Anemophily, accidental cantharophily, seed dispersal and seedling ecology of *Cycas sphaerica* Roxb. (Cycadaceae), a data-deficient red-listed species of northern Eastern Ghats

A. J. Solomon Raju* and K. Henry Jonathan

Department of Environmental Sciences, Andhra University, Visakhapatnam 530 003, India

***Cycas sphaerica* is a data-deficient, red-listed, tropical dry deciduous dioecious shrub species confined to the northern Eastern Ghats of India. It reproduces asexually and sexually. In asexual mode, bulbils arise as offshoots of the stem and produce new branches or new plants. In sexual mode, a small number of plants participate in the coning event during March–May. The plant sex ratio is strongly male-biased. The plant is typically anemophilous and effective for optimal seed set. The cones of both sexes show strong thermogenesis and odour production during the maturation process; these two processes attract *Derelomus* weevils which use male cones for feeding and breeding during which they get covered with pollen. These weevils in search of other male cones also visit female cones and effect pollination accidentally. The female cones only offer warmth to the weevils during night. The weevils diapause on male plants until the next coning season. Spotted deer (*Axis axis*), sloth bear (*Melursus ursinus*) and rainwater disperse seeds. Seeds are not dormant. Natural regeneration through sexual and asexual means is poor, which could be due to seed predation, inability of the germinating seeds and growing seedlings to compete well with the seasonal plants and grasses for the available nutrients in the soil and litter, and erratic rainfall or dry spells within the rainy season. Further, the traditional uses of this plant also contribute to the restricted population size. Therefore, concrete measures are required for the effective conservation and management of *C. sphaerica*.**

Keywords: Anemophily, bulbil reproduction, *Cycas sphaerica*, leaf and coning phenology, seed ecology.

THE family Cycadaeae represents a monotypic genus *Cycas* with about 100 species. *Cycas* is the sole living cycad group occurring in Asia[1]. In this genus, pollination information is available for a few species which include *Cycas circinalis*[2], *Cycas panzhihuaensis*[3], *Cycas seemannii*[4], *Cycas rumphii*, *Cycas thouarsii*[5], *Cycas media*[6] and *Cycas revoluta*[7]. In India, eight species exist, viz. *Cycas beddomei*, *Cycas circinalis*, *Cycas indica*, *Cycas sphaerica*, *Cycas annakailensis*, *Cycas nathorstii*, *Cycas pectinata* and *Cycas zeylanica*, with the first five species occurring only here[1]. None of the *Cycas* species occurring in India have been worked out for the pollination ecology thus far and hence the subject concerning *Cycas* genus in this country remains a virgin field. *C. sphaerica* although prominent in the literature, is poorly described even for its distributional areas and taxonomic characters. It is listed under the Data-Deficient category of the IUCN Redlist and is also included in the CITES Appendix II that allows trade in wild-cultivated seeds or plants as long as there is no detrimental impact on the survival of wild populations[8,9]. It occurs in the Eastern Ghats of Srikakulam District, Andhra Pradesh, but it was wrongly documented as *C. circinalis* in the Flora of Srikakulam by Rao and Sreeramulu[10]. In this communication, we report on the plant characteristics, demography of cone production and pollination agents, seed dispersal and seedling ecology of *C. sphaerica*. These aspects are discussed in the light of the existing related information on *Cycas* species elsewhere and on other genera of cycads.

C. sphaerica (= *C. circinalis* L. var. *orixensis* Haines) is a tropical dry deciduous shrub. Its population in the Jalantrakota Reserve Forest (lat. 18°46′N, long. 84°25′E and altitude 364 ft) in the northern Eastern Ghats of Srikakulam District, was selected for the study during 2008–2009. The site with an area of 5 km^2 is characterized by a combination of rocky and undulating terrain. Leaf characteristics and leaflet number per leaf were recorded, for which five leaves each from five male and four female plants were used. Demographic study was carried out to record the number and proportion of plants participating in the annual coning event. Five young male cones and four female cones were selected and monitored over the duration of the pollination season to record the cone development sequence. These cones were also examined for heat production during the maturation period; the temperature within and outside the cone before, during and after pollen shedding in male cone and during maturation of the female cone was measured using a thermometer. In five male cones, the arrangement and number of sporophylls, and the number of sori consisting of microsporangia were recorded. The pollen output per microsporangia/sporophyll/cone and the pollen-grain characteristics for anemophily were recorded following the protocol suggested by Dafni *et al.*[11]. A weevil species was observed on male and female cones; its feeding and breeding activities were examined in detail. This was identified to the genus level as *Derelomus* (Coleoptera: Curculionidae). Its responses to light were examined by disturbing some individuals manually within the cone. Four intact female cones were tagged and monitored at different time intervals to evaluate the role of weevils in pollen transfer from male cones. Four female cones were used to record the number of sporophylls per cone and the number of ovules per sporophyll/cone. Ten ovules were used to record the ovule characteristics. In 2009, two female cones completely free from weevils were bagged and monitored to

