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FLORAL BIOLOGY AND POLLINATION OF THREE MANGROVE SPECIES (Aegiceras floridum Roem. & Schults., Scyphiphora hydrophyllacea Gaertn. f., AND Xylocarpus granatum Koen.) IN PAGBILAO MANGROVE FOREST, QUEZON PROVINCE, PHILIPPINES

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ABSTRACT - The flowering phenology of Aegiceras floridum, Scyphiphora hydrophyllacea,and Xylocarpus granatum and the effects of pollinators on fruit set and germination were evaluated in Pagbilao Mangrove Swamp Experimental Forest. The flowers were observed from bud formation until fruiting stage. Bagging technique was used to determine the effects of pollinators on fruit set and germination.

The flowering seasons of Aegiceras floridum and Scyphiphora hydrophyllacea occurred once a year. The onset of anthesis was at 0530h with a peak at 0900h-1100h. Xylocarpus .granatum, had two to three flowering seasons in a year. The anthesis started at 1800h with a peak at 2200h.

Aegiceras floridum and Scyphiphora. hydrophyllacea shared common pollinator species, Apis dorsata and Xylocopa spp. The pollinators foraged actively during anthesis. Since Xylocarpus granatum flowers opened at night, the primary pollinators were moth species, which are generally nocturnal. The activities of the pollinators were synchronized with anthesis.

The percent fruit set of Aegiceras floridum and Scyphiphora. hydrophyllacea was 100% in both bagged and unbagged inflorescences. However, fruit abortion rates were higher in bagged flowers. In Xylocarpus granatum, low fruit set was observed in unbagged flowers and none in bagged flowers. This indicates that the species was an obligate outcrosser and requires pollinating agents.

Keywords: Floral biology, pollination, Aegiceras floridum, Scyphiphora hydrophyllacea, Xylocarpus granatum

INTRODUCTION

Pollination mechanism in a mangrove ecosystem could be best understood by looking at the interaction between floral traits and pollinating agents especially in species requiring outcrossing. Mangroves are foraged by a diverse groups of animals such as bees (Hogart, 1999; Yi-Feng Yao et al 2006), bats (Kathiresan and Bingham, 2001), hawkmoths (Hockey and de Baar, 1991), butterflies (Hill, 1992), and birds (Raju et al, 2006). In Australia, Couplanda et al (2006) observed that natural pollinators increased the fruit set of four species of mangroves. Under local conditions, most researches on mangroves were focused on vegetation analysis (Gruezo 1998), systematics (Fernando and Pancho 1980) and productivity (Codillan 2008). Even on the global scale, less is known on the biology of flowers and their pollinators, considering that

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these information are crucial in the formulation of strategy for the conservation and utilization of mangroves.

This study was conducted to determine the floral biology and pollinators of Aegiceras floridum, Scyphiphora hydrophyllacea and Xylocarpus granatum in Pagbilao Mangrove Forest. This study specifically aimed (1) to describe the floral biology of three species A. floridum, S. hydrophyllacea and X. granatum, (2) to identify the floral visitors and pollinator species, and (3) to determine the effects of pollinators on fruit set and germination.

MATERIALS AND METHODS

Study Site. The experiment was conducted at Pagbilao Mangrove Swamp Experimental Forest in Quezon Province from May 2009 to August 2010. Pagbilao Mangrove was chosen as the study area because it is one of the protected mangrove forests and declared as an Experimental and Genetic Resource Area, as well as the National Training Centre for Mangroves.

Selection of Experimental Trees: A. floridum, S. hydrophyllacea and X. granatum were chosen for this study because they bloom almost throughout the year, and their flowers are visited by bees and other species of insects. Observations were done in three sites, namely, seaward, middleward and landward sides of the mangrove swamp. In each site, nine individuals in groups of three for each species were observed.

