

# The Flowering Habit of Nipa (*Nypa fruticans* Wurmb.) in Semi-wild Stands of the Davao Region, Philippines

Junaldo A. Mantiquilla<sup>1,\*</sup>, Eufemio T. Rasco Jr.<sup>1,2</sup>,  
Abdel Majeed M. Mohammad Isa<sup>1</sup>, and Kristian Weller P. Licup<sup>1</sup>

<sup>1</sup> Department of Biological Sciences and Environmental Studies, College of Science and Mathematics, University of the Philippines Mindanao, Mintal, Tugbok District, Davao City 8022, Philippines.

<sup>2</sup> Philippine Rice Research Institute (PhilRice), Science City of Muñoz 3119, Nueva Ecija, Philippines.

\* Corresponding author. Email: junaldo2003@gmail.com. Telephone: +63 82 293 0312 local 21.

Received 25 July 2012; Revised 26 March 2013; Accepted 8 April 2013

---

## Abstract

Observations on the flowering characteristics of nipa (*Nypa fruticans* Wurmb.) were carried out on at least 70 randomly selected palms in various semi-wild stands found in the Davao Region, Philippines (i.e., Bago Aplaya, Ecoland, and Talomo) from April 2010 until February 2011. The developmental stages of inflorescence were identified, described in detail, and arbitrarily divided according to morphological changes exhibited by the inflorescence. These developmental stages are as follows: emergence (E) stage, stage 2 (S2), pre-anthesis (PA) stage, and the antheses stage, which is divided into the female receptivity (F) stage and the male anthesis (M) stage. Among the parameters measured for each stage include the length of the inflorescence from base to tip, the number and length of staminate rachillae, and the number of female flowers. For morphological characteristics comparison of this monoecious inflorescence, different stands in Carmen, Davao del Norte, were observed. The Carmen stands were significantly more fecund compared to the Davao City stands. The former had more female flower count (61 vs. 58 per pistillate head) and more staminate rachilla count (33 vs. 17 spikes) than the latter. The final inflorescence length in Carmen was significantly taller than in Davao City (117.5 cm vs. 84.3 cm), suggesting that the plants in the former had longer tapping potential for sap production. The results have implications toward the future program of nipa hybridization to produce better varieties.

**Keywords:** inflorescence development; morphology; *Nypa fruticans* Wurmb.; Philippines; pollen characterization

## Abbreviations:

ANOVA – analysis of variance

HSD – honestly significant difference

---

## Introduction

Nipa palm (*Nypa fruticans* Wurmb.) is a common component of mangrove forests of Asia and Oceania. It has a fairly wide distribution and can be found in Sri Lanka, Bangladesh, India, the Malay Peninsula and Archipelago (which includes the Philippines), and the Pacific Islands from northern Australia to the Solomons up to the Ryukus. In the Philippines, nipa grows along tidal streams and brackish swamps. It is considered economically important because it is a source of thatch, fiber, edible endosperm, wine, and paper (Corner, 1966). The inflorescence can also be tapped before it blooms to yield a sweet edible sap (Joshi et al., 2006).

The sap from inflorescence stalk is a source of sugar containing about 14% to 17% sucrose. It is used to produce fermented beverages (e.g., *tuba*) and vinegar in the Philippines. Most of the earlier research on nipa looked into the production of sugar and fuel alcohol, particularly *alcogas* (Halos, 1981; in Hamilton and Murphy, 1988).

Rasco (2011) estimated that each sap gatherer could generate PhP15,386 per month income from 1 ha of land with 2000 to 2250 plants, 750 of which flowering and producing sap half of their yield potential, which is worked on by four gatherers. A plant can yield 12.31 kg of sugar per season if a flower stalk can produce 43 L of sap per season at a sugar content of 17%.

In terms of alcoholic beverage from nipa, Rasco (2010) noted that vodka in Vinzons, Camarines Norte (*barik* in the vernacular), had 70 to 100 proof processed in indigenous distillation process, while those produced in Butuan (*laksoy*) had 70 proof for the first gallon of distillate. Important commercial use of nipa has led to initiatives in improving nipa management as well as exploring its potential. It will most likely be an alternative source of bioethanol to coconut (*Cocos nucifera* L.) (Hamilton and Murphy, 1988).

Based on traditional and molecular taxonomic classification, nipa is the only species of its genus *Nypa*, which in turn is the only genus in the subfamily *Nypoidea* (Asmussen and Chase, 2001; Judd et al., 2002; Asmussen et al., 2006; Dransfield et al., 2008). Its structural features alone isolate this genus from other palms, which leads to different taxonomic assessment (Uhl and Moore, 1971). For example, unlike most palms, nipa is structurally unique, lacking an upright trunk and instead having a horizontal stem with dichotomous branching that grows underground (Tomlinson, 1971; Joshi et al., 2006). Having Schoute's model of palm architecture (Tomlinson, 1990), nipa has

