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RESEARCH ARTICLE

Opportunistic flowering and pollinating system as a survival strategy of the coconut (*Cocos nucifera* L.), a monotypic species of the Arecaceae family

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Abstract Coconut (*Cocos nucifera* L., family Arecaceae) is a tropical, monospecific, perennial palm. It is monoecious and protandrous. Flowering and pollination biology studies carried out in the coconut in different countries, at different times of the year, and in different environmental conditions have given widely divergent results on every aspect of flowering and pollination. It has been found that the coconut palm shows the capacity to adapt its flowering and pollination biology to suit various environmental variables in order to ensure its successful pollination and seed setting. These include self pollination, cross pollination, wind pollination, insect pollination, changes in flowering biology even within an individual palm such as effecting variations in length and occurrence of male and female phases in flowering even with minor changes in temperature and rainfall. They appear to be an adaptive mechanism to ensure the successful survival of the species under natural conditions. It is therefore concluded that the coconut possesses an opportunistic flowering and pollinating system. This may be considered as an adaptive mechanism of the species to ensure its survival, possibly since the coconut palm is monospecific.

Keywords Coconut · *Cocos nucifera* L. · Floweringg bology · Pollination biology · Self pollination · Cross pollination · Survival strategy · Opportunistic pollination system

Introduction

For over a century till about the closing decades of the twentieth century, evolutionary biologists and botanists used to assume that most cross-fertilizing angiosperm species and their pollinators had co-evolved. This began with the studies of Charles Darwin on pollination syndromes in orchids in the 1860s and 1870s. This concept has been discussed in the writings of van der Pijl, Stebbins (1950), Baker (1959), Grant (1971), etc. Then, towards the close of the twentieth century, it was begun to the realized that extreme specialization in pollination systems is not so widely present as was hitherto been assumed, and specializations within pollination systems might be equally important as an evolutionary outcome. Wasser et al. (1996) observed that specialization was rare in tropical regions, more common in temperate regions, and predominant in deserts.

The immobility of flowering plants requires them to engage the services of pollen vectors to ensure cross-fertilization, or to develop the ability for self-pollination (Barrett 1998; Goodville et al. 2005; Harper and Ogden 1970, etc.). As a consequence, plants have

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developed a variety of mechanisms to reproduce, defend, survive, and compete on the landscape. These may be classified as adaptive, reproductive, variability in resource allocation, ecological, and varying the functional traits. These however require the plants to make trade-offs while responding to the environment (Harper and Ogden 1970). In order to ensure the survival of the species, "flowering plants display spectacular floral diversity, and a bewildering array of adaptations that promote mating, particularly, outbreeding" (Barrett 2010).

The coconut (*Cocos nucifera* L., Family Arecaceae) is possibly the most useful tree to the humans. Every part of the palm is put to active economic uses for food, fuel, and/or housing, wherever it occurs, but especially in the Old World tropical conditions. It is a monospecific palm. It is widely cultivated, or it occurs in natural stands throughout the tropics of the world (ca. 12 M ha worldwide, according to FAOSTAT 2014). It occurs naturally in the nearly 35,000 atolls and islands of the Pacific and Indian Oceans (Bellwood 1987, 2013). However, it is primarily categorized as an oil yielding tree. It may not be widely known that until the early 1960s, for over a century, coconut oil was the most widely traded vegetable oil in the world (Puresglove 1972). Now, it ranks only ninth out of the 14 major vegetable oils used worldwide (FAOSTAT 2014).

There are two categories of palms, the normal, widely occurring talls, and the dwarfs. The latter occurs rarely with less than 2–3% frequency in natural stands. The nature and origin of dwarf is unclear, but the general view is that they are naturally occurring mutations of talls. They are homogeneous in appearance. They bear early and their period of longevity is less than that of tall forms. They yield smaller and often fewer nuts, but since their planting density can be increased, the overall yield per unit area may be comparable to that of the talls. Of late, there is some preference for cultivating dwarfs for various reasons, including its resistance to the serious lethal yellowing disease and the superior quality of its water, which is valued as a refreshing and natural drink (Figs. 1–8).