Floral Biology: At the onset of bud formation, four sets of inflorescence per tree of each species were marked with colored tags. This is to determine the duration of the development, the opening of the buds and time of anthesis. The time of flowering such as bud formation, flower opening and flower fall were noted. Morphological and microscopic examinations of the flowers were done through actual observation of collected fresh specimens from the plant. Compound light microscope and MicronCAM^{TM}R were used in examining small parts of the flower and pollen. Photographs were taken using digital camera.

Determination of Pollen Morphology and Viability. The collected flower samples were acetolyzed using the method of Faegri and Iversen (1964). The pollen grains were examined using compound light microscope with MicronCAM^{TM}R. Pollen morphology for each species was described. The size was determined with the aid of micrometer.

Pollen grains were collected from each of the plant species and brought to the laboratory for viability test. The pollen samples were macerated on the slide and dropped with lactophenol-aniline blue. Viable pollen would absorb stain and turned blue, while non-viable pollen remained colorless.

Floral Visitors and Pollinators

The species of pollinators and other floral visitors were observed throughout the blooming period of each species. The species were counted every 15 minutes of each hour. Visual observations were complemented with digital and video camera. Representative samples of floral visitors were collected using insect net for identification. The specimens were killed in ethyl acetate, pinned and dried and sent to an insect taxonomist for proper identification and future reference.

Effects of Pollinators on Fruit Set

Bagging technique was done to determine the effect of pollinators on fruit set. In each tree, four of the selected inflorescences were bagged (Treatment 1) to prevent insects, birds and bats from entering, and limiting penetration by windborne pollen. Another four inflorescences were unbagged (Treatment 2) to allow floral visitors. Monthly observations for fruit formations were done for four months. Fruits formed from both treatments were then sown in seed boxes for germination test. All data were analyzed using SAS and comparison of means by Duncan Multiple Range Test (DMRT) .

RESULTS

Floral Biology

There was an overlap in the blooming and fruiting seasons of A. floridum, S. hydrophyllacea and X. granatum.

A.floridum bloomed from February to June. However, this was not consistent with the findings of Primavera et al (2004) in Panay, where they observed twice a year flowering. In the study site, the flower bud emergence was observed as early as February. The peak of blooming period was observed in the middle of May until early June. The flower buds of A. floridum started to open as early as 0530h, reaching the peak of anthesis at 0900-1000h (Fig. 1). It took 3 days from flowering to fruit setting. At anthesis, both the calyx and petals expanded and served as landing platform for herbivores. After the flower was pollinated, the corolla, together with the stamen and style remained in place for two to three weeks, during which the calyx bulged due to the growing fruit inside. The fruits developed three days after anthesis. At this stage, the corolla turned brownish in color. The flowering and fruiting became sequential due to the acropetal succession of the flowers. The fruit was a single-seeded capsule, curled with persistent calyx, pointed apically and filled by embryo at maturity. The fruit was cryptoviviparous in which the embryo emerged from the seed coat but not from the fruit until it abscised. The hypocotyl coming out of the seed coat had an average length of 1.5 cm. They were initially green and became brown. The fruit matured in three months. At full maturity, the fruit detached from the mother tree, floated in tidal water and settled in sticky silty mud.

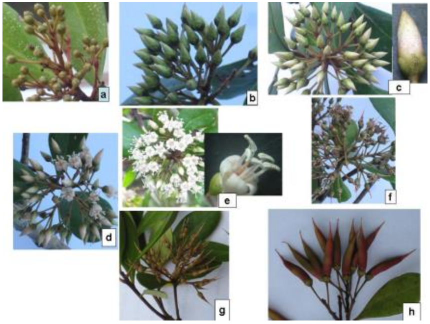

Figure 1. Anthesis and fruit development of A. floridum a-c) gradual enlargement of the flower buds (inset in c: note the dots/glands on the petals), d) asynchronous opening of the flowers in an inflorescence, e) fully opened inflorescence (inset: flexed petals exposing the anthers, f) wilted petals still attached on developing fruits, g) young fruits, and h) matured fruits still attached on the stem.