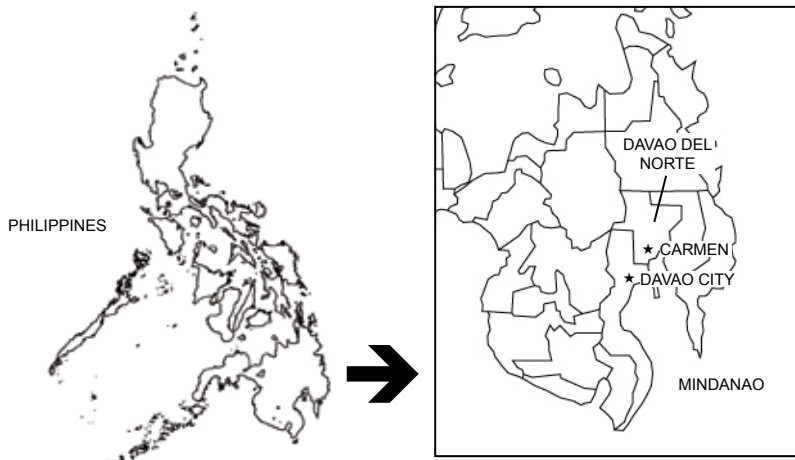
erect spirally inserted leaves measuring up to 9 m that are borne near the apex of a horizontal stem that divides in intervals. Any leaf can produce an inflorescence consisting of a monopodial axis that ends with a pistillate head and bears numerous lateral branches that terminates with staminate rachillae or male flowers (Tomlinson, 1971). Hence, it is said to be monoecious since the male and female reproductive parts are found in separate flowers on the same plant (Berg, 2012).

The primary objective of the study was to observe the reproductive biology of *N. fruticans* in the Davao Region, Philippines. The specific aim was to observe the morphological changes on inflorescence during floral development, compare the reproductive structures of nipa inflorescence in selected sites in the Davao Region (i.e., Davao City vs. Carmen, Davao del Norte), characterize the female phase and stigma receptivity, and characterize male phase and pollen morphology of nipa inflorescence.

## Materials and Methods

### Time and Place of Study

The study was conducted in the semi-wild nipa stands of the Davao Region (Figure 1) from April 2010 to February 2011. The stands in Carmen, Davao del Norte, were growing in smaller clumps inland and derived mineral-rich waters from man-made canals that cause seasonal flooding in the inland



**Figure 1.** Map showing the location of Davao City and Carmen, Davao del Norte, in the Island of Mindanao, Philippines

plains of the site. On the other hand, those found in Davao City were found in the estuaries, forming colonies near the coastal areas of Bago Aplaya and Ecoland where tributary rivers run through and empty into the Davao Gulf, which regularly inundate the palms with brackish water when tides change. In both sites, the stands may be considered semi-wild as locals practice regular deleafing of the nipa population for shingle or thatch roofing production.

The flowering habit of nipa was observed on 35 inflorescences from Bago Apalaya in Davao City (7°2'21" N, 125°32'03" E, elevation: 21 m) and Ecoland (7°3'28" N, 125°36'24" E, elevation: 19 m). The morphological characteristics of these inflorescences were compared with 23 inflorescences from two nipa stands in Carmen, Davao del Norte: Purok 17 (7°21'46" N, 125°42'13" E, elevation: 23 m) and Brgy. Ising (7°21'47" N, 125°42'33" E, elevation: 20 m). Twelve more inflorescences were selected for additional observations on pollen morphology, male phase, and stigma receptivity in Talomo, Davao City (7°2'52" N, 125°33'26" E, elevation: 29 m).

### **Inflorescence Observations**

The flowering habit of nipa was observed based on the inflorescence development. The stages were divided arbitrarily according to the morphological changes exhibited by the inflorescence. Among the parameters measured for each stage include the length of the inflorescence from base to tip, the number and length of staminate rachillae, and the number of female flowers. Only samples in Davao City gave the details of each stage because of the stands' accessibility for daily observation.

Results were subjected to a *t*-test to compare populations within Davao City (Bago Aplaya vs. Ecoland) and populations between Davao City and Carmen, Davao del Norte, using SPSS ver. 17.0.

### **Stigma Receptivity**

To determine the onset of stigma receptivity, a fine mesh bag was used to cover the pistillate head nearing anthesis to prevent possible cross-pollination. The timing of pollination includes the following treatments replicated three times: 12, 24, 36, and 48 h after opening by controlled hand-pollination. By timing the controlled pollination, the peak and the extent of stigma receptivity were determined. Pistils way past receptivity during pollination would not be fertilized resulting to a concomitant decrease in fruit set. The female flowers were pollinated by rubbing the pistillate head with the fully opened male flowers to introduce the pollen grains. The cover was removed once female flowers elongated and necrosed, indicating successful fertilization. Stigma receptivity occurred during the time of pollination. Percent receptivity per inflorescence was determined using the following formula:

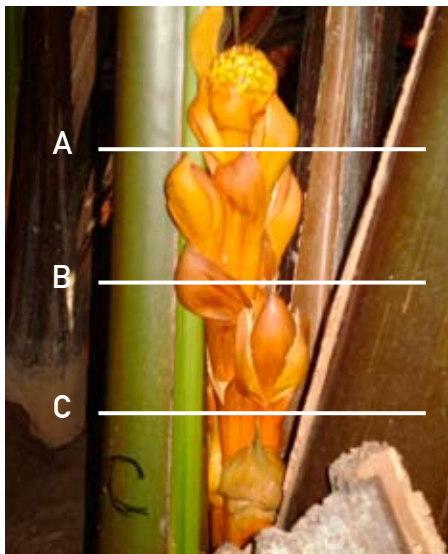
$$\text{Receptivity (\%)} = \frac{\text{Number of fertilized flowers}}{\text{Number of female flowers}}$$

The data were subjected to one-way analysis of variance (ANOVA) to determine statistical significance.