*For correspondence. (e-mail: ajsraju@yahoo.com)

evaluate the role of wind in pollination and subsequent seed set. The site and plant characteristics were also considered to evaluate the efficiency of anemophily. Four female cones were used to record seed set in open pollination. The duration of seed maturation was also observed by following four female cones periodically until maturation. Seed characteristics and seed dispersal agents were also recorded. Fifty seeds were used to evaluate seed dormancy and seed germination rate, and the study was conducted in experimental plots at Andhra University. Observations on *in situ* seed germination and seedling growth were also made. Further, observations on bulbil production and success rate were made to determine the success rate of asexual reproduction.

C. sphaerica is a medium-sized, palm-like shrub with an erect, solitary stem up to 2.36 ± 1.4 m long (range = 1–5 m) and diameter of 12–30 cm. The plant consists of a slightly swollen stem covered with thick bark which in turns bears persistent leaf bases. The apex of the stem is crowned with 23–37 pinnately compound, 135.5 ± 41.2 cm long (range 95–185 cm) leaves (Figure 1 *a*). It is dioecious, but sex determination is possible only after cone formation. Coning episode takes place during March–May. A sample size of 423 individuals showed that coning is asynchronous as male and female plants produce cones at different times within this period. The coning plants are leafless prior to cone production. In both the sexes, normally each plant produces a single cone at the apex of the stem (Figure 1 *b*). In five male plants, the stem is branched and each branch produced a single cone. A single male plant produced six cones (Figure 1 *c*). In female plants, the stem is not branched and hence each plant produced a single cone. The demography of the population showed that coning plants made up 11.58% in 2008 and 8.51% in 2009; the sex ratio was 91.83% males in 2008 and 91.66% in 2009 (Table 1).

Male cones are short stalked, compact, having narrowly ovoid woody structure, orange in colour, 36.6 ± 2.81 cm long and 10.78 ± 2.4 cm in diameter. A cone consists of 1228.5 ± 82.76 sporophylls which are arranged spirally around a central axis. All the sporophylls are fertile, except a few at its basal and apical parts. Each sporophyll is woody, brown-coloured, 6.86 ± 0.23 cm long; the upper part is expanded and extends gradually into a prominent 2.58 ± 0.3 cm long apical spine. The basal part is attached to the cone axis. The adaxial surface does not bear microsporangia, whereas the abaxial surface bears microsporangia up to the expanded part of the sporophyll. The sporangia occur in groups of 3 or 4; each such group represents a 'sorus'. Each sporophyll contains 801.5 ± 44.67 sori; each sorus contains 16,315 ± 2399 pollen grains. The total number of pollen grains per sporophyll is 13,076,472.5 ± 1,824,187. Each male cone contains 16,088,808,230 ± 2,192,694,096 pollen grains. The pollen grains are light yellow, powdery, spheroidal, 24.5 ± 0.39 μm in size, unicellular and uninucleate surrounded by thick exine and intine (Figure 1 *d*).

Male cones produce heat at maturation during which they elongate loosening the sporophylls. Just before pollen shedding, the temperature is 35.2 ± 0.83°C within the cone and 35.8 ± 1.26°C outside it. During pollen shedding, it is 40.3 ± 1.73°C within the cone and 36.1 ± 1.37°C outside it. After pollen shedding, it is 37.4 ± 1.47°C within the cone and 36.5 ± 0.63°C outside it (Figure 2). The temperature regime during the cone maturation process shows that endogenous heat production causes a rise of 4.2°C against the ambient temperature outside the cone during the pollen shedding process. At this temperature the cone produces musty odour which could be detected 50 m away; after pollen shedding, the odour gradually diminishes over a period of about 10 days. During the pollen-shedding period, the cones attract *Derelomus* (Curculionidae) weevils which remain within the cone upon arrival, and feed only on the tissues of the male cone axis during which they get dusted with pollen (Figure 1 *g*). Mating takes place after feeding. Female weevils dig holes in the cone rachis to deposit their eggs which hatch within 3 days. The larvae are creamy-white, feed in the sporophyll tissues and pupate after 3–4 days. They use black faecal pellets to construct tough, pupal cases in the basal part of the sporophylls. The adults emerge after 4–5 days, boring through the wedge-shaped part (tip) of the sporophyll (Figure 1 *h*). The adults carry pollen and fly to other male cones for feeding and breeding; while doing so they also visit female cones during which they deposit at least some pollen upon the micropyles of the ovules. The adults do not breed in female cones. They are sensitive to light and hide when disturbed. During the day they stay within the interior of the male and female cones; they are active during dusk and early evening hours only. Further, they stay within the unexposed basal areas of the stem throughout the non-reproductive phase of male plants (Figure 1 *i*), as they occur on female plants only during the coning phase.

