *Flora of Coimbatore*. Bishen Singh Mahendra Pal Singh, Dehra Dun.

DANIEL P. 2005. *Flora of Kerala*. Volume 1. Botanical Survey of India, Kolkata.

EADKONG T., PIMTON P., DAM-O P. & P. CHANNUIE 2020. Unraveling the vertical motion of *Dipterocarpus alatus* seed using Tracker. *Physica Scripta* 95(5). 055003 https://doi.org/10.1088/1402-4896/ab78b1

FYSON P.F., BOURNE E.T.G. & D.R.W. FYSON 1932. *The flora of the South Indian hill stations, Ootacamund, Coonoor, Kotagiri, Kodaikanal, Yercaud and the country round*. Government Press, Madras.

GAMBLE J.S. & C.E.C. FISCHER 1915-1936. *The flora of the Presidency of Madras*. Adlard & Son Ltd., London.

GÄRTNER S.M., LIEFFERS V.J. & S.E. MACDONALD 2011. Ecology and management of natural regeneration of white spruce in the boreal forest. *Environmental Reviews* 19: 461–478. https://doi.org/10.1139/a11-017

GREENE D.F. & E.A. JOHNSON 1990. The dispersal of winged fruits and seeds differing in autorotative behaviour. *Canadian Journal of Botany* 68(12): 2693–2697. https://doi.org/10.1139/b90-340

HAJRA P.K., NAIR V.J. & P. DANIEL 1997. *Flora of India*. Volume 4. Botanical Survey of India, Kolkata.

HAJRA P.K., RAO R.R., SINGH D.K. & B.P. UNIYAL 1995. *Flora of India*. Volume 12. Botanical Survey of India, Kolkata.

HARPER J.L., LOVELL P.H. & K.G. MOORE 1970. The shapes and sizes of seeds. *Annual Review of Ecology and Systematics* 1: 327–356. https://doi.org/10.1146/annurev.es.01.110170.001551

HENRY A.N., KUMARI G.R. & V. CHITRA 1987. *Flora of Tamil Nadu, India*. Series 1: Analysis. Volume 2. Botanical Survey of India, Kolkata.

HOOKER J.D. 1872-1897. *The flora of British India*. Volume 1-7. L. Reeve & Co., London.

KAPROTH M.A. & J.B. MCGRAW 2008. Seed viability and dispersal of the wind-dispersed invasive *Ailanthus altissima* in aqueous environments. *Forest Science* 54(5): 490–496.

LEVINE J.M. & D.J. MURRELL 2003. The community-level consequences of seed dispersal patterns. *Annual Review of Ecology, Evolution, and Systematics* 34: 549–574. https://doi.org/10.1146/annurev.ecolsys.34.011802.132400

MANCHESTER S.R. & E.L. O'LEARY 2010. Phylogenetic distribution and identification of fin-winged fruits. *The Botanical Review* 76: 1–82. https://doi.org/10.1007/s12229-010-9041-0

MANILAL K.S. 1988. *Flora of Silent Valley tropical rain forests of India*. The Mathrubhumi Press, Calicut.

MANILAL K.S. & V.V. SIVARAJAN 1982. *Flora of Calicut*. Bishen Singh Mahendra Pal Singh, Dehra Dun.

MATTHEW K.M. 1981-1983. *The flora of Tamil Nadu Carnatic*. Rapinat Herbarium, St. Joseph's College, Thiruchirapalli.

MINAMI S. & A. AZUMA 2003. Various flying modes of wind-dispersal seeds. *Journal of Theoretical Biology* 225 (1): 1–14. https://doi.org/10.1016/S0022-5193(03)00216-9

MIRLE C. & R.J. BURNHAM 1999. Identification of asymmetrically winged samaras from the Western Hemisphere. *Brittonia* 51: 1–14. https://doi.org/10.2307/2666549

MOHANAN M. & A.N. HENRY 1994. *Flora of Thiruvananthapuram, Kerala*. Botanical Survey of India, Coimbatore.

MURTHY K.S.R., RANI S.S., KARUPPUSAMY S., LALITHAMBA A. & T. PULLAIAH 2020. Tree Flora of Andhra Pradesh, India. *In*: KHASIM S.M., LONG C., THAMMASIRI K. & H. LUTKEN *Medicinal Plants: biodiversity, sustainable utilization and conservation*. Springer, Singapore. pp 33–86. https://doi.org/10.1007/978-981-15-1636-8

NAIDU M.T. & O.A. KUMAR 2015. Tree species diversity in the Eastern Ghats of northern Andhra Pradesh, India. *Journal of Threatened Taxa* 7(8): 7443–7459. https://doi.org/10.11609/JoTT.o3764.7443-59

NAIR N.C. & A.N. HENRY 1983. *Flora of Tamil Nadu, India*, Series 1: Analysis. Volume 1. Botanical Survey of India, Coimbatore.

NATHAN R. 2006. Long-distance dispersal of plants. *Science* 313(5788): 786–788. https://doi.org/10.1126/science.1124975

NATHAN R. & H.C. MULLER-LANDAU 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution* 15(7): 278–285. https://doi.org/10.1016/S0169-5347(00)01874-7

NORBERG R.A. 1973. Autorotation, self-stability, and structure of single-winged fruits and seeds (samaras) with comparative remarks on animal flight. *Biological Reviews* 48(4): 561–596. https://doi.org/10.1111/j.1469-185X.1973.tb01569.x

RAMACHANDRAN V.S. & V.J. NAIR 1988. *Flora of Cannanore district*. Botanical Survey of India, Kolkata.

RAZI B.A. 1950. A contribution towards the study of the dispersal mechanisms in flowering plants of Mysore (South India). *Ecology* 31(2): 282–286. https://doi.org/10.2307/1932393

ROSEN A. & D. SETER 1991. Vertical autorotation of a single-winged samara. *Journal of Applied Mechanics* 58(4): 1064–1071. https://doi.org/10.1115/1.2897683

SAATKAMP A., COCHRANE A., COMMANDER L., GUJA L.K., JIMENEZ-ALFARO B., LARSON J., NICOTRA A., POSCHOLD P., SILVEIRA F.A.O., CROSS A.T., DALZELL E.L., DICKIE J., ERICKSON T.E., FIDELES A., FUCHS A., GOLOS P.J., HOPE M., LEWANDROWSKII W., MERRITT D.J., MILLER B.P., MILLER R.G., OFFORD C.A., OOI M.K.J., SATYANTI A., SOMMERVILLE K.D., TANGNEY R., TOMLINSON S., TURNER S. & J.L. WALCK 2019. A research agenda for seed-trait functional ecology. *New Phytologist* 221(4): 1764–1775. https://doi.org/10.1111/nph.15502

SAHNI K.C. 1998. *The book of Indian trees*. Bombay Natural History Society, Mumbai.

