



The dual defensive strategy of *Amorphophallus* throughout its ontogeny

Kunpeng Liu, Nik Fadzly, Asyraf Mansor, Rahmad Zakaria, Nadine Ruppert & Chow Yang Lee

To cite this article: Kunpeng Liu, Nik Fadzly, Asyraf Mansor, Rahmad Zakaria, Nadine Ruppert & Chow Yang Lee (2017) The dual defensive strategy of *Amorphophallus* throughout its ontogeny, *Plant Signaling & Behavior*, 12:10, e1371890, DOI: [10.1080/15592324.2017.1371890](https://doi.org/10.1080/15592324.2017.1371890)

To link to this article: <http://dx.doi.org/10.1080/15592324.2017.1371890>



Accepted author version posted online: 25 Aug 2017.
Published online: 25 Aug 2017.



Submit your article to this journal [↗](#)



Article views: 52



View related articles [↗](#)



View Crossmark data [↗](#)

SHORT COMMUNICATION



The dual defensive strategy of *Amorphophallus* throughout its ontogeny

Kunpeng Liu^a, Nik Fadzly ^a, Asyraf Mansor ^{a,b}, Rahmad Zakaria^a, Nadine Ruppert^a, and Chow Yang Lee^a

^aSchool of Biological Sciences, Universiti Sains Malaysia, Minden, Penang, Malaysia; ^bCentre For Marine & Coastal Studies (CEMACS), Universiti Sains Malaysia, USM, Penang, Malaysia

ABSTRACT

Amorphophallus bufo is a rarely studied plant in Malaysian tropical rainforests. We measured the spectral reflectance of different developmental stages of *A. bufo* (seedlings, juveniles and adults), background soil/debris and leaves from other neighboring plant species. Results show that the leaves of *A. bufo* seedling have a similar reflectance curve as the background soil and debris. Adults and juveniles of *A. bufo* are similar to other neighboring plants' leaf colors. We hypothesize that the cryptic coloration of *A. bufo* seedlings plays an important role in camouflage and that the numerous black spots on the surface of the petioles and rachises, may serve as a defensive mimicry against herbivores.

ARTICLE HISTORY

Received 8 August 2017
Revised 21 August 2017
Accepted 22 August 2017

KEYWORDS

Plant color; cryptic color; insect mimicry; *Amorphophallus*; leaf color; reflectance analysis

Introduction

Many studies about plant defense only focus on physical deterring mechanisms (i.e., spines, thorns or prickles) or chemical mechanisms. However, some plants use unique strategies, such as warning signals (aposematic coloration) to deter herbivores,^{23,16} and cryptic colorations to avoid herbivory.⁶ For example, *Pseudopanax crassifolius* can use distinctive visual defensive strategies at different stages of their ontogeny.⁷ In scree areas, some plant species (e.g., *Lignocarpa carnosula*, *Lobelia rouhii*) have grey leaves, which resemble the grey stones in the background.³² Warning signals are not exclusive to whole leaf coloration. For instance, some *Passiflora* flowers have dark spots to mimic ants or aphid and those patterns may serve as visual deterrence for herbivore.²² Most of the studies are from the subtropical and temperate climatic zones and there is very little information on similar defensive color strategies from the tropics. A well-known example is *Macaranga bancana*, a myrmecophyte species in Malaysia's tropical rainforests. The adult stage of *M. bancana* provides food bodies for ants; in return ants help to protect the plant against herbivores.¹⁴ However, during the early stages of development (i.e. seedlings), when the soft branches of the plant cannot yet support an ant colony, the plant uses cryptic coloration as camouflage to avoid herbivory.⁸

Here, we present another example of a plant from the tropics that uses color strategy for defense throughout its ontogeny. *Amorphophallus* (Blume ex Decne), is a herbaceous plant genus from the family Araceae. There are about 200 species of *Amorphophallus*, worldwide. They are distributed from the tropical and subtropical areas of western Africa eastward into Polynesia.¹³ Traditionally, locals in China and Japan use *Amorphophallus* as food and medicine.³ Most *Amorphophallus* are pioneer species, therefore they are more likely to be found in secondary forests or forest margins compared to primary forests or dense forests. Some species can grow on exposed

surfaces such as limestone karst areas.¹³ Subterranean stems (tubers) are varied in sizes and shapes based on the species. Above the tuber, is a single petiole with a compound leaf and a single inflorescence, which will emerge when matured.¹³