The flowering season of S. hydrophyllacea started in late February until mid-June, with a peak from March to May. Like in A. floridum, there was only one flowering season per year and the flowers exhibited asynchronous development. However, it was observed that few inflorescences in several trees bloomed after the regular flowering season. The condensed cyme opened as early as 0530h with the petals slowly exposing the club-shaped stigma, reaching the peak anthesis at 0900 to 1000h (Fig. 2). The glands at the base of the corolla tube secreted nectar. The corolla remained open until the next day. The corolla of pollinated flowers wilted and the ovary gradually increased in size until maturity. Fruiting season was from April to October. The fruit was green, turned yellow as it ripened and became shiny brown when fully matured. It has 6-10 longitudinal ridges and, because of its spongy layer, it floats in water during high tide and finally settled on the sticky silty mud.

Figure 2. An thesis and fruit development of S. hydrophyllacea a-c) gradual enlargement of flower buds (inset in c: still close flower showing inferior ovary), d) gradual opening of the flower in an inflorescence (inset: opened flower showing the reflexed petals and exserted anthers and stigma at anthesis), e) gradual development of fruits (inset: enlarged ovary), f) ridges developed on immature fruits, and g) matured fruits.

The flowering pattern of X. granatum was entirely different from those of A. floridum and S. hydrophyllacea. It had three blooming periods, starting from late January to March, June to August and October to November. Inflorescence emerged mainly from the axils of the leaves at the base of the newly formed shoot or directly from the previously dormant buds or on woody shoots. The flowers were odorous and opened at night. The anthesis started at 1800h with a peak at 2100-2200h (Fig. 3), remained open until 1000h, and wilted at about 1200h. The middle flower of the cyme opened first. The corolla was creamy-white and the superior ovary was pink. There were eight stamens that were united into the tube located slightly lower than the stigma. The tree flowered profusely, but only few fruits were produced, indicating a high rate of abortion.

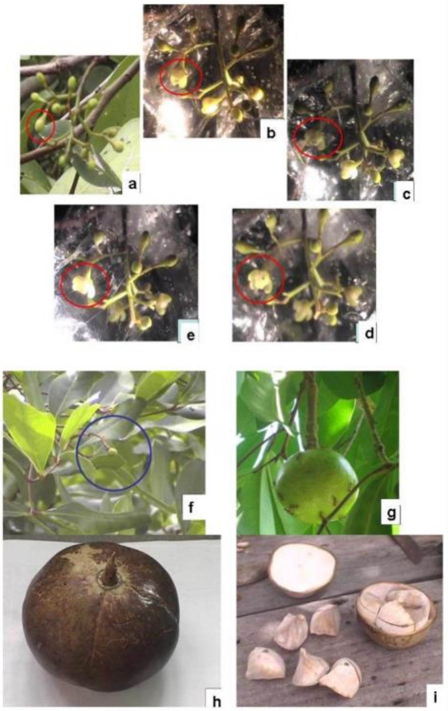

Figure 3. Anthesis and fruit development of X. granatum flower at 1800h. a) flower buds still close during the day before anthesis, b) at 1800h start opening, c-d) partially open at 1810h to 1820h, e) fully expanded flower at 1830h, f) Only one fruit produced in an inflorescence, g) Fruit is pendulous on a massive axis, h) Matured fruit i) Seeds of X. granatum (note: fruit is filled, as there is no ovule aborted since seeds are fitted completely into a fruit cavity).

Pollen grains of these three mangrove species had different sizes and morphology. The pollen grains of A. floridum were very small. Its size was 0.016 mm and with distinct annulus. It was roundish with three furrows aperture. The exine was thin and smooth. S. hydrophyllacea pollen grains were small (0.021mm). The pollen was round with circular operculum and broad and long colpi with a granular membrane. The X. granatum pollen was round, medium-sized (0.034mm) and with four furrows with pores aperture. The exine was medium.