SALDANHA C.J. 1984. *Flora of Karnataka*. Volume 1. Oxford and IBH Publishing Company, New Delhi.

SALDANHA C.J. 1996. *Flora of Karnataka*. Volume 2. Oxford and IBH Publishing Company, New Delhi.

SALDANHA C.J. & D.H. NICOLSON 1976. *Flora of Hassan district, Karnataka, India*. Amarind Publishing Company, New Delhi.

SASIDHARAN N. 2004. *Biodiversity documentation for Kerala. Part 6. Flowering plants*. Kerala Forest Research Institute, Peechi, Thrissur.

SHARMA B.D. & M. SANJAPPA 1993. *Flora of India*. Volume 3. Botanical Survey of India, Kolkata.

SHARMA B.D. & N.P. BALAKRISHNAN 1993. *Flora of India*. Volume 2. Botanical Survey of India, Kolkata.

SHARMA B.D., BALAKRISHNAN N.P., RAO R.R. & P.K. HAJRA 1993. *Flora of India*. Volume 1. Botanical Survey of India, Kolkata.

SINGH N.P., VOHRA J.N., HAJRA P.K. & D.K. SINGH 2000. *Flora of India*. Volume 5. Botanical Survey of India, Kolkata.

SNELL R.S., BECKMAN N.G., FRICKE E., LOISELLE B.A., CARVALHO C.S., JONES L.R., LICHTI N.I., LUSTENHOUWER N., SCHREIBER S.J., STRICKLAND C., SULLIVAN L.L., CAVAZOS B.R., GILADI I., HASTINGS A., HOLBROOK K.M., JONGEJANS E., KOGAN O., MONTAÑO-CENTELLAS F., RUDOLPH J., ROGERS H.S., ZWOLAK R. & E.W. SCHUPP 2019. Consequences of intraspecific variation in seed dispersal for plant demography, communities, evolution and global change. *AoB Plants* 11(4): 1–19. https://doi.org/10.1093/aobpla/plz016

SPRAGUE T.A. 1919. *Dolichandrone* and *Markhamia*. *Bulletin of Miscellaneous Information (Royal Botanic Gardens, Kew)* 1919(8): 302–314. https://doi.org/10.2307/4107551

TACKENBERG O., POSCHLOD P. & S. BONN 2003. Assessment of wind dispersal potential in plant species. *Ecological Monographs* 73(2): 191–205. https://doi.org/10.1890/0012-9615(2003)073[0191:AOWDPI]2.0.CO;2

TENNAKONE K. 2017. Aerodynamics and right-left symmetry in wind dispersal of maple, dipterocarps, conifers and some genera of Apocyanaceae and Magnoliaceae. *Journal of the National Science Foundation of Sri Lanka* 45(3): 201–217. http://dx.doi.org/10.4038/jnsfsr.v45i3.8184

THOMSON J.D. & P.R. NEAL 1989. Wind dispersal of tree seeds and fruits. *The American Biology Teacher* 51(8): 482–486. https://doi.org/10.2307/4448994

THOMPSON K., GASTON K.J. & S.R. BAND 1999. Range size, dispersal and niche breadth in the herbaceous flora of central England. *Journal of Ecology* 87(1): 150–155. https://doi.org/10.1046/j.1365-2745.1999.00334.x

VARSHNEY K., CHANG S. & Z.J. WANG 2011. The kinematics of falling maple seeds and the initial transition to a helical motion. *Nonlinearity* 25(1): C1–C8. https://doi.org/10.1088/0951-7715/25/1/C1

YASUDA K. & A. AZUMA 1997. The autorotation boundary in the flight of samaras. *Journal of Theoretical Biology* 185(3): 313–320. https://doi.org/10.1006/jtbi.1996.0299

ZHU J., LIU M., XIN Z., LIU Z. & F.M. SCHURR 2019. A trade-off between primary and secondary seed dispersal by wind. *Plant Ecology* 220: 541–552. https://doi.org/10.1007/s11258-019-00934-z

Appendix 1. List of woody angiosperms of South India with winged diaspores (Distribution & status: E-East; N-North; S-South; W-West; NE-North East; NW-North West; SE-South East; SI-South India; Sl.No.-Serial Number; SW-South West;. The IUCN threat status if any, given after asterisk).

Sl. No.	Species	Family	Habit	Flowering & Fruiting	Diaspore type	Part modified as wing	Number of wings	Distribution & Status
1.	*Acer caesium* Wall. ex Brandis	Sapindaceae	Tree	Mar-Oct	Fruit	Ovary wall	2	E Afghanistan to N & E Central China. Introduced to India
2.	*Acer oblongum* Wall. ex DC.	Sapindaceae	Tree	Feb-Sep	Fruit	Ovary wall	2	NE Pakistan to Central & S China and Indo-China. Introduced to India
3.	*Acer pseudoplatanus* L.	Sapindaceae	Tree	Apr-May	Fruit	Ovary wall	2	Europe to W Caucasus. Introduced to India
4.	*Aganope thyrsiflora* (Benth.) Polhill.	Fabaceae	Climber	Mar-Aug	Fruit	Ovary wall	2	India to S China & New Guinea
5.	*Ailanthus excelsa* Roxb.	Simaroubaceae	Tree	Dec-Jul	Fruit	Ovary wall	1	Indian subcontinent, Andaman Islands
6.	*Ailanthus integrifolia* subsp. *calycina* (Pierre) Noot.	Simaroubaceae	Tree	Jan-Apr	Fruit	Ovary wall	1	E Himalaya to Indo-China, Central & E Java
7.	*Ailanthus triphysa* (Dennst.) Alston.	Simaroubaceae	Tree	Jan-May	Fruit	Ovary wall	1	Tropical & Subtropical Asia to NE Queensland. Introduced to India
8.	*Allamanda cathartica* L.	Apocynaceae	Climber	Throughout the year	Seed	Integument	1	Tropical America. Introduced to India
9.	*Ancistrocladus heyneanus* Wall. ex J.Graham	Ancistrocladaceae	Climber	Mar-Apr	Fruit	Sepal	5	Endemic to SW India
10.	*Aspidopterys canarensis* Dalzell	Malpighiaceae	Climber	Feb-May	Fruit	Ovary wall	3	Endemic to WG *VU
11.	*Aspidopterys cordata* (B.Heyne ex Wall.) A.Juss.	Malpighiaceae	Climber	Aug-Dec	Fruit	Ovary wall	3	Endemic to India
12.	*Aspidopterys indica* (Willd.) W.Theob.	Malpighiaceae	Climber	Apr-Jan	Fruit	Ovary wall	3	Indian subcontinent to Myanmar
13.	*Berrya cordifolia* (Willd.) L. Laurent	Malvaceae	Tree	Mar-Nov	Fruit	Ovary wall	6	India to Taiwan and Central Malesia
14.	*Berrya javanica* (Turcz.) Burret	Malvaceae	Tree	Aug-Dec	Fruit	Ovary wall	10	Java, N Australia. Introduced to India
15.	*Brachypterum scandens* (Roxb.) Miq.	Fabaceae	Climber	Jun-Dec	Fruit	Ovary wall	1	Tropical & subtropical Asia to E Australia