The pollen being powdery falls off and accumulates on the adaxial side of the sporophylls which are situated below, and it is carried away into the atmosphere easily by wind. With the sloppy terrain, scanty vegetation and the area being windy during the coning season of the plant, the powdery pollen grains could be blown out effectively by wind into the atmosphere and the cones of the female plants may get deposits of pollen grains from

Table 1. Demography of *Cycas sphaerica* coning in the study area

	Jalantrakota Reserve Forest	
Plant aspect	2008	2009
Total plants	423	423
Total plants with cone	49	36
Total male cones	45	33
Total female cones	4	3

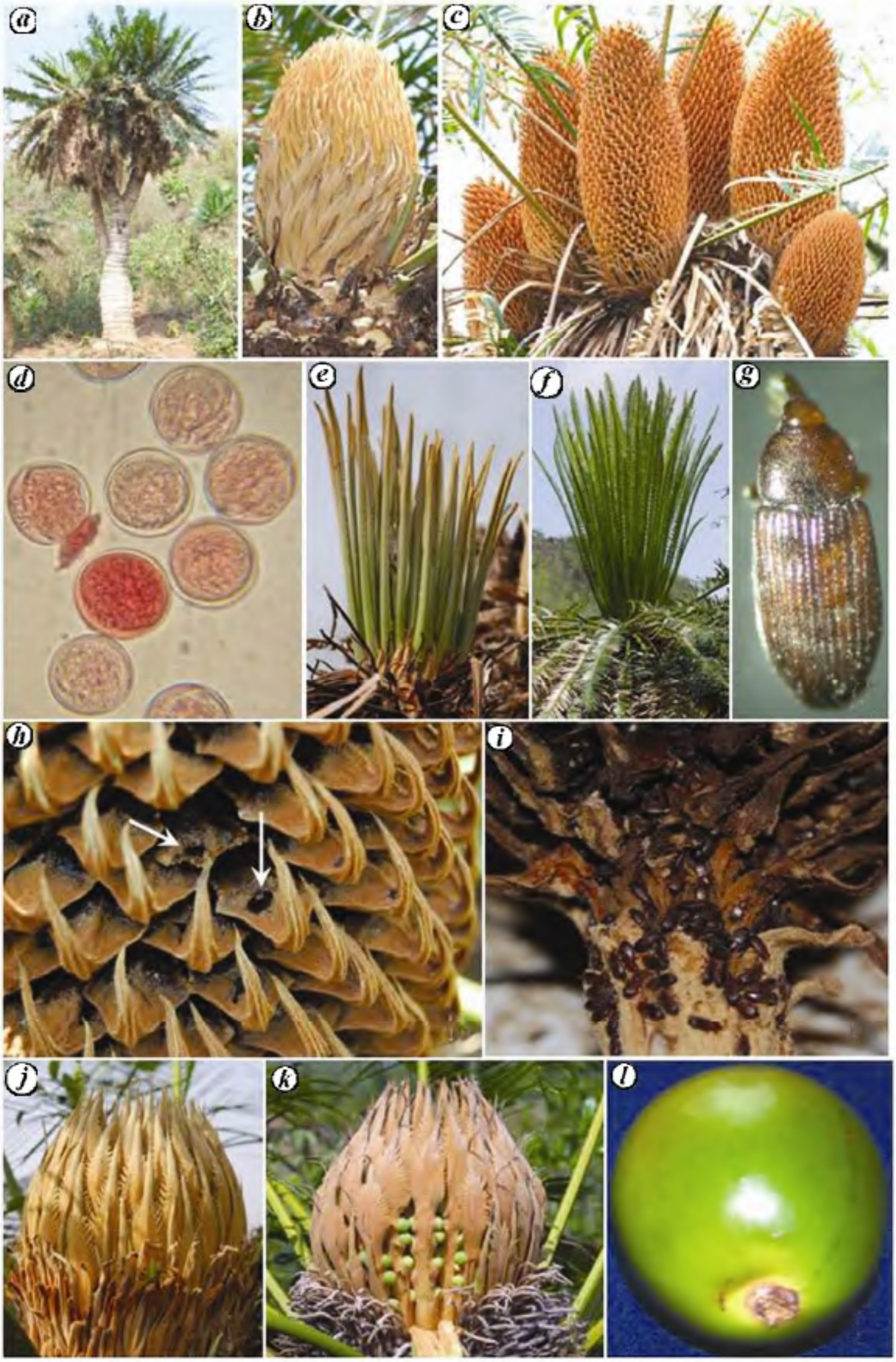

Figure 1. *Cycas sphaerica*. ***a***, A crown of leaves at the apex of the stem; ***b***, Young cone; ***c***, A single plant with six male cone; ***d***, Pollen grains; ***e***, ***f***, Leaf flushing; ***g***, *Derelomus* weevil; ***h***, Adult emerging from the hole dug by it; ***i***, Adult population; ***j***, Female cone; ***k***, Seed set in female cone, and ***l***, A close-up view of the seed.

