# Flower Color Variation in *Attalea phalerata* (Arecaceae) Revisited

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**Within the palm family, the genus *Attalea* attracts special attention from the passerby with its formidable inflorescences and infructescences that emerge among towering leaves that stretch up to 10 meters long in aborescent species. Acaulescent species also display a certain charm of their own with their elegantly tall leaves and often oversized fruits. Not only do *Attalea* species impress with their stature and beauty, they also evoke scientific interest by their fascinating reproductive biology.**

*Attalea* palms are monoecious. Most species produce unisexual inflorescences, alternating between male and female inflorescences over time, while other species switch between entirely male and androgynous, or mixed inflorescences, which present male and female flowers together on the same stalk (Henderson 2002). This unusual pattern of sex expression sparked my initial interest in the reproductive ecology of *Attalea* palms. While studying the flowering phenology of *Attalea* palms in Acre, Brazil (southwestern Amazon), I also observed a surprising variation in *Attalea phalerata* flower color. During monthly visits to *A. phalerata* populations, I usually encountered creamy-yellow inflorescences, but over the two-year study, I also observed a handful of inflorescences that displayed variations of purple and magenta flowers. For me, this was entirely unexpected, since *Attalea* palms are known for their large inflorescences with creamy-yellow flowers.

Initially, I hypothesized that the purple-colored inflorescences were a symptom of some transient environmental stress, such as cold temperatures, drought, or even fire (Tucker Lima 2009). However, I have since proven this assumption incorrect. The extensive palm collections at Montgomery Botanical Center (MBC) in Coral Gables, Florida, presented me with the unique opportunity to observe *A. phalerata* flowering continuously on a daily basis, rather than at monthly intervals, and revealed a consistent, predictable pattern of flower color change as inflorescences mature – all *A. phalerata* inflorescences change color (Fig. 1)! Rather than a response to environmental conditions, flower color in *A. phalerata* is a function of flower age that changes over time. Observations at MBC revealed that flower color changes quickly. Newly opened inflorescences display an abundance of creamy-yellow flowers color, but by the next day, new coloration spreads over the inflorescence and the flowers take on a magenta hue. Three days after opening, the flower petals appear darker magenta or purple in color and continue to gradually turn a

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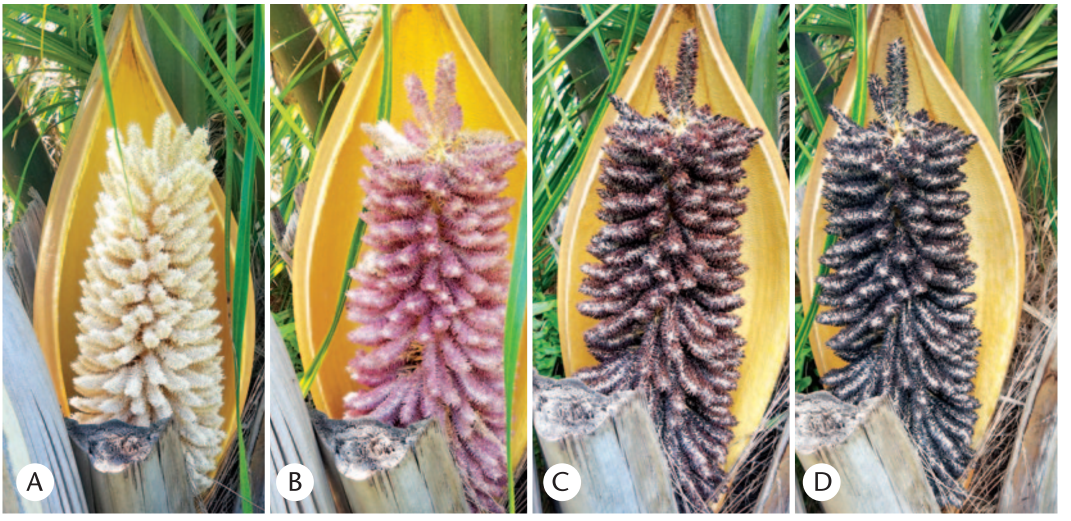
1. *Attalea phalerata* palm growing at Montgomery Botanical Center in Coral Gables, Florida (A), and staminate, or male (B, D, F) and pistillate, or female (C, E, G) inflorescences expressing a range of flower colors from creamy-yellow to magenta to purple.

darker purple to indigo over the next couple of days (Fig. 2). Not only do staminate (male) flowers follow this trajectory, but daily observations at MBC revealed that pistillate (female) flower petals change color in the same manner over time from creamy-yellow to indigo (Fig. 3). In pistillate flowers this change is sometimes relegated to the tip of each petal, but in other instances the color expands over the entire petal (Fig. 1E, G).