16.	*Butea monosperma* (Lam.) Kuntze	Fabaceae	Tree	Mar-Apr	Fruit	Ovary wall	1	Indian subcontinent to China & Indo-China
17.	*Butea superba* Roxb. ex Willd.	Fabaceae	Climber	Mar-Jul	Fruit	Ovary wall	1	India to Indo-China
18.	*Campsis radicans* (L.) Bureau	Bignoniaceae	Climber	Sep-Feb	Seed	Integument	2	Central & E U.S.A. Introduced to India
19.	*Catalpa bignonioides* Walter	Bignoniaceae	Tree	Jul-Aug	Seed	Integument	2	E Texas to S Georgia. Introduced to India
20.	*Chloroxylon swietenia* DC.	Rutaceae	Tree	Mar-Oct	Seed	Integument	1	Endemic to S India & Sri Lanka
21.	*Chukrasia tabularis* A.Juss.	Meliaceae	Tree	May-Mar	Seed	Integument	1	Indian subcontinent to S China & W Malesia
22.	*Cinchona calisaya* Wedd.	Rubiaceae	Tree	Sep-Jan	Seed	Integument	2	Central Peru to Central Bolivia. Introduced to India
23.	*Combretum albidum* G.Don.	Combretaceae	Climber	Dec-Mar	Fruit	Ovary wall	4	Endemic to S India & Sri Lanka
24.	*Combretum coccineum* (Sonn.) Lam.	Combretaceae	Climber	Apr-May	Fruit	Ovary wall	5	Madagascar. Introduced to India
25.	*Combretum latifolium* Blume.	Combretaceae	Climber	Dec-Apr	Fruit	Ovary wall	4	China to Tropical Asia
26.	*Combretum malabaricum* (Bedd.) Sujana, Ratheesh & Anil Kumar	Combretaceae	Climber	Feb-Apr	Fruit	Ovary wall	5	Endemic to SWG
27.	*Combretum nanum* Buch.-Ham. ex D.Don	Combretaceae	Shrub	Mar-Apr	Fruit	Ovary wall	4	Indian subcontinent to Myanmar
28.	*Congea tomentosa* Roxb.	Lamiaceae	Climber	Mar-Jun	Infructes-cence	Involucral bracts	3	India to China & Indo-China
29.	*Congea velutina* Wight	Lamiaceae	Climber	Jan-Apr	Infructes-cence	Involucral bracts	4	Indo-China to Sumatra. Introduced to India
30.	*Dalbergia benthamii* Prain.	Fabaceae	Climber	Feb-May	Fruit	Ovary wall	1	S China to Hainan, Taiwan. Introduced to India
31.	*Dalbergia candenatensis* (Dennst.) Prain	Fabaceae	Climber	Dec-Jun	Fruit	Ovary wall	1	Tropical & subtropical Asia to W Pacific
32.	*Dalbergia congesta* Graham ex Wight & Arn.	Fabaceae	Climber	Dec-Apr	Fruit	Ovary wall	1	Endemic to SWG *EN
33.	*Dalbergia coromandeliana* Prain.	Fabaceae	Climber	Apr-Aug	Fruit	Ovary wall	1	Endemic to S India
34.	*Dalbergia gardneriana* Benth.	Fabaceae	Climber	Nov-May	Fruit	Ovary wall	1	Endemic to S India
35.	*Dalbergia horrida* (Dennst.) Mabb.	Fabaceae	Climber	Sep-Jan	Fruit	Ovary wall	1	India to Peninsula Malaysia

36.	*Dalbergia horrida* var. *glabrescens* (Prain) Thoth. & K.K.N.Nair	Fabaceae	Climber	Nov-Apr	Fruit	Ovary wall	1	India, Indo-China
37.	*Dalbergia lanceolaria* subsp. *lanceolaria*	Fabaceae	Tree	Jan-Dec	Fruit	Ovary wall	1	Indian subcontinent to Indo-China
38.	*Dalbergia lanceolaria* subsp. *paniculata* (Roxb.) Thoth.	Fabaceae	Tree	Mar-Sep	Fruit	Ovary wall	1	Indian subcontinent to Indo-China
39.	*Dalbergia latifolia* Roxb	Fabaceae	Tree	Aug-Sep	Fruit	Ovary wall	1	Indian subcontinent, Andaman Islands, Java *VU
40.	*Dalbergia malabarica* Prain	Fabaceae	Climber	Dec-Feb	Fruit	Ovary wall	1	Endemic to WG *VU
41.	*Dalbergia melanoxylon* Guill. & Perr.	Fabaceae	Tree	Apr-Jun	Fruit	Ovary wall	1	Tropical & S Africa. Introduced to India
42.	*Dalbergia pinnata* var. *acaciifolia* (Dalzell) Thoth.	Fabaceae	Climber	Mar-May	Fruit	Ovary wall	1	Endemic to SWG
43.	*Dalbergia rostrata* Hassk.	Fabaceae	Climber	Apr-Sep	Fruit	Ovary wall	1	Tropical Asia
44.	*Dalbergia rubiginosa* Roxb.	Fabaceae	Climber	Feb-May	Fruit	Ovary wall	1	India to Bangladesh *EN
45.	*Dalbergia sericea* G.Don	Fabaceae	Tree	Feb-Sep	Fruit	Ovary wall	1	Indian subcontinent to Tibet
46.	*Dalbergia sissoides* Graham ex Wight & Arn.	Fabaceae	Tree	Feb-Aug	Fruit	Ovary wall	1	India, Java
47.	*Dalbergia sissoo* Roxb. ex DC.	Fabaceae	Tree	Throughout the year	Fruit	Ovary wall	1	S Arabian Peninsula to Myanmar
48.	*Dalbergia tinnevelliensis* Thoth.	Fabaceae	Shrub	Jan-May	Fruit	Ovary wall	1	Endemic to South India*VU
49.	*Dalbergia travancorica* Thoth.	Fabaceae	Climber	Jan-Nov	Fruit	Ovary wall	1	Endemic to SWG *EN
50.	*Dalbergia volubilis* Roxb.	Fabaceae	Climber	Feb-Jun	Fruit	Ovary wall	1	Indian subcontinent to China & Indo-China
51.	*Derris benthamii* (Thwaites) Thwaites	Fabaceae	Climber	Jun-Nov	Fruit	Ovary wall	1	Endemic to SW India & Sri Lanka *EN
52.	*Derris benthamii* var. *wightii* (Baker) Thoth.	Fabaceae	Climber	Dec-May	Fruit	Ovary wall	1	Endemic to South India
53.	*Derris brevipes* (Benth.) Baker	Fabaceae	Climber	Feb-Dec	Fruit	Ovary wall	2	Endemic to WG