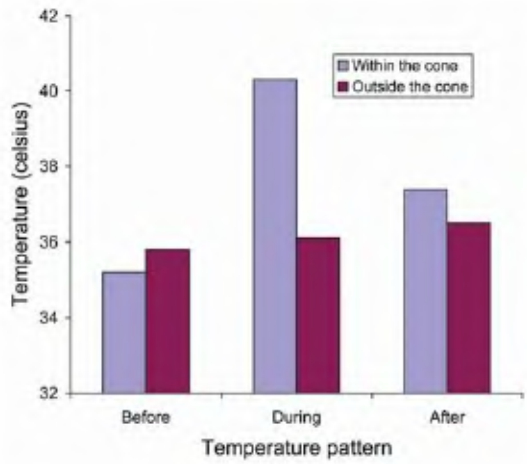

Figure 2. Temperature pattern during the course of pollen shedding in male cones of *Cycas sphaerica*.

the atmosphere. The cones of two female plants located 1 km away from the coned male plants were bagged to prevent *Derelomus* weevils, in order to assess the role of wind in pollination. The result was that both plants set seed: 57% in one and 62% in the other, suggesting anemophily. The pollen-shed male cones gradually bend to one side making way for leaf flushing (Figure 1 *e* and *f*). Each leaf has 55–130 pairs of light-green leaflets. The new leaves develop fully within three weeks and fall-off during late winter. The male plants remain leafless without coning in the consecutive year, but it is not known whether they remain so until the next coning episode.

Female plants produce cones that represent a cluster of megasporophylls resembling a cabbage-like assemblage. Each cone consists of 68.33 ± 6.18 sporophylls which are brownish-orange, tomentose and 22.46 ± 1.64 cm long (Figure 1 *j*). Each sporophyll is differentiated into a basal stalk and an upper pinnate, lanceolate and strongly dentate lamina tipped with an apical spine which is quite distinct from the lateral spines. A sporophyll bears 4.2 ± 1.11 (range 1–7) ovules on the lateral side of the stalk. A sample of 350 sporophylls of five female cones showed the following rate of ovule production: single-ovuled sporophylls are 1%, two-ovuled 4%, three-ovuled 4%, four-ovuled 46%, five-ovuled 11%, six-ovuled 26% and seven-ovuled 8%. The ovules are sessile, orthotropous, creamy-white, glabrous, globose and unitegmic. Integument remains fused with the body of the ovule, except at the apex of the nucellus where it forms a nucellar beak and a micropyle opening. The integument is three-layered with an outer fleshy layer (sarcotesta), middle smooth layer (sclerotesta) and the inner fleshy layer which remains in close association with the nucellus. In each cone, 15% of sporophylls do not contain ovules and the remaining collectively produce 243 ± 56.71 ovules out of which 100 ± 21.63 set seeds in open pollination.

Mature female cones also produce musty odour, but it is not as strong as in the male cones. During odour production, the temperature is 36.5°C within the cone and 32.7°C outside it. The pollen dispersed by wind and/or weevil reaches the nucellar surface of the ovule to effect fertilization. The diploid zygote develops into an embryo, which takes about one year for its complete development into a seed. Aborted ovules shrink, turn reddish-brown and finally become black. The fertilized ovules show slow development to form seeds. The developing seeds bulge out gradually through the gaps between the sporophylls (Figure 1 *k*). The new leaves emerge from the centre of sporophylls as soon as the ovules are fertilized, grow well during the rainy season and fall off during late winter by which time the seeds begin to mature.

The seeds are sub-globose, 4.28 ± 0.22 long, 3.55 ± 0.31 cm wide, initially green and later yellow (Figures 1 *l* and 3 *a*). The embryo is white, cellular and the upper region elongates into a suspensor. The sarcotesta eventually becomes wrinkled and at this stage the seeds fall to the ground for dispersal (Figure 3 *b* and *c*). They float in water and floating may aid in their dispersal during the rainy season. However, the terrain is rugged, stony and mostly blocks dispersal by rainwater. Spotted deer (*Axis axis*) and sloth bear (*Melursus ursinus*) feed on the sarcotesta and partly on the sclerotesta of the seeds; while doing so they disperse the seeds. The sarcotesta decomposes naturally exposing the sclerotesta to enable seed germination (Figure 3 *d*). Seed-germination experiments have indicated that the seeds are not dormant; they germinate in about a month if the soil is consistently wet; if not, seed mortality occurs (Figure 3 *e*–*h*). Seed germination rate is 80%. A few seeds germinate *in situ* and the seedlings grow slowly; 15 seedlings were evidenced in 2008 and 11 in 2009 in the entire study area. Both sexes of the plant also reproduce by bulbils during the rainy season; the bulbils arise mostly from the basal area of the stem (Figure 3 *i*–*k*). A single male plant produced 11 bulbils at the terminal part of the stem. Normally, each plant produces 5–13 bulbils, out of which only 2–3 germinate to produce new plants upon detachment from the stem. A few bulbils remain on the stem and form new branches (Figure 3 *l*).