### The Male Phase and Pollen Characterization

For male phase observation, the nipa inflorescence was arbitrarily divided into three regions: upper, middle, and lower regions (Figure 2). The entire duration of this phase was observed from the anthesis of the first staminate rachilla at the top and down to the lowest staminate rachilla. One-way ANOVA was used to determine the statistical significance among the three regions and Tukey's honestly significant difference (HSD) test was used for mean comparison.

For pollen sampling, some rachillae were severed from the palms found in Talomo, Davao City, for pollen characterization. They were brought to the laboratory for collection in vials and hydration using 1:1 distilled water: glycerine solution (Walker, 1999). Microscopic observations were conducted in three replications to characterize pollen according to color, shape, aperture, and other ornamentation on the exine or pollen wall.



**Figure 2.** Arbitrary regions of nipa inflorescence for male phase observation: (a) upper, (b) middle, and (c) lower regions.

## Results and Discussion

### Inflorescence Development in Davao City

Nipa palms were found to be flowering throughout the observation period but only few produced inflorescence. The flowering palms were mostly found in the periphery of the stands near or along the river banks such as those observed in Bago Aplaya and Talomo, Davao City. This clearly shows the influence of the environment on the palms, with the availability of nutrients and sunlight inducing the flowering of the palms.

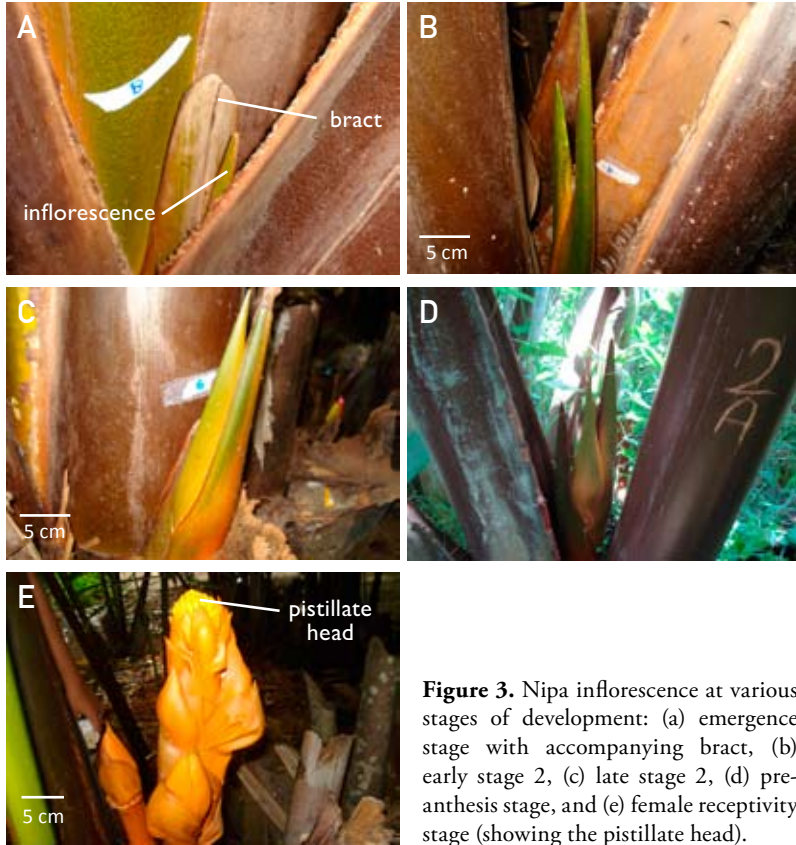
Based on the 35 palms in the semi-wild stands of Davao City, the developmental stages of the inflorescence were divided into five different arbitrary stages based on distinguishable morphological characteristics: emergence (E) stage, stage 2 (S2), pre-anthesis (PA) stage, anthesis by female receptivity (F) stage, and male anthesis (M) stage.

The inflorescence at emergence (E) stage was found to be axillary and green, protruding between the fronds of the palm (Figure 3a). Although identifying inflorescence from a developing leaf posed a challenge initially, the differences eventually became apparent, the former being flat in contrast to a cylindrical emerging spear leaf. A brown thin bract flanked the inflorescence at the middle by the frond. During the later part of this stage, the inflorescence eventually developed yellowing along its length. The mean height of the inflorescence reached 8.90 cm (Table 1). However, the age cannot be determined as this was beyond the scope of the study.