Botany and systematics

The coconut (*Cocos nucifera* L.) belongs to the family Arecaceae, subfamily Arecoideae (one of five subfamilies), tribe Cococeae (one of 13 tribes), and subtribe Attaleineae (one of three subtribes). The genus *Cocos* L. is monospecific (Dransfield et al. 2008). The members of the subtribe are predominantly South American in distribution, but there are two genera in Madagascar (*Parajubaea, Vaonioala*), and one in South Africa (*Jubaeopsis*) (Dransfield et al. 2008). Phylogenetic studies by various authors have shown that it has no close relations, but relatively they show some affinities with three genera, *Syagrus, Attaleina*, and *Parajubaea* (Baker et al. 2009; Meerow et al. 2009, 2014). The results are, however, not very consistent (cf., Gunn 2004; Baker et al. 2009; Meerow et al. 2009, 2114; Baker and Couvreur 2013a, b).

Fig. 1 A normal bearing coconut palm (ca. 40 years old)

The coconut is a monoecious and protrandrous palm. Both the male and female flowers are borne on the same inflorescence. The inflorescence is called a spadix and the fruit, the coconut, is a drupe. Under normal conditions in the tropics, a palm produces 10–14 inflorescences in an year. They are borne in leaf axils. Not all the leaf axils produce fruits or since some

Fig. 2 A mature coconut inflorescence (spadix)

Fig. 3 A newly opened spadix with the first male flower open

inflorescences abort prematurely for various reasons (Menon and Pandalai 1958; Child 1953; Dransfield et al. 2008).

The spadix is 1.0–1.5 m long and the inflorescence, 0.8–1.0 m long. It is pale yellow to creamy in colour. It consists of a rachis with 10–30 rachillae, with each rachilla bearing 50–200 or more male flowers, and 0–3 female flowers at their base. Mature male flowers are 7–9 mm long and female flowers—which are nearly spherical, 2.5–4.0 cm long. Normally, the male flowers are protandrous. They open from the distal to the near end of the rachilla. Male flowers open for 6–10 h from early morning. Under average situations, all the male flowers of a spadix complete their flowering in 19–25 days. The 10–50 female flowers open typically 2–4 days after the male flowering is completed. They complete their flowering in 5–7 days. This facilitates cross fertilization. However, in some situations, for instance, when the number of leaves produced exceeds 12 annually—and consequently, the number of spadices too,—the spadix subtended by the succeeding leaf may open when the female flowers of the preceding inflorescence are still open and the stigma are receptive. Then the pollens from the succeeding spadix could be pollinating the female flowers of the preceding spadix. When this happens, it facilitates self fertilization.

In dwarfs, typically, the male flowering is completed in 14–18 days and the female flowering in 3–6 days. The female flowering phase takes place within the male phase, generally towards its end period. This generally ensures self pollination.

Pollination biology

Fair amount of work has been done on this aspect from 1913. However, comprehensive studies covering even one flowering cycle have not been done on this aspect yet.

Fig. 4 Nonreceptive female flowers in newly opened spadix

Early botanists (Muller in 1883; Knuth in 1909; Jack and Sands 1929) had believed that coconut was wind-pollinated. This might have been because the coconut possesses several characteristics favouring anaemophily (wind-pollination), such as nonsynchronized male and female flowering cycle, abundant pollen production, absence of any strong flower colour and odour, location of male flowers on the upper portion and female flowers at the bottom of the inflorescence, and presence of protandry.

During the early twentieth century, some scientists had proposed that coconut is insect-pollinated (Furtado 1924), and a third group, that it is both insect- and wind-pollinated (Aldaba 1921; Marechal 1928; Patel 1938, etc.). Henderson (1986), in his review of the pollination system in the Palmae family, had observed that the coconut is both insect- and wind-pollinated, but predominantly insect-pollinated. Anaemophily, he observed, was a derived condition. This view has been endorsed by some others also (Silberbauer-Gottesberger 1990). Incidentally, coconut possesses also some characteristics of insect pollination. They include copious production of pollen and nectar, extended period of stigma receptivity, possibly, heavier pollen grains, and so on.

Let us now look at some of the studies in flowering and pollination biology in the coconut that are relevant to our enquiry here.

In recent years, a few detailed experimental studies have been the carried out on the pollination biology in the coconut. They were done in different regions of the world, in different seasons of the year, and under varied environments. We shall now review them very briefly in the context of this study. The latest review was of Thomas and Rajkumar (2013).

Patel (1938) conducted his work in the farms at Kasaragod and Nileshwar (44 km south of Kasargod), both in Kerala, India (12°–13°N Lat., 6 m amsl; 3600 mm rainfall annually) in 80–120 palms each for two successive years (Tables 1, 2). Nearly three-fourths of the spadices opened during the summer months of February–May. The opening was relatively low during the post-monsoon and cooler months of October–January. The average interval (in days) between the opening of successive spadices showed a tendency to be more during the monsoon months, July–September (Table 2) and less during the late summer months, April–May. The data indicated clearly that various weather parameters have marked effects on both the periodicity of spadix opening and length of flowering cycles.