Many *Amorphophallus* species are famous for their giant inflorescence and carrion smell. Individual plants of *Amorphophallus* are monoecious. A single spadix is wrapped by the spathe, which can protect the female flowers at the lower part and male flowers at the upper part. The carrion smell is the outcome of a simple chemical composition that can attract carrion beetles for pollination (Kate & Hetttersched [18]). Flowers of *A. johnsonii* will trap carrion beetles in their lower spathe for overnight and produce sticky pollen so that the carrion beetle can carry pollen when it escapes from the spadix of the flower.¹ Small staphylinid beetles and sweat bees are also found as visitors in some *Amorphophallus* species.¹³ The *Amorphophallus* seed dispersers are not well documented. Birds, such as hornbills and Bulbuls, were found carrying colored berries of some *Amorphophallus* species.¹³

Amorphophallus bufo (Ridl) is a native species from Peninsular Malaysia. Its tuber is globose and above the tuber is the petiole, which is around 30 to 100 cm in size. The petiole and the rachises are normally mottled reddish or brown in color, and some mottles are irregularly attached on the surface. Young leaves emerge from the tuber within 20 cm, and their colors are always reddish and brown. After the seedling stage, the leaf color changes to green and the margins of the adult leaves are reddish purple. Every leaflet has the shape of a narrow to oblanceolate ellipse with a slightly undulate margin.

Similarly to *Macaranga bancana*, we suggest that *Amorphophallus bufo* changes its defensive strategies with ontogeny. We measured the color reflectance of leaves of adults, juveniles and seedlings of *A. bufo*. The background (soil/ debris) color as well as other neighboring plant seedlings' leaf color reflectance were

also measured and compared with each other. We hypothesized that seedling stage of *A. bufo* uses camouflage as the color reflectance of *A. bufo* seedling leaves are similar to the background, but different from other neighboring plants seedling leaves. Furthermore, *A. bufo* share the same ecosystem with *Macaranga* species as well as many myrmecophytes. Herbivores in the same habitat should have experience of encountering ant defense. Therefore, the black spots on the petiole and rachises of *A. bufo* may serve by ant mimicry as a warning signal against herbivores. We also hypothesized that the plant uses a dual color defense strategy through different life stages.

Methods

The *A. bufo* samples were collected from Bukit Genting Hill, Penang, Malaysia (GPS N 5.308, E 100.220). The height of adult *A. bufo* were around 30 cm above the ground, juveniles were 20 cm high and seedlings were 10 cm high (Fig. 1a). The adults had green leaves similar to other neighboring plant species, while seedling leaves were reddish and brown (Fig. 1b, c). Juvenile leaf color was at an intermediate tone between adults and seedlings (Fig. 1c). Spectral measurements were conducted using Ocean Optics Jazz spectrophotometer with Tungsten lamp light source and analyzed using SpectraSuite software. Spectral measurement protocols followed.⁸ We took the spectral measurement of three *A. bufo* seedlings. Three *A. bufo* juveniles' spectral reading as well as three adults of *A. bufo*'s reading was also recorded. For comparison, we also measured the background spectral reading by measuring the debris and soil in the sampling area. Leaves of eleven other species of seedlings (located within 5 meter radius of the *A. bufo*) were also measured with the same protocol. One *A. bufo* adult plant was brought back from the forest and planted in a pot at the USM Plant house to observe its growth pattern. We could not target any specific herbivores of *A. bufo* since there are many different herbivores species in the tropical rainforests. Furthermore, there is a lack of research on herbivory of *A. bufo*. Following the methods from Fadzly et al.,⁸ we also ran Principal Component Analysis (PCA) using JMP software. We use the Robust estimation method to analyze the data.

Results

The reflectance curve of adult *A. bufo* was similar to the reflectance curve of other seedlings at a peak wavelength of 550 nm (Fig. 2). This particular wavelength is known as visible green light. Green leaves of most plants reflect green light from the sunlight with a peak around 550 nm wavelength. However, the reflectance curve of *A. bufo* seedlings and juveniles were not similar to the adult *A. bufo* or other neighboring plant seedlings. Their curves were more similar to the spectral curve of the background reflectance. Their reflectance curves did not show any peak at 550 nm area of wavelength. The pattern of *A. bufo* seedlings and juveniles were almost similar along the wavelengths of 400 nm to 650 nm (within the visible light wavelength). This shows that the seedlings and juvenile leaves were different from their own adult leaves or from other neighboring plant seedling leaves. They do not reflect green light, but have a dark-brown color similar to the background color of soil