Upon digging into the published literature on *Attalea* palms, I came across only a few images or mention of purple-colored flowers in species considered part of the *Attalea phalerata* complex (Barbosa Rodrigues 1903 [as *A. kewensis*], Glassman 1999, Lorenzi et al. 2004, Fava et al. 2011). So, purple *Attalea* flowers are not a new discovery, per se; however, I know of no published investigation into the details of flower color change in this species, and as far as I know, only Fava et al. (2011) acknowledged the change in staminate flower color from creamy-yellow to purple over time. Other than a singular historical illustration under the name of *Attalea kewensis* (Barbosa Rodrigues 1903), ours is the first published record of purple coloration in pistillate flowers of *Attalea phalerata*.

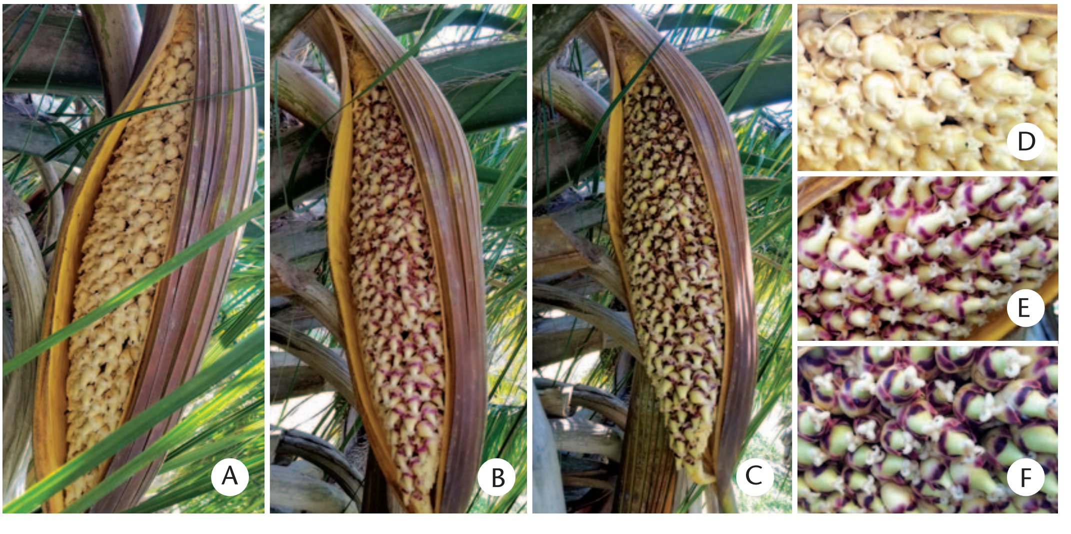


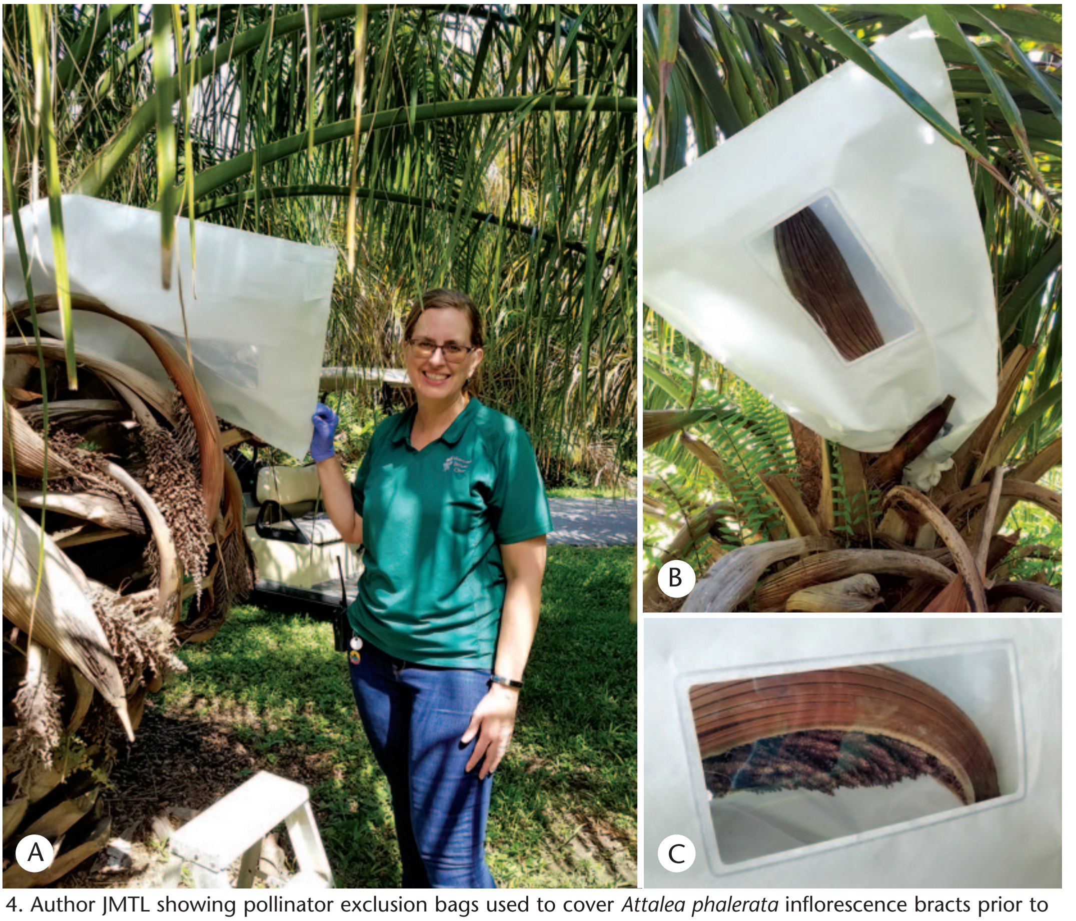

2. Flower color change sequence over time in an *Attalea phalerata* palm growing at Montgomery Botanical Center in Coral Gables, Florida. The staminate (male) inflorescence displays creamy-yellow colored flowers on first day of opening (A), but subsequently, over the next three to four days, flowers change to a magenta hue (B), then purple (C), and finally indigo (D).

Records of flowering in other *Attalea* species report only creamy-yellow flowers. Our findings related to patterns of flower color change in *A. phalerata* spawned a new set of questions about why only this particular species diverges from the