54.	*Derris brevipes* var. *coriacea* Baker	Fabaceae	Climber	Feb-Oct	Fruit	Ovary wall	2	Endemic to SWG
55.	*Derris canarensis* (Dalzell) Baker	Fabaceae	Climber	Sep-Jan	Fruit	Ovary wall	2	S India, Sri Lanka, Taiwan
56.	*Derris elliptica* (Wall.) Benth.	Fabaceae	Climber	Mar-Jun	Fruit	Ovary wall	2	Indo-China to New Guinea
57.	*Derris heyneana* (Wight &Arn.) Benth.	Fabaceae	Climber	Feb-May	Fruit	Ovary wall	2	SW India, Laos
58.	*Derris thothathri* Bennet	Fabaceae	Climber	Dec-Mar	Fruit	Ovary wall	2	Endemic to SWG *VU
59.	*Derris trifoliata* Lour.	Fabaceae	Climber	Jan-Oct	Fruit	Ovary wall	1	S Somalia to S Africa & W Pacific. Introduced to India
60.	*Dioscorea alata* L.	Dioscoreaceae	Climber	Jul-Dec	Seed	Integument	1	Tropical Asia
61.	*Dioscorea belophylla* (Prain) Voigt ex Haines	Dioscoreaceae	Climber	Oct-Mar	Seed	Integument	1	Indian subcontinent
62.	*Dioscorea bulbifera* L.	Dioscoreaceae	Climber	Sep-Dec	Seed	Integument	1	Tropical & subtropical Old World
63.	*Dioscorea esculenta* (Lour.) Burkill	Dioscoreaceae	Climber	Sep-Dec	Seed	Integument	1	Tropical Asia. Introduced to India
64.	*Dioscorea glabra* Roxb.	Dioscoreaceae	Climber	Aug-Dec	Seed	Integument	1	Indian subcontinent to Malaya
65.	*Dioscorea hamiltonii* Hook.f.	Dioscoreaceae	Climber	Oct-Dec	Seed	Integument	1	Indian subcontinent to Taiwan & Peninsula Thailand
66.	*Dioscorea hispida* Dennst.	Dioscoreaceae	Climber	Sept-Oct	Seed	Integument	1	Tropical & subtropical Asia to N. Australia
67.	*Dioscorea intermedia* Thwaites	Dioscoreaceae	Climber	Oct-Jan	Seed	Integument	1	Sri Lanka. Introduced to India
68.	*Dioscorea kalkapershadii* Prain & Burkill.	Dioscoreaceae	Climber	Sep-Dec	Seed	Integument	1	India to Bangladesh
69.	*Dioscorea oppositifolia* L.	Dioscoreaceae	Climber	Jan-May	Seed	Integument	1	S India, Sri Lanka, E Himalaya to Myanmar
70.	*Dioscorea pentaphylla* L.	Dioscoreaceae	Climber	Sep-Dec	Seed	Integument	1	Tropical & subtropical Asia to N Australia
71.	*Dioscorea pubera* Blume	Dioscoreaceae	Climber	Oct-Jan	Seed	Integument	1	Central Himalaya to W Malesia
72.	*Dioscorea spicata* B.Heyne ex Roth	Dioscoreaceae	Climber	Aug-Dec	Seed	Integument	1	S India, Sri Lanka, Bangladesh
73.	*Dioscorea tomentosa* J.Koenig ex Spreng.	Dioscoreaceae	Climber	Jul-Nov	Seed	Integument	1	India to Bangladesh, Sri Lanka
74.	*Dioscorea wallichii* Hook.f.	Dioscoreaceae	Climber	Oct-Nov	Seed	Integument	1	India, China, Bangladesh, Myanmar, Thailand
75.	*Dioscorea wightii* Hook f.	Dioscoreaceae	Climber	Jul-Nov	Seed	Integument	1	Endemic to SWG *CR
76.	*Dipterocarpus bourdillonii* Brandis	Dipterocarpaceae	Tree	Jan-Jun	Fruit	Sepal	2	Endemic to WG *CR

77.	*Dipterocarpus indicus* Bedd.	Dipterocarpaceae	Tree	Dec-Jul	Fruit	Sepal	2	Endemic to Western Ghats *VU
78.	*Dodonaea viscosa* Jacq.	Sapindaceae	Shrub	Jan-Sep	Fruit	Ovary wall	2-3	Pantropical
79.	*Dodonaea viscosa* subsp.*angustifolia* (L.f.) J.G.West	Sapindaceae	Shrub	Throughout the year	Fruit	Ovary wall	3	Tropics & subtropics
80.	*Dolichandrone arcuata* (Wight.) C.B.Clarke	Bignoniaceae	Tree	Oct-Feb	Seed	Integument	2	Endemic to S India
81.	*Dolichandrone atrovirens* (Roth) K.Schum.	Bignoniaceae	Tree	Jan-May	Seed	Integument	2	Endemic to S India
82.	*Dolichandrone falcata* (Wall. ex DC.) Seem.	Bignoniaceae	Tree	Throughout the year	Seed	Integument	2	India to Bangladesh
83.	*Dolichandrone spathacea* (L.f.) K.Schum.	Bignoniaceae	Tree	Jun-Aug	Seed	Integument	2	Tropical & Subtropical Asia to W Pacific
84.	*Eriolaena candollei* Wall.	Malvaceae	Tree	Mar-Oct	Seed	Integument	1	India to S China & Indo-China
85.	*Eriolaena hookeriana* Wight. & Arn.	Malvaceae	Tree	Feb-Mar	Seed	Integument	1	Endemic to India & Sri Lanka
86.	*Eriolaena lushingtonii* Dunn.	Malvaceae	Tree	Jun-Aug	Seed	Integument	1	Endemic to SW India *VU
87.	*Eriolaena quinquelocularis* (Wight & Arn.) Drury	Malvaceae	Tree	Jul-Dec	Seed	Integument	1	India to China
88.	*Eriolaena stocksii* Hook.f. & Thomson ex Mast.	Malvaceae	Tree	May-Sep	Seed	Integument	1	Endemic to India
89.	*Fernandoa adenophylla* (Wall. ex G.Don) Steenis	Bignoniaceae	Tree	Oct-May	Seed	Integument	2	India to Peninsula Malaysia
90.	*Firmiana colorata* (Roxb.) R.Br.	Malvaceae	Tree	Jan-Jun	Fruit	Ovary wall	1	Indian Subcontinent to China (S. Yunnan) and Sumatera.
91.	*Getonia floribunda* Roxb.	Combretaceae	Climber	Jan-May	Fruit	Sepal	5	India to China & Peninsula Malaysia
92.	*Grevillea robusta* A.Cunn. ex R.Br.	Proteaceae	Tree	Jun-Sep	Seed	Integument	1	New South Wales, Queensland. Introduced to India
93.	*Gyrocarpus americanus* subsp. *americanus*	Hernandiaceae	Tree	Dec-Apr	Fruit	Tepals	2	E Tropical Africa to Pacific, Central Mexico to Venezuela
94.	*Handroanthus impetiginosus* (Mart. ex DC.) Mattos	Bignoniaceae	Tree	Not known	Seed	Integument	2	Central Mexico to S Tropical America. Introduced to India