Next, stage 2 (S2) occurred 23.60 d after emergence. In this stage, the inflorescence split from its much taller prophyll, the outermost sheath called spathe (Figure 3b), due to the expanding base and increasing length of the inflorescence. At the early part of S2, the inflorescence remained predominantly green except the newly exposed surface from the spathe. However, as the stage progressed, some inflorescence (i.e., 12 out of 35 samples) developed distinct morphological changes, such as the pronounced bulking at the base, the lengthening of the inflorescence, and the yellowing of its length, except at the ridges of the spathe (Figure 3c).

Moreover, the duration of the inflorescence development at stage 2 became shorter prior to anthesis. It took 10.2 d for the inflorescence to reach pre-anthesis with a mean height of 43.6 cm. This means that the growth of the inflorescence was observed to be accelerating (Figure 4) accompanied by morphological changes in preparation for sexual maturity of male and female reproductive structures.

The penultimate stage is the pre-anthesis (PA) stage or the stage prior to the opening of the female and male flowers. The inflorescence began to grow rapidly, with the main axis becoming apparent and the lateral branching becoming eminent (Figure 3d). The leathery bracts that enclosed the flowers

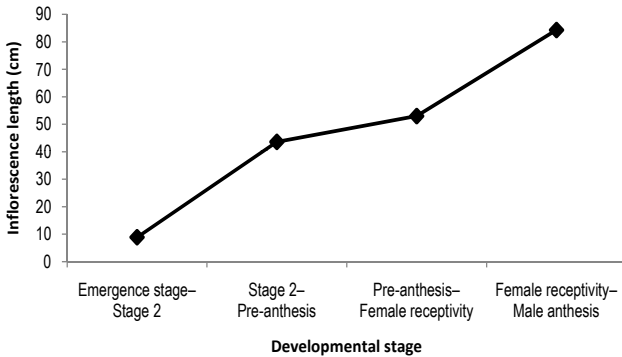


**Figure 3.** Nipa inflorescence at various stages of development: (a) emergence stage with accompanying bract, (b) early stage 2, (c) late stage 2, (d) pre-anthesis stage, and (e) female receptivity stage (showing the pistillate head).

**Table 1.** Estimated intervals between development stages and corresponding length of inflorescence produced by nipa palms in Davao City, Philippines

Developmental stage	Number of days	Inflorescence length (cm)
Emergence to stage 2	23.60 (4.50)	8.90 (1.86)
Stage 2 to pre-anthesis	10.20 (1.84)	43.60 (4.52)
Pre-anthesis to female receptivity	6.60 (2.03)	53.00 (5.12)
Female receptivity to male anthesis	1.00 (0.00)	84.30 (9.23)
Total	41.40 (7.83)	-

**Note:** Standard deviations are given inside parentheses.



**Figure 4.** The inflorescence length (cm) of nipa at different developmental stages

eventually developed bright hues (between yellow-orange to orange). On the average, this stage lasted 6.60 d before anthesis, with the inflorescence reaching a mean height of 53 cm.

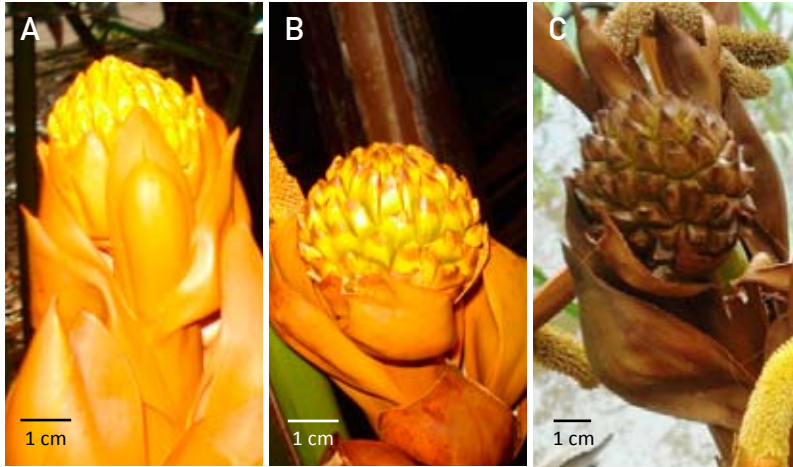
The ultimate stage is the anthesis stage. Nipa is considered protogynous; hence, stigma receptivity occurs first before the pollen grains are shed. Female receptivity (F) stage is characterized by the emergence of bright yellow pistillate head, which is composed of clustered female flowers, out of the bract. Receptivity was exhibited by the presence of glistening nectar on the stigma of the female flowers (Figure 3e).