C. sphaerica shows leaf flushing after pollen shedding in male plants and after fertilization of ovules in female plants whereas non-reproductive plants stay leafless, suggesting that leaf flushing is not an annual event and is associated with the coning event in both sexes. Leaf shedding occurs in late winter in both sexes which have coned in the previous year. It is not clear whether the non-reproductive plants remain leafless until their next coning phase; a longer period of study is required for confirmation. The leaf-flushing activity in coned plants enables gain in the lost energy in both sexes and also to supply the photosynthate for the growing seeds in female plants.

The study suggests that coning activity in *C. sphaerica* is not an annual event. Participation of a few plants in the annual coning event has been shown to be a typical fea-

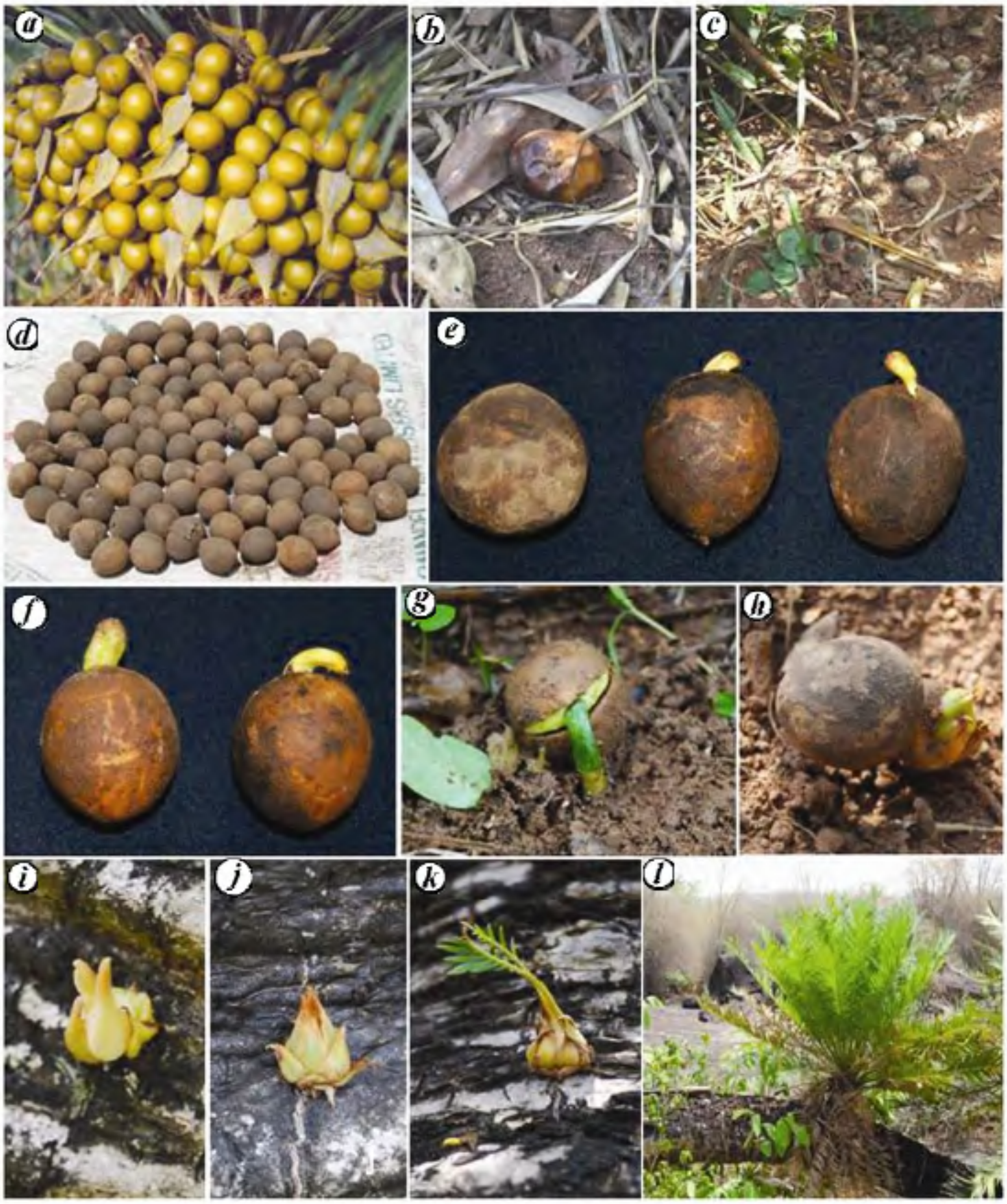

Figure 3. *Cycas sphaerica*. ***a***, Mature seeds; ***b***, Blackening seed coat; ***c***, Fallen seeds; ***d***, Seeds with smooth sclerotesta; ***e–h***, Seed germination stages; ***i***, ***j***, Bulbil stages; ***k***, Bulbil germination on the mother plant, and ***l***, Bulbil producing another branch on the mother plant.

ture of cycad populations and this is possibly because of high resource cost associated with such massive reproductive structures[12–15]. The strikingly male-biased sex ratio evidenced in this study appears to be an inbuilt evolved strategy to assure pollen receipt by most of the ovules and to achieve optimal seed set in coned female plants. Such a male-biased sex ratio has also been reported in *Lepidozamia peroffskyana*[16].

Tang[17] reported that in cycads, male and female cones number from one to several per plant. In *C. sphaerica*, the number of male cones is equivalent to the number of stem branches per plant and branching seems to be a result of bulbil growth on the mother plant. Each male plant normally produces a single cone, whereas a few produce more than one and up to a maximum of six cones. Female plants also reproduce by bulbil mode, but their stems are not branched and hence invariably produce a single cone per plant, suggesting that bulbils either detach from the mother plant or perish while still on the mother plant. Published reports indicate that *C. circinalis* is pollinated exclusively by wind[2]; *C. panzhihuaensis* and *C. seemanni* by wind and beetles[3,4]; *C. rumphii*, *C. thouarsii* and *C. media* by beetles[5,6], and *C. revoluta* primarily by beetles[7]. Further, thermogenesis and odour production occur during the process of maturation of cones of both sexes in *C. rumphii*, *C. thouarsii* and *C. revoluta*; the odour attracts beetles in both sexes and the beetles visiting the cones effect pollination[5]. In *C. sphaerica*, heat and odour resulting from developmental and metabolic processes in male cones are strong, whereas they are relatively weak in female cones. Further, the weevil-exclusion experiment with two-coned female plants demonstrated that optimal seed set occurs in the absence of weevil activity. All of these suggest that the plant is not adapted for entomophily. Proctor *et al.