In a second experiment, Patel studied the effect of seasons on female flower production. The material used was the same as in the previous experiment. The palms showed much variation in the number of female flowers produced during different months. This was apparent even when the average member of female flowers/spadix were compared. These observations had been also taken for 2 years and at both the locations. Even though the trend of the direction of the change was similar, the monthly data showed variability both between the years and the two locations (Table 2).

Whitehead (1965) studied flowering biology in Jamaica [18°N lat.; 2500 mm evenly distributed rainfall for 6–12 months in both tall (30 + 30 + 6 in three varieties) and dwarf (12 + 18 on two varieties/forms)]. The region receives 2500 mm evenly distributed rainfall in an year. In contrast to the general observation, he found ‘considerable possibilities for

Table 1 Monthly variation in spadix production

Month	Monthwise per cent spadix production*		Average interval (in days) between successive spadix openings*	
1	2		3	
	Nileswar	Kasaragod	Nileswar	Kasaragod
January	4.7	8.0	54.4	28.4
February	10.1	7.8	54.1	27.0
March	16.9	9.5	28.9	26.8
April	13.1	10.8	21.5	24.8
May	11.7	9.5	24.3	27.6
June	6.5	7.9	27.9	25.0
July	7.1	8.3	37.7	27.3
August	8.2	7.6	48.3	29.5
September	7.1	7.7	38.3	29.1
October	5.8	8.3	32.9	27.6
November	6.1	7.3	34.6	27.0
December	2.5	7.5	41.3	26.9

Adapted from Patel (1938), Table 54

* Data collected for 2 years (1933, 1934) at two locations, Nileswar (65 palms) and Kasaragod (63 palms)

Table 2 Monthly variation in female flower production

1	No. of female flowers produced/palm* 2	No. of female flowers produced/spadix* 3	Per cent female flower produced/month* 4	Per cent female produced/month* 5	Average number of female flowers spadix* 6
January	21.1	20.9	6.8	7.5	6.4
February	28.7	30.6	9.3	6.8	10.2
March	35.3	34.8	11.6	16.1	9.3
April	44.9	33.8	14.5	14.9	10.7
May	36.8	33.3	11.9	17.8	15.2
June	29.9	31.0	9.6	9.2	15.1
July	25.6	26.1	8.4	7.6	12.3
August	20.2	22.9	7.3	6.7	10.6
September	19.9	21.7	6.5	6.0	8.7
October	18.6	18.9	6.2	4.5	7.8
November	14.2	16.6	4.6	3.3	6.9
December	13.5	14.1	4.4	1.2	6.1

Adapted from Patel (1938), Table 66

* Data from two locations and 2 years (1933 + 1934) except in column 6 (data for only 1933)

self-pollination due to overlap of inflorescence, and in one variety, due to overlapping of male and female flowers opening within an inflorescence'. The dwarf palms too showed varietal difference in the extent of male and female flowering overlapping, with the red varieties showing more complete overlapping.

Sholdt and Mitchell (1967) studied different aspects of pollinations biology in Hawaii (21°N lat.) on about 30 palms (in two lots) in two experiments for a total of 12 months. They recorded 51 insect species visiting the flowers. Seven among them were most frequent: honey bees (*Apis mellifera*), black earwig

(*Cheliosoches morio*), wasps (*Pollistes exclamans, P. macaensis, P. olivaceus*), and ants (*Paracrechina longi, Phedole megaphala*). Twelve insect species visited the coconut only occasionally, and 26 others were rare visitors. Wasps were foraging on only nectar, and no pollen was found on their bodies or in their guts. In ants, pollen grains were found on only those collected from male flowers. The earwigs fed on both pollen and nectar. While earwigs were present in large numbers on male flowers (200 or more), only 1–2 of them were found on female flowers. The honey bees, at the same time, were present in great numbers on both the male and female flowers. They appeared to be the most common pollinating agent in Hawaii. However, wind pollination accounted for 3.2–4.1% of fruit setting. Through the authors have not stated so, the data presented in the paper shows that seed setting was slightly higher in palms standing on the windward side than on the leeward side.