The pollen of the A. floridum S. hydrophyllacea, and X. granatum had 71.09%, 69.34% and 60.4% viability respectively.

Floral Visitors and their Foraging behavior

Aegiceras floridum

The pollinator species observed visiting the flowers of A. floridum were carpenter bees, Xylocopa spp. and giant bees, Apis dorsata (Fig. 4). There were three species of carpenter bees, Xylocopa (Koptortosoma) bombiformis, Xylocopa. (Koptortosoma) chlorina and X. (Koptortosoma) bakeriana). Other minor species were Vespa sp., Halictus sp., Chrysomya sp. and Calliphora sp. The wasp, Vespa sp .were observed preying on adult flies while Halictus sp., Chrysomyia sp. and Calliphora sp. collected both pollen and nectar.

Figure 4. a) Xylocopa sp. and b) A. dorsata foraging on A. floridum flowers

Scyphiphora hydrophyllacea

A total of 15 species of insects visited S. hydrophyllacea. The pollinator species were Xylocopa spp., A. dorsata (Fig. 5) andTetragonula biroi. However, the populations of T. biroi were scarce, and not consistently observed in the flowers. Hence, they may not be considered as true biotic pollinators for the species.

Like in A. floridum, S. hydrophyllacea remained open throughout the night. The bees continuously exploited nectar and pollen.

Figure 5. a) Xylocopa sp. and b) A. dorsata foraging on S. hydrophyllacea flowers

Xylocarpus granatum

Both diurnal and nocturnal insects belonging to the order Coleoptera, Diptera, Hemiptera visited the flowers of X. granatum. Hymenoptera, Lepidoptera, Neuroptera, Orthoptera and Trichoptera. The activities of the floral visitors synchronized with anthesis, which started at 1800h. The flowers remained open until the next day with full pollen presentation until 1000h. The diurnal pollinator species were the native bees (Fig.6). The Dipterans, Conopidae, Syrphidae and Tabanidae collected pollen, while the Coleopterans were feeding on petals. Since X. granatum can be considered as night flowers, the moths were the most important pollinators. They collected nectar from the flowers. The pollen grains that adhered to their hairy bodies were transferred to another flower. The moths stayed in the flower for 5-7 seconds.

Figure 6. a) Apis cerana hovering around X. granatum flowers b) the same A. cerana in the left figure trapped after collecting pollen (note: the loaded pollen sacs).

Effect of Pollinators on Fruit set

The number of flowers that developed into fruits in A. floridum and S. hydrophyllacea did not significantly vary among treatments. The percent fruit set of both species was 100% in bagged and unbagged treatments. All the fruits in unbagged flowers reached maturity. However, the fruits from bagged flowers had high abortion rates. When the fruits were sown in seed boxes, the percent germination of seeds from the unbagged was significantly higher than the bagged treatment. On the other hand, the percent germination of seeds from S. hydrophyllacea was relatively low (19.91%).

Lower fruit set, (5.52%) was observed in unbagged flowers of X. granatum with an abortion rate of 98.48%. However, all the fruits germinated. The bagged flowers did not yield any fruit.

DISCUSSION

Floral Biology

The differences in the number of blooming periods of the three mangrove species within a year may be attributed to regional climate patterns. Pagbilao has Type II climate, where there is no dry season but minimal rainfall from March to May. This may be the reason why A. floridum and S. hydrophyllacea bloomed only once a year, coinciding with the months with minimal rainfall. On the contrary, Panay, which falls under Type 1 Climate has long dry spells, from November to April, that allows at least two blooming periods for A. floridum and S. hydrophyllacea (Coronas 1920).

Among the three species, X. granatum was least affected by climatic patterns. Three blooming periods were observed throughout the year. This could be a strategy of this species, because of its low fruit setting despite the enormous number of flowers it produces.