95.	*Heritiera littoralis* Aiton	Malvaceae	Tree	Jul-Mar	Fruit	Ovary wall	1	SE Kenya to Mozambique & W Pacific. Introduced to India
96.	*Heritiera papilio* Bedd.	Malvaceae	Tree	Jan-May	Fruit	Ovary wall	1	Indian subcontinent to Myanmar
97.	*Heterophragma quadriloculare* (Roxb.) K.Schum.	Bignoniaceae	Tree	Dec-Feb	Seed	Integument	2	Central & S India to Bangladesh
98.	*Hildegardia populifolia* (DC.) Schott & Endl.	Malvaceae	Tree	Feb-Aug	Fruit	Ovary wall	1	Endemic to SE India
99.	*Hiptage benghalensis* (L.) Kurz.	Malpighiaceae	Climber	Jan-Nov	Fruit	Ovary wall	3	Tropical & subtropical Asia
100.	*Holoptelea integrifolia* (Roxb.) Planch.	Ulmaceae	Tree	Dec-Mar	Fruit	Ovary wall	1	Indian subcontinent to Indo-China, E Borneo
101.	*Hopea canarensis* Hole	Dipterocarpaceae	Tree	May-Jul	Fruit	Sepals	2/3	Endemic to S India *EN
102.	*Hopea glabra* Wight & Arn.	Dipterocarpaceae	Tree	Jan -Jul	Fruit	Sepals	2	Endemic to WG *EN
103.	*Hopea jacobi* C.E.C.Fisch.	Dipterocarpaceae	Tree	Jan-Jul	Fruit	Sepals	2	Endemic to SWG *CR
104.	*Hopea parviflora* Bedd.	Dipterocarpaceae	Tree	Jan-Jun	Fruit	Sepals	2	SW & S India *VU
105.	*Hopea ponga* (Dennst.) Mabb.	Dipterocarpaceae	Tree	Mar-Jun	Fruit	Sepals	2	Endemic to SWG *VU
106.	*Hopea racophloea* Dyer	Dipterocarpaceae	Tree	Feb-May	Fruit	Sepals	2/3	Endemic to S India
107.	*Hymenodictyon obovatum* Wall.	Rubiaceae	Tree	Jun-Oct	Seed	Integument	1	Endemic to WG
108.	*Hymenodictyon orixense* (Roxb.) Mabb.	Rubiaceae	Tree	Jul-Jan	Seed	Integument	1	Indian subcontinent to S Central China & Indo-China, Philippines
109.	*Jacaranda mimosifolia* D.Don.	Bignoniaceae	Tree	Dec-Jul	Seed	Integument	1	Bolivia to NW Argentina. Introduced to India
110.	*Kamettia caryophyllata* (Roxb.) Nicolson & Suresh	Apocynaceae	Climber	Sep-Jan	Seed	Integument	2	Endemic to SWG
111.	*Kydia calycina* Roxb.	Malvaceae	Tree	Oct-Jan	Fruit	Bracts (Epicalyx)	4-6	Indian subcontinent to China & Indo-China

112.	*Lagerstroemia indica* L.	Lythraceae	Shrub	Jun-Nov	Seed	Integument	1	Central Himalaya to S China & Indo-China. Introduced to India
113.	*Lagerstroemia microcarpa* Wight	Lythraceae	Tree	Jun-Feb	Seed	Integument	1	Endemic to WG
114.	*Lagerstroemia parviflora* Roxb.	Lythraceae	Tree	Feb-May	Seed	Integument	1	Indian subcontinent to Myanmar
115.	*Lagerstroemia speciosa* (L.)Pers.	Lythraceae	Tree	Mar-Nov	Seed	Integument	1	China to Tropical Asia
116.	*Loeseneriella africana* var. *obtusifolia* (Roxb.) N.Halle	Celastraceae	Climber	Jul-Sep	Seed	Integument	1	India, Sri Lanka, Indo-China
117.	*Loeseneriella bourdillonii* (Gamble) D.C.S.Raju	Celastraceae	Climber	Mar-May	Seed	Integument	1	Endemic to SWG
118.	*Lophopetalum wightianum* Arn.	Celastraceae	Tree	Dec-Jul	Seed	Integument	1	Indian subcontinent to W Malesia *LC
119.	*Mansoa alliacea* (Lam.) A.H.Gentry	Bignoniaceae	Climber	Sep-Feb	Seed	Integument	2	Lesser Antilles to S Tropical America. Introduced to India
120.	*Markhamia stipulata* (Wall.) Seem.	Bignoniaceae	Tree	Not known	Seed	Integument	2	Bangladesh to S China & Indo-China
121.	*Mezoneuron cucullatum* (Roxb.) Wight & Arn.	Fabaceae	Climber	Feb-Apr	Fruit	Ovary wall	1	S & E India to China & W & Central Malesia
122.	*Mezoneuron hymenocarpum* Wight & Arn. ex Prain	Fabaceae	Climber	Sep-Jan	Fruit	Ovary wall	1	China to Tropical Asia & N Queensland
123.	*Millingtonia hortensis* L.f.	Bignoniaceae	Tree	Mar-Aug	Seed	Integument	1	S Central China to Malesia. Introduced to India
124.	*Moringa concanensis Nimmo* ex Dalzell & A.Gibson	Moringaceae	Tree	Feb-Jun	Seed	Integument	3	Pakistan to NW India
125.	*Moringa oleifera* Lam.	Moringaceae	Tree	Nov-Mar	Seed	Integument	3	NE Pakistan to NW India
126.	*Neuropeltis malabarica* Ooststr.	Convolvulaceae	Climber	Nov-Mar	Fruit	Floral bract	1	Endemic to SWG
127.	*Nyctocalos cuspidatum* (Blume) Miq.	Bignoniaceae	Climber	Not known	Seed	Integument	1	Assam to Indo-China, Central & E Malesia
128.	*Oroxylum indicum* (L.) Kurz.	Bignoniaceae	Tree	Jul-Dec	Seed	Integument	1	S China to Tropical Asia
129.	*Pajanelia longifolia* (Willd.) K.Schum.	Bignoniaceae	Tree	Jan-Jun	Seed	Integument	1	S India to W Malesia
130.	*Pandorea jasminoides* (Lindl.) K.Schum.	Bignoniaceae	Climber	Dec-May	Seed	Integument	1	E Queensland to NE New South Wales. Introduced to India