typical creamy-yellow flowers presented by the other 30 species of *Attalea* (Henderson 2020). What role, if any, does floral color change play in the reproductive biology of this palm? Observations of other *Attalea* species at MBC, including *Attalea humilis*, *Attalea cohune*, *Attalea guayacule*, *Attalea brasiliensis*, *Attalea butyracea*, *A. speciosa*, *A. crassispatha* and *A. brejinhoensis* confirm that flowers in these species usually maintain yellowish, cream-colored flowers through anthesis and until flowers begin to drop a few days later. In a couple species (*A. butyracea* and *A. speciosa*), we did observe flower petals turning a brownish-tan color as inflorescences aged but never purple.

Flower color change is relatively common among plant species, occurring across as many as 78 different angiosperm families (Weiss 1995, Raguso & Weiss 2015, Yan et al. 2016).

3. Flower color change in a pistillate (female) *Attalea phalerata* inflorescence growing at Montgomery Botanical Center in Coral Gables, Florida. The new flowers display a creamy-yellow color on first day of opening (A, D), then change to magenta by the second day (B, E) and purple by the third day (C, F).



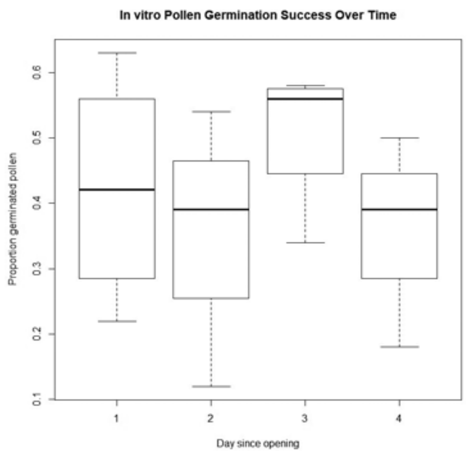



4. Author JMTL showing pollinator exclusion bags used to cover *Attalea phalerata* inflorescence bracts prior to opening (A). Each breathable bag has a front window enabling visualization of flower color during and after anthesis without opening the bag (B, C).