Floral traits influence pollination mechanism. In A. floridum, the protandrous flowers and the close proximity of the position of the styles and stigma to dehisced anthers at the onset of anthesis facilitate self pollination. The acropetal succession of the flowers of both A. floridum and S. hydrophyllacea flowers extends the flowering period. Likewise, the succession of the flower's opening in an inflorescence extends the visitation rate or feeding of the herbivores, including pollinator species.

The three species have perfect flowers, having both male and female parts within a flower. They have the possibility of self-pollination but can be able to outcross by other means (Simpson, 2006). The stalk of A. floridum and X. granatum and subsessile S. hydrophyllacea helps in relative positioning of the flowers for pollination and fruit dispersal. It also supports the flower to hold larger visitors like Xylocopa spp. and giant honey bees, A. dorsata during foraging. The filamentous stamen of A. foridum and S. hydrophyllacea made the anthers of these species being exerted of protruding beyond the perianth. It makes the pollen available for the foraging large visitors. In addition, the reflexed petals of both A. floridum and S. hydrophyllacea serve as landing platform for these large insects. However, X. granatum has sessile anthers so that it was inserted or included within the perianth. Thus, small insects with proboscis like moth species and A. cerana, which have extended mouth parts, can gather the pollen and nectar. Furthermore, only the expanded calyx served as landing platform of this plant and can accommodate lightweight visitors.

Pollinators and Foraging Behavior

The carpenter bees, Xylocopa spp. and giant bees, Apis dorsata seemed to be the most important pollinators in a mangrove ecosystem, especially of species with diurnal anthesis like A. floridum and S. hydrophyllacea. They are considered as true biotic pollinators because they consistently visited the flowers, carried pollen and transferred them to the stigma during a visit. The two species coexisted in the foraging site and there was no apparent competition between the two species. This can be attributed to the abundant pollen and nectar sources since the flowers bloomed at the same time.

Among the three species, X. granatum was the only species that had nocturnal anthesis that started at 1800h. The strong scent of the flowers served as cue for the visitors. It was also likely that Apis cerana could pollinate X. granatum. The extended anthesis until 1000h enabled the bee to exploit the nectar and pollen. Smaller bees like A. cerana were able to penetrate into the interior of the corolla tube and could therefore get to the pollen which will explain their relative number foraging during the day. Its small size matched the size of the flower. The absence of Xylocopa spp. and A. dorsata in the flowers of X. granatum during the day was perhaps due to the relative inaccessibility of its pollen. Unlike in A. floridum and S. hydrophyllacea whose anthers and pointed stigma protrude well above the corolla, X. granatum's anthers were situated just below the inner lip of the corolla tube beside the disk-like stigma. This location and the cup-like structure of the corolla presented a barrier for larger species like Xylocopa and A. dorsata. Larger species of bees, like Xylocopa spp. had close affinity to pollen flowers with well presented poricidal anthers and flowers with a steady state-flowering strategy similar to Passiflora edulis.

The ability of the Xylocopa spp. to forage at night was one strategy to escape predators and minimize completion. The foraging activity at night, dusk or dawn has been observed in several species of bees, including Apidae, where the Xylocopa spp. belongs (Warrant, 2007). Among the species of Xylocopa studied, only one is obligately nocturnal, and this is Xylocopa tranquebarica (Somanathan et al, 2008). The rest of the species are known to be crepuscular (Warrant et al 2004). In this study, it was not ascertained whether the Xylocopa spp. were strictly nocturnal or crepuscular, since the observations were only until 1800h.

Pollen viability

High viability of the pollen of A. floridum and S. hydrophyllacea contributed to high production of fruits from both bagged and unbagged inflorescences. Although flower and fruit abortion in X. granatum were high, good quality of seeds in developed fruits were produced. Given the importance of pollen development and function in sexual plant reproduction, it is obvious that pollen viability is a prerequisite for hybrid production (Bots et al, 2005).