131.	*Plumeria obtusa* L.	Apocynaceae	Tree	Dec-Jun	Seed	Integument	1	Florida Keys, Caribbean, SE Mexico to Guatemala. Introduced to India
132.	*Plumeria rubra* L.	Apocynaceae	Tree	Nov-Apr	Seed	Integument	1	Mexico to Venezuela. Introduced to India
133.	*Podranea ricasoliana* (Tanfani) Sprague	Bignoniaceae	Climber	Nov-Jun	Seed	Integument	2	S Tropical & S Africa. Introduced to India
134.	*Polyspora obtusa* (Wall. ex Wight &Arn.) Niissalo & L.M.Choo	Theaceae	Tree	Oct-May	Seed	Integument	1	Endemic to S India
135.	*Pristimera arnottiana* (Wight) R.H.Archer	Celastraceae	Climber	Feb-Mar	Seed	Integument	1	Endemic to India & Sri Lanka
136.	*Pterocarpus dalbergioides* Roxb. ex DC.	Fabaceae	Tree	Sep-Jan	Fruit	Ovary wall	1	Endemic to Andaman Islands. Introduced to India *VU
137.	*Pterocarpus indicus* Willd.	Fabaceae	Tree	Oct-Jan	Fruit	Ovary wall	1	Tropical & subtropical Asia to W Pacific *EN
138.	*Pterocarpus marsupium* Roxb.	Fabaceae	Tree	Sep-Oct	Fruit	Ovary wall	1	Indian subcontinent
139.	*Pterocarpus santalinus* L.f.	Fabaceae	Tree	Sep-Jan	Fruit	Ovary wall	1	Endemic to S India *EN
140.	*Pterocymbium tinctorium* var. *javanicum* (R.Br.) Kosterm.	Malvaceae	Tree	Jan-May	Fruit	Ovary wall	1 (2-lobed)	Indo-China to Malesia. Introduced to India
141.	*Pterolobium hexapetalum* (Roth) Santapau & Wagh.	Fabaceae	Climber	Mar-Aug	Fruit	Ovary wall	1	Indian subcontinent to Myanmar
142.	*Pterospermum acerifolium* (L.) Willd.	Malvaceae	Tree	May-Jun	Seed	Integument	1	Nepal to China & Peninsula Malaysia
143.	*Pterospermum diversifolium* Bl.	Malvaceae	Tree	Dec-Apr	Seed	Integument	1	Indo-Malesia
144.	*Pterospermum obtusifolium* Wight ex Mast.	Malvaceae	Tree	Mar-Aug	Seed	Integument	1	Endemic to SWG
145.	*Pterospermum reticulatum* Wight. & Arn.	Malvaceae	Tree	Jan-Nov	Seed	Integument	1	SW India, Myanmar *VU
146.	*Pterospermum rubiginosum* B.Heyne ex G.Don	Malvaceae	Tree	Nov-Apr	Seed	Integument	1	Endemic to SWG
147.	*Pterospermum suberifolium* (L.) Raeusch.	Malvaceae	Tree	Jun-Apr	Seed	Integument	1	Indian subcontinent to Myanmar

148.	*Pterospermum xylocarpum* (Gaertn.) Oken	Malvaceae	Tree	May–Jul	Seed	Integument	1	Endemic to S India
149.	*Pterygota alata* (Roxb.) R.Br.	Malvaceae	Tree	Apr–May	Seed	Integument	1	Indian subcontinent to China & Sumatera, S Hainan
150.	*Pyrostegia venusta* (Ker Gawl.) Miers	Bignoniaceae	Climber	Dec–Jun	Seed	Integument	2	Tropical & subtropical areas
151.	*Radermachera xylocarpa* (Roxb.) Roxb. ex K.Schum.	Bignoniaceae	Tree	Mar–Apr	Seed	Integument	2	Endemic to India
152.	*Reissantia grahamii* (Wight) Ding Hou	Celastraceae	Climber	Jan–May	Seed	Integument	1	Tropical Asia
153.	*Reissantia indica* (Willd.) N. Halle	Celastraceae	Climber	Mar–Apr	Seed	Integument	1	Indo-Malesia
154.	*Schrebera swietenioides* Roxb.	Oleaceae	Tree	May–June	Seed	Integument	1	India to Indo-China
155.	*Shorea robusta* C.F.Gaertn.	Dipterocarpaceae	Tree	Feb–Jul	Fruit	Sepals	3–5	Indian subcontinent to SE Tibet
156.	*Shorea roxburghii* G.Don	Dipterocarpaceae	Tree	Feb–Jun	Fruit	Sepals	3–5	S India, Indo-China to NW Peninsula Malaysia *VU
157.	*Shorea tumbuggaia* Roxb.	Dipterocarpaceae	Tree	Mar–Jul	Fruit	Sepals	3–5	Endemic to SE India *EN
158.	*Smythea bombaiensis* (Dalzell) S.P.Banerjee & P.K.Mukh.	Rhamnaceae	Climber	Feb–Jun	Fruit	Ovary wall	1	Endemic to WG
159.	*Soymida febrifuga* (Roxb.) A.Juss.	Meliaceae	Tree	Feb–Jul	Seed	Integument	2	Indian subcontinent to Myanmar
160.	*Spathodea campanulata* P.Beauv.	Bignoniaceae	Tree	Nov–May	Seed	Integument	1	W Tropical Africa to Uganda & Angola. Introduced to India
161.	*Spatholobus parviflorus* (Roxb. ex G.Don) Kuntze	Fabaceae	Climber	Sep–Apr	Fruit	Ovary wall	1	Indian subcontinent to China & Indo-China
162.	*Spatholobus purpureus* Benth. ex Baker	Fabaceae	Climber	Jan–Mar	Fruit	Ovary wall	1	India, Myanmar
163.	*Sphenodesme involucrata* (C.Presl) B.L.Rob.	Lamiaceae	Climber	Dec–Mar	Infructescence	Involucral bract	6	India to China & N Sumatera
164.	*Sphenodesme involucrata* var. paniculata (C.B.Clarke) Munir	Lamiaceae	Climber	Dec–May	Infructescence	Involucral bract	6	S India, Myanmar

