Flower Color Variation in *Attalea phalerata* (Arecaceae)

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Over the past few years, I have been conducting a phenology study of the arborescent palm *Attalea phalerata* Mart. ex Spreng. in southwestern Amazonia. Although botanical records have consistently reported yellow flowers on *A. phalerata* inflorescences, I observed multiple cases of non-yellow staminate flowers. Flower color varied from dark purple to violet, or a mixture of yellow-orange to magenta flowers within the same male inflorescence (Fig. 1; hereafter I refer to non-yellow flowers as purple). This article reports on field observations of flower color polymorphism in *A. phalerata* and discusses possible explanations for this anomaly.

Field observations

Phenology

I monitored flowering phenology of *Attalea phalerata* in Acre, Brazil, between January 2006 and December 2007. Using binoculars, I observed flowering from the ground at monthly intervals at six study sites (three actively grazed pastures and three areas of old-growth tropical moist forest). At each site I observed 12 reproductive palms. Between July to December 2007, observations were reduced to two sites per habitat. For each individual I recorded sex and reproductive phase of all inflorescences – closed inflorescence buds (bracts), inflorescences in anthesis (open flowers) and dried, post-anthesis inflorescence structures. I also categorized crown illumination on a scale of zero to five by counting the number of sides of the palm crown directly exposed to sunlight (four lateral sides plus top) (Bechtold 2003). Within old-growth forest, *A. phalerata* is mainly a lower canopy palm.

Attalea species alternate between pistillate, staminate, and sometimes hermaphroditic inflorescences on the same plant. During 24 months of observations of 72 *A. phalerata* palms, I registered only four instances of hermaphroditic inflorescences. The remaining inflorescences were either exclusively pistillate or exclusively staminate. The majority of *A. phalerata* staminate inflorescences initiated flowering at the beginning of the dry season between May and June, peaked in September at the end of the dry season, and dwindled during the wet season (Fig. 2). Palms growing in old-growth forest were more likely to suspend inflorescence production for a short

1. Color variation from yellow to dark purple in *Attalea phalerata* staminate inflorescences observed in eastern Acre, Brazil.

period each year between February and April, whereas pasture palms produced inflorescences continuously year-round. Still, pasture palms mimicked the overall seasonal patterns of flowering peaks and lulls in the forest.

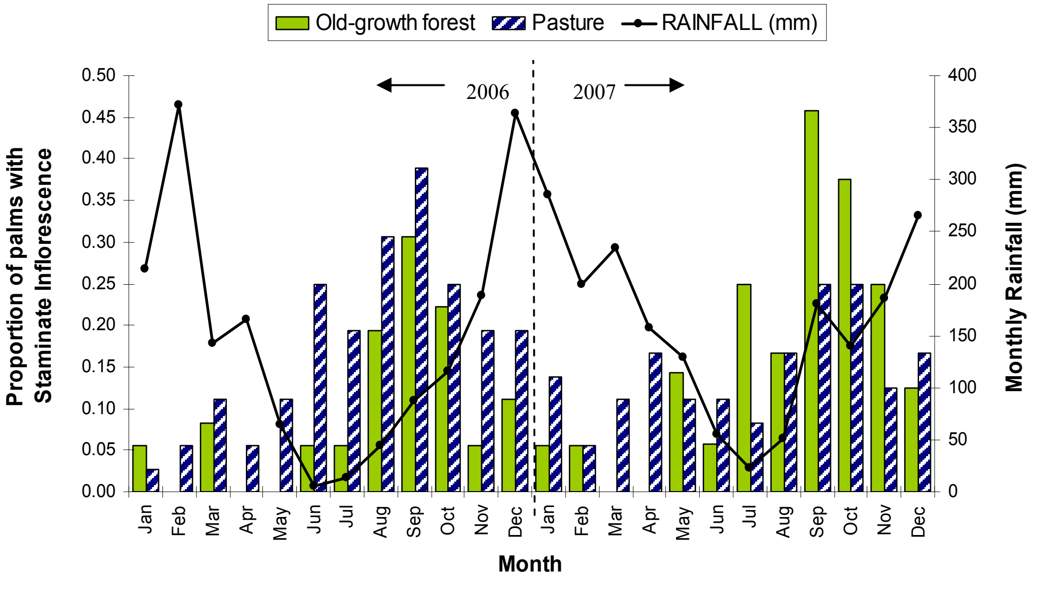
Flower color variation

To my surprise, of 55 male inflorescences observed in anthesis, the majority (55%) produced purple flowers rather than the