### Stigma Receptivity

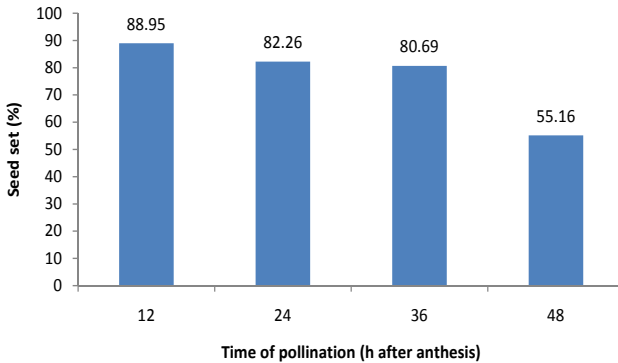
Hand pollination done 12 h after anthesis showed an 88.95% seed set. This high seed set would imply that even before the first male flower opened in the same inflorescence, most of the stigmas were already receptive, suggesting the cross-pollinating nature of the palm. The percentage decreased gradually as the flowers matured: 82.26% seed set at 24 h after anthesis, then 80.69% seed set at 36 h after anthesis. But at 48 h after anthesis, seed set dropped to 55.16% (Figures 5 and 6). This sudden drop of seed set was found to be statistically significant (d.f. = 3 and 8,  $F = 7.374$ ,  $P = 0.11$ ), indicating that most of the stigma must have been way beyond receptivity after 48 h. In coconut, a female flower remains receptive for 1 to 3 d. The duration of female and male phases are known to be affected by climatic environment (Santos et al., 1995).

The male anthesis (M) stage, on the other hand, occurred a day after the onset of the F stage. The increase in the number of laterals and the subsequent elaborate branching signaled the approach of male anthesis. At the onset of this stage, the staminate rachillae borne at the topmost laterals opened up while other lateral branches gradually increased in height. Once proximate to the pistillate head, the staminate rachillae of these lateral branches initiated





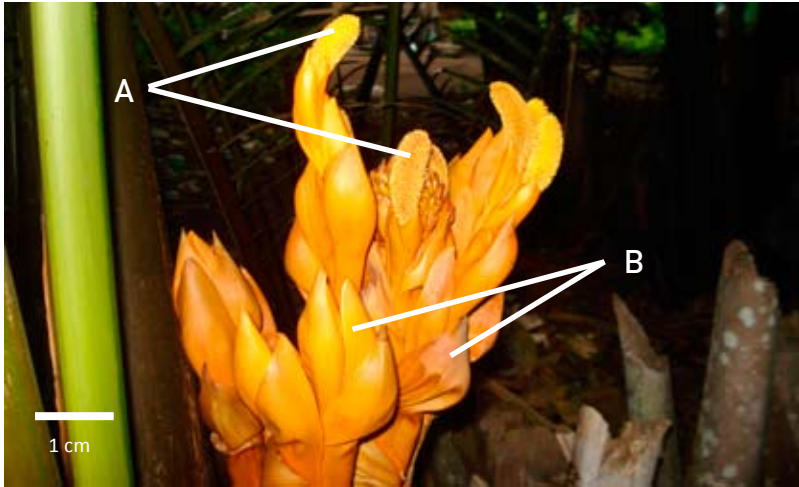
**Figure 5.** Nipa inflorescence with (a) unpollinated female flowers, (b) pollinated female flower, and (c) female flower two-weeks after pollination



**Figure 6.** Comparison of stigma receptivity of nipa inflorescence at different time intervals

anthesis. Sometimes, some lateral branches surpassed the main axis of the inflorescence (Figure 7).

The entire duration of inflorescence development of nipa was estimated at around 41 d, with the female receptivity occurring in about 40 d (Table 1). These characteristics are essential in the timing of pollination for the future hybridization program of nipa if varieties will be identified. Also, the duration of inflorescence development may have implications in the formation



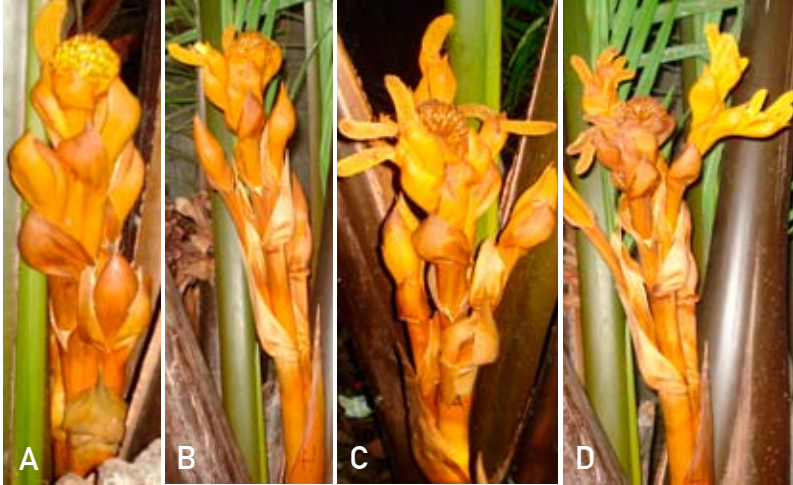
**Figure 7.** Nipa inflorescence at male anthesis: (a) opened and (b) enclosed staminate rachillae

of infructescence and tapping preparations that require special mechanical practices to initiate sap flow.

### Male Phase of Nipa

Borges (2008) described the male phase as the duration from which the first anthesis of an inflorescence occurs until all staminate rachillae dry out. The nipa inflorescence was divided arbitrarily into three regions to observe the male phase. Chronologically, the male phase followed these regions where onset of anthesis occurred first on staminate rachilla way above the pistillate head followed by other rachillae in the upper region, then the middle region, and finally the lower region (Figure 8). Rasco (2011) observed that the male flowers at the bottom, which were more numerous, opened much later after fruit set, indicating a cross-pollinating habit. Generally, the anthesis of male inflorescence across the arbitrary regions is associated by the elongation of lateral branches surpassing the height of the female inflorescence.