165.	*Stereospermum chelonoides* (L.f.) DC.	Bignoniaceae	Tree	Jan-Aug	Seed	Integument	2	Indian subcontinent to Indo-China
166.	*Stereospermum tetragonum* DC.	Bignoniaceae	Tree	Feb-Oct	Seed	Integument	2	S China & Sumatera
167.	*Swietenia macrophylla* G.King.	Meliaceae	Tree	Apr-Jan	Seed	Integument	1	Central America. Introduced to India
168.	*Swietenia mahagoni* (L.) Jacq.	Meliaceae	Tree	Apr-Jan	Seed	Integument	1	West Indies & Central America. Introduced to India
169.	*Symphorema involucratum* Roxb.	Lamiaceae	Climber	Mar-Apr	Infructes-cence	Involucral Bract	6	India to China
170.	*Tabebuia aurea* (Silva Manso) Benth. & Hook.f. ex S.Moore	Bignoniaceae	Tree	Mar-Apr	Seed	Integument	2	Peru to Brazil & N Argentina. Introduced to India
171.	*Tabebuia pallida* (Lindl.) Miers	Bignoniaceae	Tree	Feb-Apr	Seed	Integument	2	Leeward Islands, Windward Islands. Introduced to India
172.	*Tabebuia rosea* (Bertol.) Bertero ex A.DC.	Bignoniaceae	Tree	Dec-Jun	Seed	Integument	2	Mexico to Ecuador. Introduced to India
173.	*Tecoma castanifolia* (D. Don) Melch.	Bignoniaceae	Tree	Throughout the year	Seed	Integument	2	W Ecuador. Introduced to India
174.	*Tecoma stans* (L.) Juss. ex Kunth.	Bignoniaceae	Tree	Throughout the year	Seed	Integument	2	Tropical & Subtropical America. Introduced to India
175.	*Tecomaria capensis* (Thunb.) Spach	Bignoniaceae	Shrub	Throughout the year	Seed	Integument	2	Tanzania to S Africa. Introduced to India
176.	*Terminalia arjuna* (Roxb. ex DC.) Wight & Arn.	Combretaceae	Tree	May-Nov	Fruit	Ovary wall	5	Indian subcontinent
177.	*Terminalia elliptica* Willd.	Combretaceae	Tree	Apr-May	Fruit	Ovary wall	5	Indian subcontinent to Indo-China
178.	*Terminalia paniculata* B.Heyne ex Roth	Combretaceae	Tree	Aug-Feb	Fruit	Ovarywall	3	Endemic to S India
179.	*Toona ciliata* M.Roem.	Meliaceae	Tree	Feb-May	Seed	Integument	2	S China to tropical Asia
180.	*Toona sureni* (Blume) Merr.	Meliaceae	Tree	Apr-May	Seed	Integument	2	S Central China to tropical Asia. Introduced to India
181.	*Tristellateia australasiae* A.Rich.	Malpighiaceae	Climber	Sep-May	Fruit	Ovary wall	6-8	Comoros, Indo-China to Nansei-shoto & W Pacific. Introduced to India
182.	*Ventilago denticulata* Willd.	Rhamnaceae	Climber	Sep-Jun	Fruit	Ovary wall	1	Indian subcontinent to China & Indo-China
183.	*Ventilago gamblei* Suess.	Rhamnaceae	Climber	Jan-Feb	Fruit	Ovary wall	1	Endemic to S India & Sri Lanka

184.	*Ventilago goughii* Gamble	Rhamnaceae	Climber	March	Fruit	Ovary wall	1	Endemic to S India
185.	*Ventilago madraspatana* Gaertn.	Rhamnaceae	Climber	Dec-Mar	Fruit	Ovary wall	1	India to China, Indo-China, Java to Lesser Sunda Islands
186.	*Zanonia indica* L.	Cucurbitaceae	Climber	Sept-Jan	Seed	Integument	1	Endemic to S India & Sri Lanka

Appendix 2. Pattern of development of wings in diaspores of South Indian woody angiosperms

Part modified to wing	Mode of wing development	Species
Ovary wall	Unidirectional	*Acer caesium* Wall. ex Brandis, *A. oblongum* Wall. ex DC., *A. pseudoplatanus* L., *Berrya cordifolia* (Willd.) L.Laurent, *B. javanica* (Turcz.) Burret, *Butea monosperma* (Lam.) Kuntze, *B. superba* Roxb. ex Willd., *Firmiana colorata* (Roxb.) R.Br., *Heritiera littoralis* Aiton, *H. papilio* Bedd., *Hildegardia populifolia* (DC.) Schott & Endl., *Pterocymbium tinctorium* var. *javanicum* (R.Br.) Kosterm., *Pterolobium hexapetalum* (Roth) Santapau & Wagh., *Smythea bombaiensis* (Dalzell) S.P. Banerjee & P.K.Mukh., *Spatholobus parviflorus* (Roxb. ex G.Don) Kuntze, *S. purpureus* Benth. ex Baker, *Ventilago denticulata* Willd., *V. gamblei* Suess., *V. goughii* Gamble, *V. maderaspatana* Gaertn.
	Bidirectional	*Aganope thyrsiflora* (Benth.) Polhill., *Ailanthus excelsa* Roxb., *A. integrifolia* subsp. *calycina* (Pierre) Noot., *Ailanthus triphysus* (Dennst.) Alston., *Brachypterum scandens* (Roxb.) Miq., *Dalbergia benthamii* Prain., *D. candenatensis* (Dennst.) Prain, *D. congesta* Graham ex Wight & Arn., *D. coromandeliana* Prain., *D. gardneriana* Benth., *D. horrida* (Dennst.) Mabb., *D. horrida* var. *glabrescens* (Prain) Thoth. & K.K.N.Nair, *D. lanceolaria* L.f. subsp. *lanceolaria*, *D. lanceolaria* subsp. *paniculata* (Roxb.) Thoth., *D. latifolia* Roxb., *D. malabarica* Prain, *D. melanoxylon* Guill. & Perr., *D. pinnata* var. *acaciifolia* (Dalzell) Thoth., *D. rostrata* Hassk., *D. rubiginosa* Roxb., *D. sericea* G.Don, *D. sissoides* Graham ex Wight & Arn., *D. sissoo* Roxb. ex DC., *D. tinnevelliensis* Thoth., *D. travancorica* Thoth., *D. volubilis* Roxb., *Derris brevipes* (Benth.) Baker, *D. brevipes* var. *coriacea* Baker, *D. canarensis* (Dalzell) Baker, *D. elliptica* (Wall.) Benth., *D. heyneana* (Wight & Arn.) Benth., *D. thothathrii* Bennet
	3-directional	*Hiptage benghalensis* (L.) Kurz., *Terminalia paniculata* B.Heyne ex Roth
	Multidirectional	*Aspidopterys canarensis* Dalzell, *A. cordata* (B.Heyne ex Wall.) A.Juss., *A. indica* (Willd.) W.Theob., *Combretum albidum* G.Don., *C. coccineum* (Sonn.) Lam., *C. latifolium* Blume., *C. malabaricum* (Bedd.) Sujana, Ratheesh & Anil Kumar, *C. nanum* Buch.-Ham. ex D.Don, *Dodonaea viscosa* Jacq., *D. viscosa* subsp. *angustifolia* (L.f.) J.G.West, *Terminalia arjuna* (Roxb. ex DC.) Wight & Arn., *T. elliptica* Willd., *Tristellateia australasiae* A.Rich.