1. (*continued*) Color variation from yellow to dark purple in *Attalea phalerata* staminate inflorescences.

familiar yellow flowers. During two years of monthly phenological observations, I recorded 19 purple staminate inflorescences in anthesis in pastures (on 15 different palms) and 11 in forests (on nine different palms). Over the same two-year period, I observed 14 yellow staminate inflorescences in pastures (on 12 different palms) and 11 in forest (on ten different palms). Some *A. phalerata* individuals alternated between purple and yellow flowers, while a few palms (n=5) repeatedly produced purple flowers. Of the 22 *A. phalerata* individuals with purple flowers, more than half (n = 12) also produced the better known yellow flowers either before or after a purple flowering event, indicating phenotypic

2. Proportion of *Attalea phalerata* palms with staminate inflorescence and monthly rainfall from January 2006 until December 2007 in pastures and old-growth forests in Acre, Brazil.



3. Purple coloration of petal tips on flowers of an *Attalea phalerata* pistillate inflorescence in eastern Acre, Brazil.

plasticity within individual palms. In one case, a single palm exhibited one yellow and one purple inflorescence simultaneously. Both yellow and purple inflorescences were observed in anthesis, and the colors remained constant as they developed. I also observed purple coloration at the tips of creamy yellow petals of *A. phalerata* pistillate flowers (Fig. 3), but only three pistillate inflorescences were observed in anthesis during the entire study period.

Staminate flower color variation occurred not only within and among individual palm trees, but also in both the wet (November to April) and dry seasons (May to October), across different habitats (pasture and forest), and on a regional scale dispersed over 100 km^2. Purple flowers appeared at various times throughout the year, although mostly during the dry season, which corresponds to the peak flowering season of *A. phalerata* (Fig. 2, Tab. 1). Most flowering anthesis events occurred between observation visits, and for these I was unable to determine flower color.

Color polymorphism in palms

Flower color polymorphism in plants is common in nature and appears within genera, within species, and even within isolated populations. Several examples from herbaceous and other short-lived plants, both wild and cultivated, exist in the research literature (Armbruster 2002). Larry Noblick (pers. comm.) detected flower color variation between yellow and magenta in *Attalea* palms near Corumba, Mato Grosso do Sul, Brazil, in the Pantanal region, but to my knowledge no records of within-species color variation in palm inflorescences have been published.

Palms, such as the lipstick palm, *Cyrtostachys renda*, with its bright red crown shaft, *Geonoma epetiolata,* with reddish purple underside of

Table 1. Number of yellow and purple-shaded staminate inflorescences of *Attalea phalerata* observed in anthesis in pasture and old-growth forest during monthly visits in (a) 2006 when I observed 36 reproductive individuals in pastures and 36 in old-growth forests, and (b) 2007 when I observed 36 individuals in each habitat until June and 24 in each habitat from June-December.

(a) 2006		J	F	M	A	M	J	J	A	S	O	N	D	TOTAL
PASTURE	Purple-shaded (no. palms=11)	0	0	0	0	1	3	0	3	2	0	2	2	13
	Yellow (no. palms=9)	1	0	0	0	0	1	1	1	0	2	2	1	9
OLD-GROWTH FOREST	Purple-shaded (no. palms=6)	0	0	0	0	0	1	0	2	2	0	1	1	7
	Yellow (no. palms=4)	0	0	0	0	0	1	0	1	0	1	1	1	4
	TOTAL	1	0	0	0	1	5	1	7	4	3	6	5	33

(b) 2007		J	F	M	A	M	J	J	A	S	O	N	D	TOTAL
PASTURE	Purple-shaded (no. palms=4)	0	1	1	0	0	0	0	0	3	1	0	0	6
	Yellow (no. palms=5)	0	0	0	1	0	0	0	3	1	0	0	0	5
OLD-GROWTH FOREST	Purple-shaded (no. palms=4)	0	0	0	0	1	1	0	0	0	0	2	0	4
	Yellow (no. palms=7)	0	0	0	0	0	0	0	3	2	1	1	0	7
	TOTAL	0	1	1	1	1	1	0	6	6	2	3	0	22

young leaves (Blanco & Martén-Rodríguez 2007), and various palm genera with purple fruits (e.g., *Euterpe*, *Bactris*, *Butia*, *Coccothrinax*), testify to widespread anthocyanin production within Arecaceae. Anthocyanins (a flavonoid sub-group) are responsible for most orange, red, purple and blue flower colors and occur in almost all vascular plants (Grotewold 2006). Harborne et al. (1974) found flavonoid pigments (glycosides) specifically in the flowers of ten different palm species, and a few studies have identified other types of flavonoids in the vegetative structures of *Attalea* and other cocosoid palm species (Williams et al. 1983, Williams et al. 1985). Still, the question remains as to what drives flower color variation in *A. phalerata*.