Sholdt and Mitchell (1967) had observed further that the interval between the opening of successive spadices was shortest during August, and longest during February. 'In relation to temperature, the interval was shorter during the months with high mean temperatures and longer during the months with low mean temperatures', they had observed. The correlation coefficient was $r = -0.962$ (significant at 1% level). In their data, the palms in the windward plots showed a slightly lower interval between successive spadices (average 24.1 days; range, 11–40 days) as compared to those on the leeward side (average, 27.7 days; range, 10–57 days). The agrees with the findings of Patel (1938).

Free et al. (1975) studied pollination biology on Malayan Dwarf in Jamaica (18°N lat.). Honey bees were the most common insects, but wasps and ants too were present. Nearly two-thirds of the wasps (68%) were observed on male flowers, and the rest (32%) on female flowers. At the same time, as much as 98% honey bees were observed on male flowers, and only 2% on female flowers. Half the bees visiting the female flowers had pollen loads. The bee population peaked at 11.00 a.m., and then, it diminished by midday. A secondary peak appeared in the afternoon. Maximum pollen gatherers were found during 10.00 a.m.–11.00 a.m. However, honey bees continued to collect pollen grains throughout the day. As many as 99% of the bees visiting male flowers and 67% bees visiting female flowers were carrying pollen. In wasps, the respective figures were 36 and 16%, respectively.

Kevan and Blades (1989) observed in Maldives (6°–10°S lat.) that wind was the main pollinating agent. Kevan had found that honey bees are absent in the islands. Maldives is a group of more over 1000 small coral islands dotting the Indian Ocean, about 800 km south of Indian peninsula. Only 202/1190 of them are populated. Most islands have naturally growing stands of coconut palms.

Devanesan et al. (2009), working in Trivandrum (southwest India, 10°N lat.) recorded 30 insect species on coconut palms comprising of bees, butterflies, beetles, ants, wasps, and bugs. Honey bees were the dominant group. They recorded four species, *Apis cerane indica* (Indian bee), *A. mellifera* (Italian bee), *A. florae* (little bee), *A dorsata* (rock bee), and *Trigona irridipennis* (stingless bee). The Indian bee was the most common visitor.

Fig. 5 A fully open inflorescence

Fig. 6 Female flowers with two receptive ones

Fig. 7 An open spadix showing three female flowers that have completed their receptive phase

Ashburner et al. (2001) observed that in Gazelle Peninsula (Papua New Guinea, 6°S lat.), 96.3% palms were insect-pollinated, and only 3.7%, wind-pollinated. Two halictid bee species belonging to the genus *Homalietus* accounted for most pollinations. The receptive pistillate phase partially overlapped the staminate phase of the subsequently opening inflorescence. Fourteen insect species were observed on the inflorescence (Coleoptera, 2 spp., Dermoptera, 2 spp., Diptera, 2 spp., Hemiptera, 2 spp.). Among them, six species visited only the staminate flowers, and the remaining eight species visited both the male and female flowers. The extent of self-pollination was estimated to be 31.3% (range: 12.4–47.8%). It varied with season and palms varieties. The authors inferred that the coconut in the area had mixed pollination.

Melendez-Ramirez et al. (2004) carried out some detailed studies on this aspect in Yucatan peninsula, Gulf of Mexico (21°N lat.). They used five palm ecotypes. They recorded 83 insect species visiting the palms. The most abundant were those belonging to Hymenoptera (89.8% honey bees, *Apis mellifera*) and the rest consisted of Branconidoeae (wasps, *Vespoidea* including *Polistop* spp.), Formicideae (ants), and those belonging to Hemiptera, Homoptera, and Thysanoptera (1.0% each), Diptera (4.9%), and Coleoptera (4.3%). Ants did not have any effect on nut production. Insect populations were maximum during the rainy (July–October) season.

The authors estimated that self pollination (geitenomy) caused 19% fruit set, xenogamy (cross-fertilization) caused 30% fruit set, cross fertilization by wind (anaemophily) 10% fruit set, and entomophily 40% setting. Entomophily consisted of mellitophily (bees), myophily (flies), and carantherophily (beatles). They found that the introduced honey bee, *Apis mellifera*, showed the most appropriate foraging behavior, visiting both pistillate and staminate flowers. They were also the most efficient pollinators. The population of the visitors did not change with the

Fig. 8 An inflorescence that has just completed flowering

seasons, but it changed with palm ecotypes, with the maximum on Atlantic Talls. They concluded that coconut has a mixed mating strategy.