The durations of the male phase of these inflorescence regions appear longer in the middle and lower regions (Table 2), again indicating a cross-pollinating habit. These staminate rachillae can become potential sources of pollen for receptive female flowers from other nipa palms. However, mean differences did not reveal statistical significance across regions between the samples from two locations in Davao City. Apparently, the duration of the male phase is an inherent characteristic of the palm rather than being largely influenced by its environment. The whole duration of the male phase would



**Figure 8.** The male phase of nipa showing antheses in different arbitrary regions of the inflorescence: (a) first staminate rachilla, (b) upper region, (c) middle region, and (d) lower region

**Table 2.** Duration of the male phase in three different regions of inflorescence among samples from Davao City, Philippines

Site	Upper region	Middle region	Lower region	Whole plant
Bago Aplaya ( $n = 28$ )	5.28 (1.11)	5.75 (1.32)	5.53 (0.99)	14.17 (1.61)
Ecoland ( $n = 7$ )	5.14 (1.06)	4.71 (0.95)	5.42 (1.27)	13.28 (1.97)
Both sites ( $n = 35$ )	5.25 (1.09)	5.54 (1.31)	5.51 (1.03)	14.00 (1.69)

**Note:** Standard deviation given inside parentheses.

appear shorter than the sum of the durations of each region because of overlapping antheses. Overall, the male phase in samples from Bago Aplaya was longer than those from Ecoland (Table 2). The duration of the entire male phase for samples taken from Davao City was estimated at 14 d (Table 2). This duration is close to the male phase of coconut (*Cocos nucifera*), which is between 16 to 22 d (Perera et al., 2006). For coconut, this phase can reach up to 20 d depending on the season and variety (Santos et al., 1995).

### Pollen Characterization

Separate flowering palms from the stands in Talomo, Davao City, were randomly selected as pollen sources for characterization. Under light microscopy, various features of pollen grains were noted (Figures 9 and 10).

Pollen grains were spheroidal and yellow. The acetolyzed pollen grains burst open through their aperture (Figure 9), which is particularly zonasulcate where the aperture is perpendicular to the equatorial region (Chumchim and Khunwasi, 2011). The intact pollen grains had visible fully formed exine or outer wall (Figure 10) with uniform spine lengths. The images suggest that these spheroidal pollens of living nipa having spines of almost equal sizes fit the descriptions of Kessler and Harley (2009).

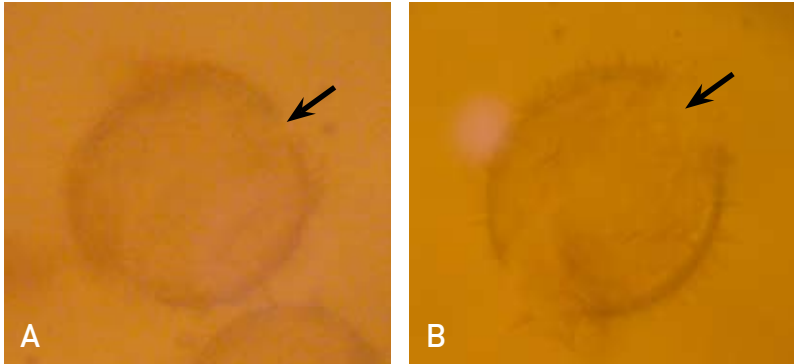
### **Morphological Characteristics of Nipa Inflorescence**

Within Davao City, the average number of female flowers per inflorescence was 58.0 for the nipa stand in Bago Aplaya and 59.7 for those in Ecoland. Mean differences were not statistically significant. In general, palms in Davao City produced a mean of 58.3 female flowers per inflorescence at F stage (Table 3). On the other hand, those in Carmen, Davao del Norte, produced a mean of 61.3 female flowers. The *t*-test of the mean differences between the two areas revealed to be statistically significant (Table 4). This suggests that the inland stands of Carmen were more fecund compared to the estuarine stands of Davao City. Nevertheless, these counts are twice as high as the count reported by Uhl (1972) at 30 female flowers per pistillate head, which is based on samples from New Guinea and Florida, United States.