Possible explanations for color polymorphism in *Attalea phalerata* flowers

To try and uncover the reasons for flower color variation in *A. phalerata*, I used Pearson's Chi-squared Test to examine relationships between flower color and four variables: (1) habitat (old-growth forest versus pasture) (χ^2 = 1.01 , d.f. = 1, p = 0.32), (2) season (wet versus dry) (χ^2 = 0.799 , d.f. = 1, p = 0.37), (3) year (2006 versus 2007) (χ^2 = 1.84 , d.f. = 1, p = 0.17), and (4) crown illumination (χ^2 = 10.67, d.f. = 5, p = 0.06). Results revealed no significant associations with flower color. Crown illumination, or light availability, was marginally significant, but the absence of an association between habitat and flower color precluded any strong linkage between crown illumination and flower color, since the two habitats we compared – pasture and forest – represent two extremes in light availability.

A common explanation for color variation within and among species is pollinator selective pressures (Hannan 1981). Pollinators respond to various floral signals – color, shape, size, fragrance, temperature – and these preferences exert selective pressures on the plant to optimize reproductive success (Levin & Brack 1995, Meléndez-Ackerman et al. 1998). Studies of *A. phalerata* pollination are scarce; however, nitidulid beetles from the genus *Mystrops* are most likely the principal pollinators (Moraes et al. 1996). Beetles respond to floral signals of increased temperature and fragrance, rather than color, and *Attalea* flowers are known to mature quickly, heating up before anthesis (Henderson 2002). I observed insects, apparently pollinators, actively feeding on purple inflorescences, so purple flowers do not appear to deter pollinators. Further research may help determine if purple staminate flowers negatively affect fertilization, fruit set and reproductive success in *A. phalerata*.

Associations between anthocyanins in vegetative organs and flowers and environmental stresses may also help explain flower color variation in *A. phalerata*. In vegetative organs, plants manufacture anthocyanins to protect against environmental stresses, such as herbivory (Fineblum & Rausher 1997), photo-damage (Close & Beadle 2003) and drought (Levin & Brack 1995). Plants also synthesize pigments in response to extreme environmental conditions, such as cold temperatures (Stiles et al. 2007) and nitrogen deficiency (Bonguebartelsman & Phillips 1995). Finally, Armbruster (2002) found linkages between anthocyanins in vegetative organs and their presence in flowers. Selection pressures related to environmental heterogeneity and stress tolerance may be responsible for plant anthocyanin production in general, helping maintain flower color polymorphism within and among species (Warren & MacKenzie 2001).

Final Considerations

Until now, *A. phalerata* inflorescence color in southwestern Amazonia has been reported only as yellow or cream-colored (Evandro Ferreira, pers. comm.). Anthocyanins present in the plant to various degrees likely account for the various shades of purple observed. The question remains as to what provokes the differences in anthocyanins seen in these palms. Flower color is not genetically fixed in *A. phalerata*, since yellow inflorescences often followed the production of purple inflorescences on the same plant. If environmental stress is responsible for flower color variation in *A. phalerata*, three sources of stress come to mind: (1) Intermittent cold fronts pass through the region each year during the early dry season, dropping temperatures into the lower teens (ºC) (cf. Stiles et al. 2007); (2) A severe drought in 2005 induced soil moisture stress and could have indirectly augmented susceptibility to herbivory or pathogen attack; and (3) Extensive fires during the 2005 drought killed a large number of pollinators, and palms may have reacted with a different flower color to attract alternative pollinators. *Attalea phalerata* is a broadly distributed species, found throughout the southern and western periphery of the Amazon region, including Brazil, Bolivia and Peru, as well as the planalto of Brazil, Bolivia and Paraguay (Henderson et al. 1995). More detailed studies of this species' flowering phenology and variation in flower color over its geographical range are warranted to understand what triggers deviations in *A. phalerata* flower color and how flower color variation affects the ecology of this species.

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