*[18] stated that anemophilous species produce typically non-sticky pollen grains that disperse singly and easily. In the habitat of such species, every square metre must receive around a million pollen grains to make pollination reasonably certain. Hall *et al.*[16] reported that pollen would be even higher in the habitat of anemophilous gymnosperm species, since the micropyles of ovules are not exposed to open air but are sheltered behind a barrier of megasporophylls. In *C. sphaerica*, the coning male plants produce trillions of light, dry and powdery pollen grains at the population level and disperse singly and easily into the air. The meteorological conditions for airborne pollen transport are optimal during the coning season of the plant and hence anemophily is highly effective. These findings are in agreement with those of Faegri and van der Pijl[19] and Proctor *et al.*[18], who stated that genuinely anemophilous plants are characterized by mechanisms to ensure that the pollination phase is perfectly timed so that the pollination event is initiated when meteorological conditions for airborne pollen transport are optimal. Kono and Tobe[7] reported that in *C. revoluta* wind is effective for pollination only when both males and females grow densely in windy, open areas. The plant site of *C. sphaerica* is an open area with sparse vegetation and windy, and facilitates pollen flow easily from male to female cones due to which ovules receive pollen and get fertilized. The airborne pollen penetrates well into the female cone, although it slightly exposes the ovules and the same is substantiated by the weevil-exclusion experiment, suggesting that *C. sphaerica* is anemophilous.

Norstog and Fawcett[20] reported that the Curculionid weevil, *Rhopalotria mollis* uses *Zamia furfuracea* for breeding and develops possibily up to six generations within the coning period lasting two months. *C. sphaerica* attracts *Derelomus* weevils during the coning period and the weevils use the cones for communal sexual display to choose their partners. The weevils feed on the cone-axis tissue, then mate and use sporophyll tissue for feeding and breeding; they produce a single generation of offspring within two weeks on a male cone. Likewise they may produce eight generations within the three-month period of the annual coning episode. The adults that emerge are covered with pollen and then depart in search of other male cones during which they also visit female cones, thus effecting pollination. They fly short distances and the flight activity is confined to dusk and early evening hours due to their sensitivity to sunlight. As the area is windy, the weevils may be driven off by wind, thus increasing the distance of pollen transport by it. On female cones, the weevils attempt to collect food from the micropyle region of the ovules, but this region does not have any fluid or fluid-like substances, and such attempts result in pollen transfer to the micropyle from where pollen enters the archegonia. They do not breed on female cones, but they may use them for warmth during the night. Therefore, *Derelomus* weevils effect pollination only accidentally; pollination by beetles is referred to as cantharophily[19].