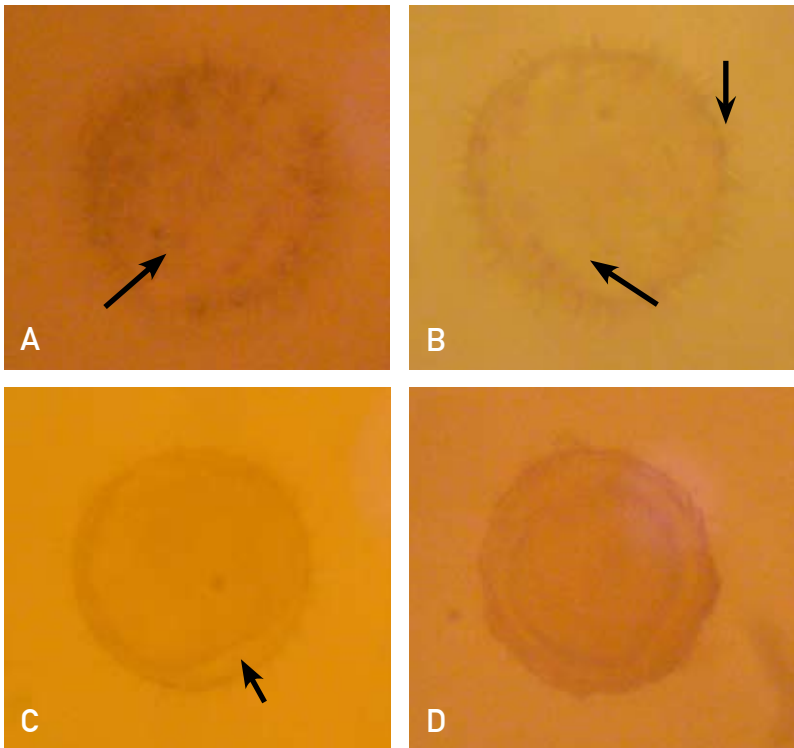
In Davao City, the mean inflorescence length at maturity observed in Bago Aplaya was significantly higher than that observed in Ecoland (86.04 cm vs. 77.32 cm) (Table 3). However, the mean inflorescence length at maturity observed in Davao City was lower than that observed in Carmen (84.3 cm vs. 117.50 cm), and the difference proved to be statistically significant (Table 4).

Inflorescence length may have implications on the development of the peduncle during fruit development as a conduit for sap collection. According to Hamilton and Murphy (1988), tapping life depends on the length of stalk. Long peduncles have a much longer tapping period than short ones and can provide higher sap yield if adequate pretapping activities were done to improve sap flow. One such practice, known as *takdug* in Surigao, Northern Mindanao, involve kicking and beating the peduncle during 3 weeks to 1 month of growth. Anecdotal accounts from tappers suggest the immediate drying of sap when *takdug* is not performed.

Nipa stands in Bago Aplaya produced 18 staminate rachillae per inflorescence while those in Ecoland produced 15. The mean lengths of these male flowers from palms in the Bago Aplaya and Ecoland sites were measured at 5.76 cm and 5.47 cm, respectively (Table 3). The *t*-test revealed that the difference of the male spike lengths between these areas were not significant. These results suggest that site differences produce variations in inflorescence height and staminate rachilla count even in nipa stands that are in proximity to each other.



**Figure 9.** Acetolyzed nipa pollen grains split (a) and burst (b) by their apertures (400×)



**Figure 10.** Intact nipa pollen grains (a, b) showing apertures encircling their spheres with spines in polar view, and in equatorial view (c, d) (400×)

**Table 3.** Mean inflorescence characteristics at full maturity of nipa palms in Davao City, Philippines

Site	Number of inflorescence	Inflorescence height (cm)	Staminate rachilla count	Staminate rachilla lengths (cm)	Female flower count
Bago Aplaya	28	86.04 (9.04)*	18.07 (3.30)*	5.76 (0.87)	58.00 (5.08)
Ecoland	7	77.32 (3.74)*	14.71 (2.81)*	5.47 (0.71)	59.70 (5.29)
Both sites	35	84.30 (9.23)	17.40 (3.45)	5.70 (0.84)	58.31 (5.08)

**Notes:**

Standard deviations are given inside parentheses.

\* Significant at 5%

**Table 4.** Mean inflorescence characteristics at full maturity of nipa palms in the Davao Region, Philippines

Site	Number of inflorescence	Inflorescence height (cm)	Staminate rachilla count	Staminate rachilla lengths (cm)	Female flower count
Davao City	35	84.30 (9.23)*	17.40 (3.45)*	5.70 (0.84)*	58.31 (5.08)*
Carmen	23	117.50 (16.60)*	33.22 (6.36)*	7.00 (0.90)*	61.30 (6.07)*
Both sites	58	97.46 (20.63)	23.67 (9.14)	6.22 (1.07)	59.50 (5.64)

**Notes:**

Standard deviations are given inside parentheses.

\* Significant at 5%

However, the palm population in Carmen produced more and much longer male flowers compared to those in Davao City. Palms in Carmen had a mean count of 33 staminate rachillae per inflorescence with a mean length of 7.00 cm (Table 4). The differences between these floral characters were found to be statistically significant across locations.

## Summary and Conclusion

This study is primarily aimed to understand the flowering habit of nipa by observing semi-wild stands in the Davao Region, Philippines. It was observed that the entire duration of inflorescence development occurred in about 41 d, confirming nipa as protogynous—i.e., anthesis of the female flowers on day 40 was one day ahead of the male flowers, suggesting the cross-pollinating habit of the palm. Stigma receptivity peaked 12 h after the onset indicated by the highest seed set, which significantly declined 48 h after. The male phase, beginning on the day 41, ranged from 13 to 14 d, shedding pollen basipetally, i.e., from top to bottom laterals. Pollen was found to be spherical with uniform spine length, yellow, and zonosulcate aperture as reported elsewhere.