Among palm species, however, I know of no published record of flower color change, other than Fava et al. (2011). Scientific research links flower color change to pollinator attraction. In many cases, color change corresponds with availability of floral rewards, such as nectar or pollen (Casper & La Pine 1984, Niesenbaum et al. 1999, Oberrath & Bohning-Gaese 1999). Usually, color change indicates post-reproductive flowers, thereby increasing pollination efficiency by directing pollinators to fertile, rewarding flowers (Raguso & Weiss 2015, Delph & Lively 1989). In some species, researchers have identified a direct link between color change and pollen deposition on the stigma, loss of stigma receptivity, or developing pollen tubes (Lamont 1985, Nuttman & Wilmer 2003, Pereira et al. 2011). Sometimes plants also retain color-changed flowers to increase overall flower abundance and draw long-distance attention of key pollinators (Weiss 1991, Oberrath & Bohning-Gaese 1999, Nuttman et al. 2006).

To test whether flower color change in *A. phalerata* is related to pollinator visitation or pollen deposition in the case of pistillate flowers, we bagged 16 still closed inflorescence bracts at MBC and observed their flower color through the first week after opening. We used specialized breathable bags with a "window" for viewing (PBS International pollination bags, size 2D.4-1W; Fig. 4). In all cases, both staminate and pistillate flowers changed color from creamy-yellow to purple over the course of a few days. Thus, we can say with certainty that neither pollinator visitation, nor pollination itself triggers flower color change in *A. phalerata*.

Other related explanations for flower color change include the signaling of pollen viability or stigma receptivity. If color change signals post-reproductive flowers in *A. phalerata*, pollen viability and stigma receptivity should peak during the creamy-yellow phase and be significantly lower or even undetectable in



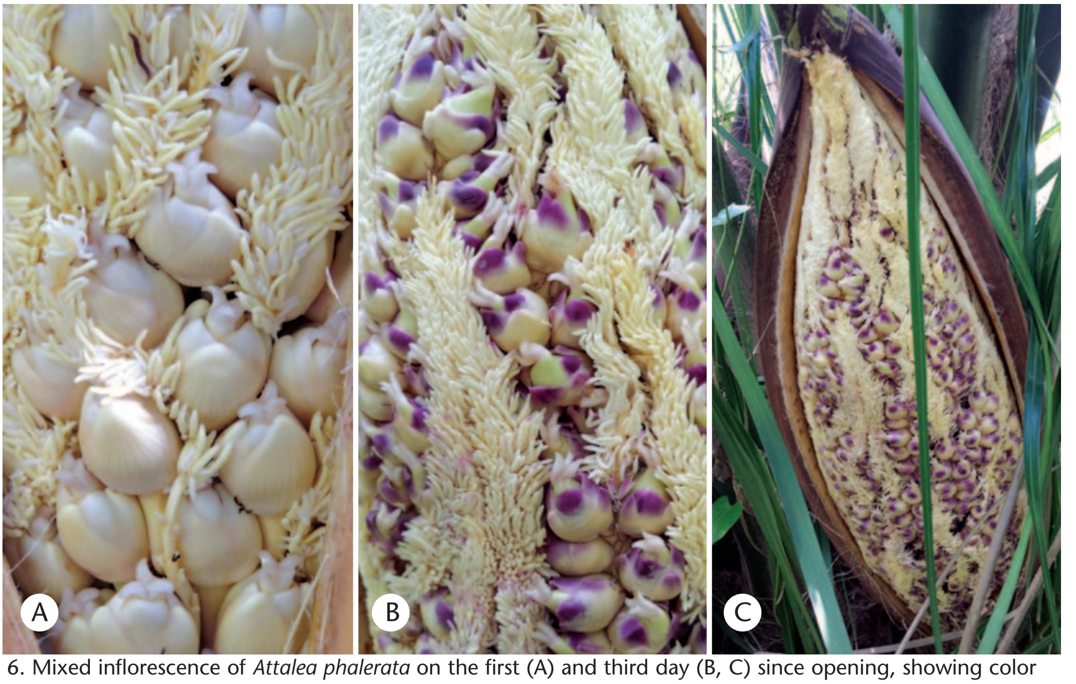

5. Proportion of *Attalea phalerata* pollen that successfully germinated *in vitro* on day 1, day 2, day 3, and day 4 after bract opening, based on pollen samples collected from six different inflorescences at Montgomery Botanical Center in Coral Gables, Florida.