In *C. sphaerica*, the weevils produce offspring on dry and dead rachis of male cones after pollen shedding, suggesting that their presence does not cost the male plants in anyway. The weevils seem to be attracted to both sexes of the plant due to similar colour and odour of the cones. Estragole is the main volatile compound that produces odour; it acts as both an attractant and a deterrent to insects or herbivores[21,22]. We assume that the odour may act as a pheromone and the weevils use this as a cue to reach the male cone at the time of pollen shedding, or female cone at maturation. The weevil enjoys an ecological niche with this plant which offers protective colouration, shelter, warmth, feeding and breeding environment in male cones; and protective colouration, shelter and warmth in female cones. Similar ecological niche offered to other beetle pollinators has been reported in *Zamia furfuracea*[23] and *Chamaerops humilis*[24]. In *C. sphaerica*, the weevils diapause on male plants in the unexposed areas throughout the non-reproductive phase of the plant without any feeding and breeding. They become active again during the coning season of *C. sphaerica*, suggesting that the reproductive continuity of weevils from season to season is related to their year-to-year survival in diapause on the male plant. The presence of diapausing weevils on *C. sphaerica* may be used as a key to identify plant sex during the non-reproductive phase.

In cycads, almost all parts of the plant produce toxins, the concentration of which varies with each part. The seeds also contain toxins, usually have brightly coloured sarcotesta and attract a variety of birds and mammals. These animals feed on the fleshy sarcotesta and disperse the seeds which are protected by a hard sclerotesta[25]. The sarcotesta is barely toxic, or if it does contain toxins, the animals feed on this layer and somehow cope like many animals do with toxic angiosperm fruits[6,26]. The spotted deer and sloth bear feed on the sarcotesta of *C. sphaerica* and disperse seeds with sclerotesta intact. Other animals such as rodents and birds are also present at the plant site but we never found them feeding on the seeds of *C. sphaerica*. Rainwater also disperses the seeds, but the rugged terrain of the area does not permit dispersal far away from the parent sites. Charlton *et al.*[23] and Norstog and Nicholls[6] reported that in cycad seeds, the endosperm and the embryo are well supplied with toxins for protection against herbivores. Despite the toxicity of the inner part of the *Zamia* seed, a specialized weevil uses it for its breeding[25]. The absence of seed infestation in *C. sphaerica* may suggest that its seeds are highly toxic and hence no insect uses them for breeding. Seeds germinate readily if the soil conditions are favourable, if not they perish. This is evidenced in our experiments. As the area is covered with litter and other organic debris during the rainy season, *in situ* seed germination could not be assessed. We could only count the seedlings finally established and growing slowly at the plant site. Poor natural regeneration from the seeds may be attributed to seed predation, inability of the germinating seeds and growing seedlings to compete well with the seasonal plants and grasses for the available nutrients in the soil and litter, and erratic rainfall or dry spells within the rainy season.

C. sphaerica also reproduces asexually by bulbils during the rainy season and adds new plants to the existing populations each year. Since it is asexual reproduction, bulbils produce new plants of the same sex from which they are produced. The success rate of bulbils depends on the same factors which have been mentioned for the natural regeneration from sexual means. Despite its ability to reproduce sexually and asexually, *C. sphaerica* has restricted population size in the study site and also restricted distribution range confined to the northern Eastern Ghats of India. Further, the traditional uses of this species are also decimating its population size. Our field studies show that the locals collect its feathery leaves, especially from young plants for selling them in the local florist market. The leaves are used for making bouquets. The tender leaves are used for making vegetable curry. Young stems are cut to remove pithy material for food preparation. Male cones are collected for use as a repellent against mosquito bites. These various uses are a great threat to the survival of the species in the course of time. Therefore, further studies are required to utilize this species commercially without affecting its distributional areas and population size.