Stigma receptivity data imply that in controlled pollination, breeder intervention should be made within a day from female anthesis to ensure higher seed set. Emasculation of male flowers can be scheduled in about 37 d from emergence to ensure removal of topmost laterals, which should have been well differentiated by this time. In reproductive biology studies, emasculation can also be employed in understanding the pollination strategy of this palm, whether pollination is insect- or wind-driven. Familiarization of pollen morphology will also allow studies on viability of pollen in storage and on insect pollinators.

In comparing morphological characteristics of inflorescence between different locations, both staminate rachilla and female flower counts were higher in the inland stands of Carmen, Davao del Norte, than those in the estuaries of Davao City. Those in Carmen stands are almost twice higher in number than those reported outside the Philippines. The inflorescence mean length in Carmen stands was higher.

These inflorescence attributes can provide a clue on the tapping potential of nipa as longer or taller inflorescence is assumed to produce higher sap yield due to its longer tapping time. However, it has to be validated by further studies. Also, growing nipa inland is not impossible as evidenced by the nipa stands in Carmen, Davao del Norte, whose palm inflorescences exhibited better morphological characteristics despite growing in areas not considered to be a natural habitat of nipa. This study is an initial step towards identifying parents that have higher potential of sap yield for hybridization should varieties be identified in the future.

## References

- Asmussen, C.B., and M.W. Chase. 2001. Coding and noncoding plastid DNA in palm systematics. *Am. J. Bot.* 88(6): 1103–1117.
- Asmussen, C.B., J. Dransfield, V. Deickmann, A.S. Barfod, J.C. Pintaud, and W.J. Baker. 2006. A new subfamily classification of the palm family (Arecaceae): Evidence from plastid DNA phylogeny. *Bot. J. Linnean Soc.* 151: 15–38.
- Berg, L.R. 2012. *Introduction to botany*. Cengage Learning Asia, Philippines.
- Borges, R.M. 1998. Gender in plants: 2. More about why and how plants change sex. *Resonance* 3(11): 30–39.
- Chumchim, N., and C. Khunwasi. 2011. Pollen morphology of true mangrove species in Thailand. *Proceedings of the 5th Botanical Conference of Thailand*, Kasetsart University, Bangkok, Thailand, 30 March–01 April 2011.
- Corner, E.J.H. 1966. *The natural history of palms*. University of California Press, Berkeley.
- Dransfield, J., N.W. Uhl, C.B. Asmussen, W.J. Baker, M.M. Harley, and C.E. Lewis. 2008. *Genera Palmarum: Evolution and classification of palms*. 2nd ed. Kew Publishing, UK.
- Halos, S.C. 1981. Nipa for alcogas production. *Canopy* 7(8): 15.
- Hamilton, L.S., and D.H. Murphy. 1988. Use and management of nipa palm (*Nypa fruticans*, Arecaceae): A review. *Econ. Bot.* 42(2): 206–213.
- Joshi, L., U. Kanagaratnam, and D. Adhuri. 2006. *Nypa fruticans*—Useful but forgotten in mangrove reforestation programs? *World Agroforestry Centre*, Bogor, Indonesia.
- Judd, W.S., C.S. Campbell, E.A. Kellogg, P.F. Stevens, and M.J. Donoghue. 2002. *Plant systematics: A phylogenetic approach*. 2nd ed. Sinauer Associates, Sunderland, MA.
- Kessler, R., and M. Harley. 2009. *Pollen: The hidden sexuality of flowers*. Firefly Books, New York, NY.
- Perera, P.I.P., I.P. Wickremasinghe, and W.M.U. Fernando. 2006. Morphological, cytogenetic and genotypic differences between spicata and ordinary tall coconut (*Cocos nucifera* L.). *J. Nat. Sci. Foundation Sri Lanka* 36(1): 103–108.
- Rasco, E.T. Jr. 2010. Biology of nipa palm (*Nypa fruticans* Wurm., Arecaceae) and its potential for alcohol production. *Asia Life Sci.* 19(2): 373–388.



- Santos G.A., P.A. Batugal, A. Othman, L. Baudouin, and J.P. Labouisse. 1995. Manual on standardized research techniques in coconut breeding. International Plant Genetic Institute (IPGI), Rome, Italy.
- Tomlinson, P.B. 1971. The shoot apex and its dichotomous branching in the *Nypa* palm. *Ann. Bot.* 35: 865–879.
- Tomlinson, P.B. 1990. The structural biology of palms. Oxford University Press, New York, NY.
- Uhl, N.W. 1972. Inflorescence and flower structure in *Nypa fruticans* (Palmae). *Am. J. Bot.* 59(7): 729–743.
- Uhl, N.W., and H.E. Moore Jr. 1971. The palm gynoecium. *Am. J. Bot.* 58: 945–992.
- Walker, D. 1999. Studying pollen. *Micscape Magazine*, UK. 3 January 2012. <http://www.microscopy-uk.org.uk/mag/artjul99/pollen.html>.