purple-colored flowers. This would mean, however, that flowers are only fertile for up to 24 hours. To explore whether flower color change in *A. phalerata* is linked to pollen viability, we have begun to study germination rates in pollen collected at MBC from *A. phalerata* flowers during the first days after opening. To assess viability, we followed the *in vitro* pollen germination protocol described in Dafni et al. (2005), germinating pollen in Boric Acid medium mixed with a 20% sucrose concentration. Pollen samples were incubated at 26ºC for approximately 18 hours. We then used a hemocytometer to count germinated and ungerminated pollen grains using a compound microscope. Germination rate was calculated as the proportion of germinated pollen grains out of 300 grains systematically counted in each of four gridded quadrants on the hemocytometer. Preliminary results from six sampled inflorescences showed no clear pattern of loss in pollen viability over the first four days after bract opening, when flowers change from creamy-yellow to purple (Fig. 5). Although suggestive, further research is needed to better determine the relationship between pollen viability and flower color.

We also tested stigma receptivity of pistillate flowers over the first few days after inflorescence opening using two different methods: the application of hydrogen peroxide droplets and peroxidase test paper (Peroxtesmo KO, CTL Scientific Supply Corp) to the stigma, as described in Dafni et al. (2005). Both procedures are designed to test for the presence of peroxidase. This enzyme reflects receptivity; however, these tests can also give false positives if pollen is already present on the stigma (Kearns & Inouye 1993). We administered both tests on several different *A. phalerata* palms and found positive evidence of peroxidase on pistillate flowers both before and after color change. Further tests are needed to support these preliminary results.

One surprising finding was that the mere presence or absence of pollen seems to be linked with petal color in the staminate flowers. Shortly after the *A. phalerata* bract opens to expose its creamy-yellow flowers, anthers normally dehisce, and when jiggled, the inflorescence releases a large cloud of pollen. This continues to be true over the first 3 or 4 days after opening, regardless of flower color. On multiple occasions, however, we observed staminate inflorescences with no apparent burst of pollen when bumped. Flowers on these inflorescences also failed to change color, and upon closer examination, we found that the anthers contained no pollen. This also held true for mixed inflorescences, where only pistillate flowers exhibited color change but not the staminate flowers (Fig. 6). In *Attalea* species, mixed inflorescences are often functionally female with sterile male flowers (Anderson et al. 1988, Voeks 2002).

Flower color in *A. phalerata* does not seem to be a reliable indicator of pollen viability but may signal pollen availability. If color change to purple signals the presence of pollen, the question becomes, who is the palm signaling? And what about pistillate flowers? Could female flowers that do not change color also be sterile? The main pollinators of *A. phalerata* identified by Fava et al. (2011) are *Celetes* sp. *Colopterus* sp. *Mystrops* sp. and *Madarini* indet.*1*. These beetles are attracted to heat produced by thermogenesis. Temperatures peak just before the inflorescence opens, and accompanying scents released as volatiles also draw the beetles. Since both the heat and scent diminish quickly after the inflorescence is exposed (Fava et al. 2011), it is unlikely that color change plays a role in attracting the beetles. So, what purpose does the subsequent flush of purple serve? Does it somehow encourage the beetles to leave the inflorescence and visit another for cross-pollination? Or does the darkening color ensure a warmer environment for developing beetle eggs?




6. Mixed inflorescence of *Attalea phalerata* on the first (A) and third day (B, C) since opening, showing color change in pistillate but not in staminate flowers. Staminate flowers are void of pollen.

Could it possibly be attracting a secondary pollinator?

This paper revisits the question of flower color in *A. phalerata*, correcting an erroneous assumption that this palm displays two distinct types of inflorescences: one creamy-yellow and another purple (Tucker Lima 2009). Instead, daily observations revealed a predictable pattern of flower color change after the inflorescence opens. Whether this pattern has ecological significance or is simply a consequence of the passage of time remains to be proven, and our new discoveries have prompted many questions. The fact that *A. phalerata* is the only *Attalea* species to exhibit flower color change seems to hint at a deeper significance, but so far the usual explanations have come up short. Complementary *in situ* pollination studies to identify pollinators and their behavior are needed to explore possible associations between native pollinators and flower color. At MBC we shall continue our investigations into both the physiology and the ecology of flower color change and hope to shed light on the mechanisms, triggers, and possible reasons behind this mystery.

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