	Elliptical surrounding	*Derris benthamii* (Thwaites) Thwaites, *D. benthamii* var. *wightii* (Baker) Thoth., *D. trifoliata* Lour., *Holoptelea integrifolia* (Roxb.) Planch., *Pterocarpus dalbergioides* Roxb. ex DC., *P. indicus* Willd., *P. marsupium* Roxb., *P. santalinus* L.f.
Integument	Unidirectional	*Chloroxylon swietenia* DC., *Chukrasia tabularis* A.Juss., *Dioscorea bulbifera* L., *D. hispida* Dennst., *D. kalkapershadii* Prain & Burkill., *D. pentaphylla* L., *D. tomentosa* J.Koenig ex Spreng., *Eriolaena candollei* Wall., *E. hookeriana* Wight. & Arn., *E. lushingtonii* Dunn., *E. quinquelocularis* (Wight & Arn.) Drury, *E. stocksii* Hook.f. & Thomson ex Mast., *Lagerstroemia indica* L., *L. microcarpa* Wight, *L. parviflora* Roxb., *L. speciosa* (L.) Pers., *Loeseneriella africana* var. *obtusifolia* (Roxb.) N.Halle, *L. bourdillonii* (Gamble) D.C.S.Raju, *Plumeria obtusa* L., *P. rubra* L., *Polyspora obtusa* (Wall. ex Wight & Arn.) Niissalo & L.M.Choo, *Pristimera arnottiana* (Wight) R.H.Archer, *Pterospermum acerifolium* (L.) Willd., *P. diversifolium* Bl., *P. obtusifolium* Wight ex Mast., *P. reticulatum* Wight. & Arn., *P. rubiginosum* B.Heyne ex G.Don, *P. suberifolium* (L.) Raeusch., *P. xylocarpum* (Gaertn.) Oken, *Pterygota alata* (Roxb.) R.Br., *Reissantia grahamii* (Wight) Ding Hou, *R. indica* (Willd.) N.Halle, *Schrebera swietenioides* Roxb., *Swietenia macrophylla* G.King., *S. mahagoni* (L.) Jacq.
	Bidirectional	*Campsis radicans* (L.) Bureau, *Catalpa bignonioides* Walter, *Cinchona calisaya* Wedd., *Dolichandrone arcuata* (Wight.) C.B.Clarke, *D. atrovirens* (Roth) K.Schum., *D. falcata* (Wall. ex DC.) Seem., *D. spathacea* (L.f.) K.Schum., *Fernandoa adenophylla* (Wall. ex G.Don) Steenis, *Handroanthus impetiginosus* (Mart. ex DC.) Mattos, *Heterophragma quadriloculare* (Roxb.) K.Schum., *Kamettia caryophyllata* (Roxb.) Nicolson & Suresh, *Mansoa alliacea* (Lam.) A.H.Gentry, *Markhamia stipulata* (Wall.) Seem., *Mezoneuron cucullatum* (Roxb.) Wight & Arn., *M. hymenocarpum* Wight & Arn. ex Prain, *Podranea ricasoliana* (Tanfani) Sprague, *Pyrostegia venusta* (Ker Gawl.) Miers, *Radermachera xylocarpa* (Roxb.) Roxb. ex K.Schum., *Soymida febrifuga* (Roxb.) A.Juss., *Stereospermum chelonoides* (L.f.) DC., *S. tetragonum* DC., *Tabebuia aurea* (Silva Manso) Benth. & Hook.f. ex S.Moore, *T. pallida* (Lindl.) Miers, *T. rosea* (Bertol.) Bertero ex A.DC., *Tecoma castanifolia* (D.Don) Melch., *T. stans* (L.) Juss. ex Kunth., *Tecomaria capensis* (Thunb.) Spach, *Toona ciliata* M.Roem., *T. sureni* (Blume) Merr., *Zanonia indica* L.
	Multidirectional	*Moringa concanensis* Nimmo ex Dalzell & A.Gibson, *M. oleifera* Lam.
	Elliptical surrounding	*Allamanda cathartica* L., *Dioscorea alata* L., *D. belophylla* (Prain) Voigt ex Haines, *D. glabra* Roxb., *D. esculenta* (Lour.) Burkill, *D. hamiltonii* Hook.f., *D. intermedia* Thwaites, *D. oppositifolia* L., *D. pubera* Blume, *D. spicata* B.Heyne ex Roth, *D. wallichii* Hook.f., *D. wightii* Hook.f., *Grevillea robusta* A.Cunn. ex R.Br., *Hymenodictyon obovatum* Wall., H. orixense (Roxb.) Mabb., *Jacaranda*

		mimosifolia D.Don., *Lophopetalum wightianum* Arn., *Millingtonia hortensis* L.f., *Nyctocalos cuspidatum* (Blume) Miq., *Oroxylum indicum* (L.) Kurz., *Pajanelia longifolia* (Willd.) K.Schum., *Pandorea jasminoides* (Lindl.) K.Schum., *Spathodea campanulata* P.Beauv.
Perianth	Sepal/tepal without further development	*Getonia floribunda* Roxb.
	Sepal/tepal with further development	*Ancistrocladus heyneanus* Wall. ex J.Graham, *Dipterocarpus bourdillonii* Brandis, *D. indicus* Bedd., *Gyrocarpus americanus* Jacq., *Hopea canarensis* Hole, *H. glabra* Wight & Arn., *H. jacobi* C.E.C.Fisch., *H. parviflora* Bedd., *H. ponga* (Dennst.) Mabb., *H. racophloea* Dyer, *Shorea robusta* C.F.Gaertn., *S. roxburghii* G.Don, *S. tumbuggaia* Roxb.
Bract	Floral bract	*Neuropeltis malabarica* Ooststr.
	Involucral bract	*Congea tomentosa* Roxb., *C. velutina* Wight, *Kydia calycina* Roxb., *Sphenodesme involucrata* (C.Presl) B.L.Rob., *S. involucrata* var. *paniculata* (C.B.Clarke) Munir, *Symphorema involucratum* Roxb.