Effect of Pollinators on Fruit Set

The very high percentage of fruit set in A. floridum and S. hydrophyllacea, suggests that these species are not obligately vector–dependent and set fruit with autogamy. However, native bees contribute additional pollination and increase fruit set rate by effecting self-and cross-pollination. The result shows that both plants are self-compatible. This pollination mechanism implies that these plants possess mixed breeding system. The abundance of fruits formed even in bagged flowers means they were self-fertile. In S. hydrophyllacea, the anthers dehisce introrsely before the flower opens. In addition, the pollen adherent outside the style may promote selfing. Mangroves have species with both self-pollinating and cross-pollinating systems. Sometimes they would retain the need for self fertility if they are primarily colonizing an area and need to establish populations in isolated localities. On the other hand, high percentage of fruit abortion on bagged or self-fertilized treatments may indicate some inbreeding depression (Clarke and Myerscough, 1991) or poor nutrition.

The absence of fruit in bagged inflorescence indicates that X. granatum. is an obligate outcrosser and achieve pollination by insect as vectors. This species have profuse flowers but high incidence of flower and fruit abortion occurred. Normally, only one fruit appeared from a single inflorescence. In some cases, production of more flowers elevates male fitness by dispersing additional pollen. The excess flowers are functionally staminate and the overproduction is a form of pollinator–mediated competition for access to males that would provide reproductive assurance. Accordingly, the overproduction of flowers and the subsequent abortion of immature fruits are both mechanism by which plants can match fruit production to the available resources. This may provide a larger pool from which superior fruits can be selectively matured. Likewise, it is a means of uncoupling the roles of flowers in pollinator attraction and pollen dispersal from their role in seed production (Raju et al. 2006). This is true in X. granatum because fruits are always filled, as there are no ovules aborted. Seeds are fitted completely into a fruit cavity.

Another factor that may have contributed to high floral and fruit abortion of X. granatum was the predation or herbivore by Coleopterans and Orthopterans Lepidopterans and a species of Crustacean that caused the premature abscission of heavily damaged flowers and fruits.

SUMMARY AND CONCLUSION

A. floridum and S. hydrophyllacea bloomed once in a year. The peak of the blooming period of both species was in the middle of May until early June. The flower buds of both species started to open as early as 0530 h reaching a peak of anthesis at 0900-1100h. Fruits were developed three days after anthesis. X. granatum flowering seasons occur three times a year. The floral anthesis started at 1800h and remained open until 1000h.

Numerous insects visited the three mangrove species. The pollinators of A. floridum and S. hydrophyllacea were Xylocopa spp. and Apis dorsata, while X. granatum were pollinated by moth. The pollinators collected pollen or nectar, and when they landed on the flower, the pollen grains attached to their hairy body. As they transfer from flower to flower of the same species, the pollen grains are deposited into the stigma, hence, pollination is effected.

The percent fruit set of A. floridum and S. hydrophyllacea was 100% in both bagged and unbagged inflorescence. However, fruit abortion rates were high in bagged flowers. When the fruits were grown, those from unbagged flowers had higher germination than those from bagged flowers. The low percentage germination of seeds of A. floridum was compensated by the numerous flowers it produced. In X. granatum, low fruit set was observed in unbagged flowers and none in bagged flowers. It suggests that this species was obligate outcrosser and achieves pollination by insect as vectors.

Twenty four hours after anthesis, pollen of the A. floridum S. hydrophyllacea, and X. granatum had 71.09%, 69.34% and 60.4% viability, respectively. The relatively high percentage of pollen viability contributes to the reproductive success of the species.

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STATEMENT OF AUTHORSHIP

The authors had equal contribution to the research. The first author conducted the experiment, undertook write up and literature search; while the second author identified pollinators/visitors, formulated recommendations and reviewed the manuscript.

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