1. Lindstrom, A. J. and Hill, K. D., The genus *Cycas* (Cycadaceae) in India. *Telopea*, 2007, **11**, 463–488.
2. Niklas, K. J. and Norstog, K., Aerodynamics and pollen grain depositional patterns on *Cycad megatrobili*: implications on the reproduction of three cycad genera (*Cycas*, *Dioon* and *Zamia*). *Bot. Gaz.*, 1984, **145**, 92–104.
3. Wang, Q., Li, C. L., Yang, S. Y., Huang, R. and Chen, F. L., Pollination biology of *Cycas panzhihuaensis* L. Zhou et. and S.Y. Yang. *Acta Bot. Sin.*, 1997, **39**, 156–163.
4. Keppel, G., Notes on the natural history of *Cycas seemannii* (Cycadaceae). *South Pac. J. Nat. Sci.*, 2002, **19**, 35–41.
5. Vorster, P., Comments on *Cycas revoluta. Encephalartos*, 1995, **42**, 25–26.
6. Norstog, K. J. and Nicholls, K. J., *The Biology of the Cycads*, Cornell University Press, Ithaca, New York, 1997.
7. Kono, M. and Tobe, H., Is *Cycas revoluta* (Cycadaceae) wind- or insect-pollinated? *Am. J. Bot.*, 2007, **94**, 847–855.
8. Donaldson, J. (ed.), *Cycas: Status Survey and Conservation Action Plan*, IUCN – The World Conservation Union, UK, 2003.
9. Hill, K. D., Chen, C. J. and Loc, P. K., Regional overview: Asia. In *Cycads: Status Survey and Conservation Action Plan* (ed. Donaldson, J.), IUCN/SSC Cycad Specialist Group, IUCN – The World Conservation Union, Cambridge, UK, 2003, pp. 25–30.
10. Rao, R. S. and Sreeramulu, S. H., *Flora of Srikakulam District, Andhra Pradesh, India*, Indian Botanical Society, Meerut, 1986.
11. Dafni, A., Kevan, P. G. and Husband, B. C., *Practical Pollination Biology*, Enviroquest, Ltd, Cambridge, 2005.
12. Clark, D. A. and Clark, D. B., Temporal and environmental patterns of reproduction in *Zamia skinneri*, a tropical rainforest cycad. *J. Ecol.*, 1987, **75**, 135–149.
13. Ornduff, R., Size distribution and coning behaviour of the Australian cycad *Lepidozamia peroffskyana. Aust. J. Ecol.*, 1989, **14**, 241–245.
14. Ornduff, R., Features of the reproductive biology of *Macrozamia* species and *Cycas media* in Australia. In Proceedings of CYCAD90, The Second International Conference on Cycad Biology (eds Stevenson, D. W. and Norstog, K. J.), Palm and Cycad Societies of Australia, Brisbane, 1993, pp. 121–124.
15. Vovides, A. P., Spatial distribution, survival and fecundity of *Dioon edule* (Zamiaceae) in a tropical deciduous forest in Veracruz, Mexico, with notes on its habitat. *Am. J. Bot.*, 1990, **77**, 1532–1543.
16. Hall, J. A., Walter, G. H., Bergstrom, D. M. and Machin, P., Pollination ecology of the Australian cycad *Lepidozamia peroffskyana* (Zamiaceae). *Aust. J. Bot.*, 2004, **52**, 333–343.
17. Tang, W., Heat production in cycad cones. *Bot. Gaz.*, 1987, **148**, 165–174.
18. Proctor, M., Yeo, P. and Lack, A., *The Natural History of Pollination*, Harper Collins, London, 1996.
19. Faegri, K. and van der Pijl, L., *The Principles of Pollination Ecology*, Pergamon Press, Oxford, 1979.
20. Norstog, K. J. and Fawcett, P. K. S., Insect-cycad symbiosis and its relation to the pollination of *Zamia furfuracea* (Zamiaceae) by *Rhopalotria mollis* (Curculionidae). *Am. J. Bot.*, 1989, **76**, 1380–1394.
21. Pellmyr, O. and Thien, L., Insect reproduction and floral fragrances: keys to the evolution of angiosperms. *Taxon*, 1986, **35**, 76–85.
22. Azuma, H. and Kono, M., Estragole (4-allylanisole) is the primary compound in volatiles emitted from the male and female cones of *Cycas revoluta*. *J. Plant Res.*, 2006, **119**, 671–676.
23. Charlton, T. S., Marini, A. M., Markey, S. P., Norstog, K. and Duncan, M. W., Quantification of the neurotoxin 2-amino-3-(methylamino)-propanoic acid (BMAA) in Cycadales. *Phytochemistry*, 1992, **31**, 3429–3432.
24. Anstett, M. C., An experimental study of the interaction between the dwarf palm (*Chamaerops humilis*) and its floral visitor *Derelomus chamaeropsis* throughout the life cycle of the weevil. *Acta Oecol.*, 1999, **20**, 551–558.
25. Schneider, D., Wink, M., Sporer, F. and Lounibos, P., Cycads: their evolution, toxins, herbivores and insect pollinators. *Naturwissenschaften*, 2002, **89**, 281–294.
26. Nair, J. J., Toxic compounds in cycads, M S thesis, University of Natal, Durban, South Africa, 1990.

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