Discussion and conclusion

A review of the floral and pollination biology studies conducted on the coconut in different tropical regions of the world indicate the following:

1. The coconut, *Cocos nucifera*, possesses characteristics that favour both self and cross-pollination, and also, both wind- and insect- pollination.
2. Dwarf palms are prodominantly self fertilized. This is ensured by the female flowering taking place within the male flowering phase.
3. Tall forms are protandrous under standard/normal conditions. Female phase begins 1–4 days after the male flowering phase is completed. This promotes cross fertilization.
4. Extended period of longevity of the pollen (up to 7–8 days) seems to provides a back-up assurance for self-pollination to take place.
5. Even small increases in daily average temperatures or small variations in day length, as occurring in the tropics, bring about marked changes in the duration of the male phase. This may be ensuring better synchrony in the male and female phases of flower opening.
6. Several insect species are able to successfully transfer pollen grains from male to female flowers. Though various honey bee species are the predominant pollen carriers, other insect species such as ants, wasps, and thrips, also carry pollen grains from male to female flowers.
7. In Maldives, where no honey bees are known to be present (Kevan 1989), and the coconut constitutes the dominant vegetation, pollination is done only by winds. Nuts yields in Maldives are comparable to those obtained in similar regions occurring elsewhere.

The coconut palm produces copious amounts of both pollen and nectar. The former attribute is a characteristic of wind pollination, and the latter of insect pollination. Generally, pollen grains are actively foraged by honey bees (except in Maldives, where honey bees are not present; cf. Kevan 1989). Various species of honey bees are the most common and most numerous floral visitors everywhere else. The coconut palm permits a whole range of foraging insects. Even, bats and birds have been reported as foragers.

All the above attributes indicate that the coconut palm has an in–built mechanism to adjust its flowering cycle to suit the varying environmental changes, which, in its turn, ensures pollination, self- or cross-pollination, or both. Their extent and range vary with the country, season, and sometimes, even landraces. This is yet another indication of the coconut palm having a nonspecialized and a generalized and adaptive pollinating system.

Another characteristic that may be unique to the coconut palm among the cultivated plants is that it produces flowers and seeds round the year. Further, coconut is a perennial plant, which, when it once crosses the juvenile phase (in 3–4 years under average conditions), continues to flower and produce seeds (nuts) for several decades till its senescence and death.

Added to these are the flowering and pollination biology strategies of coconut palm, which is apparently capable of adapting itself to changing tropical environments. They are able to produce seeds, both by self- and cross-pollination, and produce normal progenies that do not show any changes in viability, vigour, and productivity. They are capable of setting seeds both by wind- and insect pollination. Several species of insects are also able to carry out pollination. We can therefore conclude that the coconut palm, *Cocos nucifera* L., possesses an opportunistic system of pollination.

The coconut, *Cocos nucifera* a monotypic species. Phylogenetic studies have not shown any taxon having consistent sister relationship with the genus *Cocos*. Various studies have shown differing results. The nearest extant genus to *Cocos* are *Parajubaea* (Baker et al. 2009). *Syagrus*, and *Attalea* (Meerow et al. 2009, 2014), all of them are native of the Neotropics. The genus *Cocos* has been suggested to have evolved 10–15 Mya. Consequently, the coconut is genetically a very isolated species. Hence, it would have become necessary for the coconut to develop 'out-of-the-box' strategies for its perpetuation and survival in nature. It is therefore reasonable to assume that *Cocos nucifera* has assumed an opportunistic system of pollination to ensure its propagation and perpetuation in nature.

From the evolutionary perspective, the adoption of the opportunistic pollination system by the coconut, can be reckoned as a survival strategy of a monotypic species. The adaptive value and importance of characters such as pollination biology under natural selection has been stressed by evolutionary biologists such as Stebbins, Grant, and Baker.

Wasser et al. (1996) had observed that from the ecological point of view, plant strategies responding to environmental challenges include mechanisms and responses that plants use to reproduce, defend, survive and compete in nature. They may be adaptive, reproductive, resource allocation- wise, and or functional trait-wise.

Mixed mating strategies, as prevalent in the coconut, are found commonly in plants (Goodville et al. 2005). This strategy is intermediate between outcrossing and selfing. But, the rate of selfing can vary both among closely related species and even among populations within a species. This attribute can respond rapidly to natural selection. Beccara and Lloyd (1992) have pointed out that this process of assuring reproduction is tantamount to ensuring 'the best of both the worlds.' In general, plants alter their strategies and their growth rates to suit ecological niches (Harper and Ogden 1970).

It is therefore concluded that the mixed mating strategy found in the coconut provides the species with the evolutionary assurance needed for its survival.

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