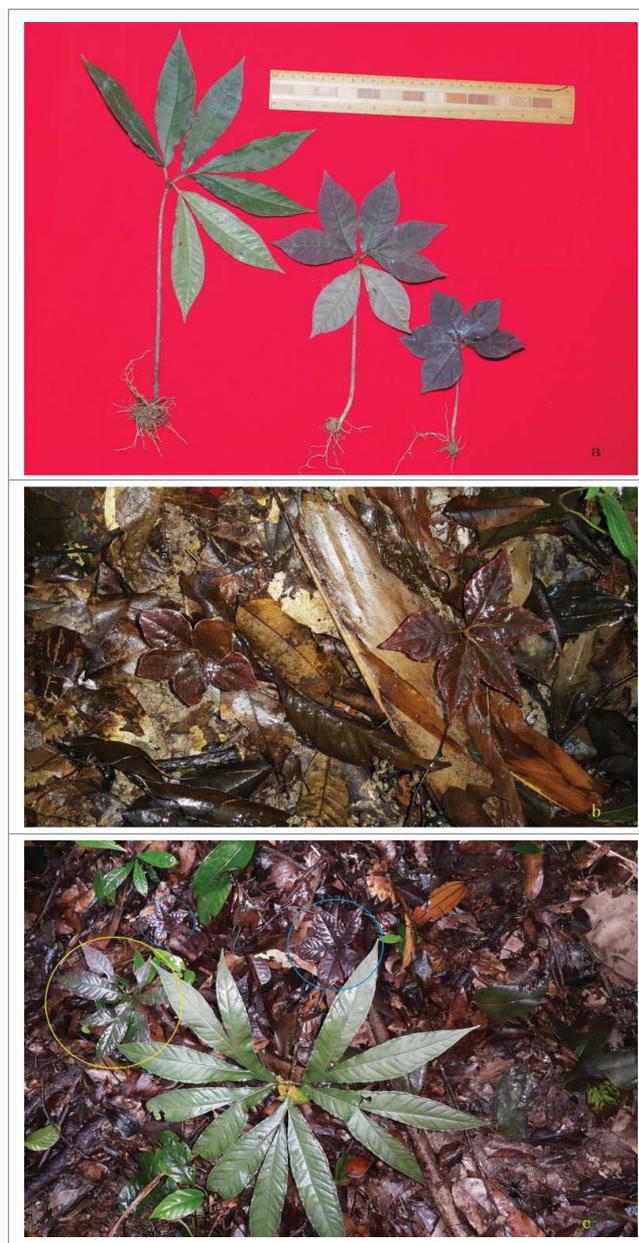


Figure 1. 1a: The three stages of *A. bufo*: adult (left), juvenile (center) and seedling (right). Full length of the ruler is 30.5 cm as a scale. **Figure 1b:** The cryptic colors of *A. bufo* seedlings matches the dead dry leaves and soil in the background. **Figure 1c:** All the three stages of *A. bufo* in its natural environment. The blue circle shows the seedling, the yellow circle shows the juvenile and the large green adult is in the center.

and debris. The light intensity of *A. bufo* juveniles were higher than *A. bufo* seedlings, which means that they were the intermediate hue with a slightly green reflectance, but still retaining the dark brown colors.

The principle component 1 and principle component 2 accounted for 92% of the variation (Fig. 3). In detail, PC1 accounts for the majority of the variation, which was 72%, and PC2 represents the remaining 20% of the variation. Table 1 shows the eigenvector values for PC1 and PC2. The average adult *A. bufo* and average neighboring species were clustered in the same region. Average background, seedling, and juvenile *A. bufo* were clustered together in a separate region from the previous component. The average background and the average

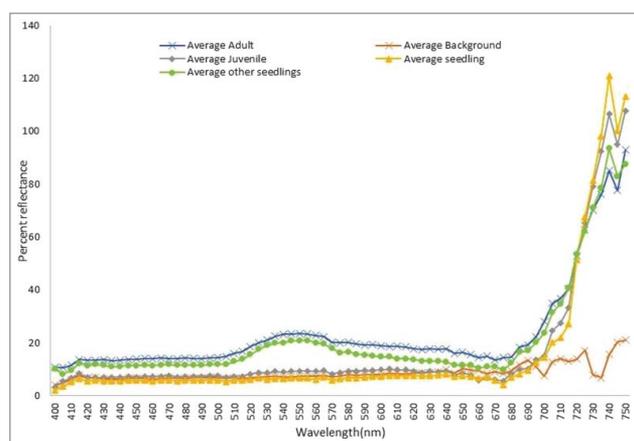


Figure 2. The spectral reflectance results from 400 nm to 750 nm wavelengths.

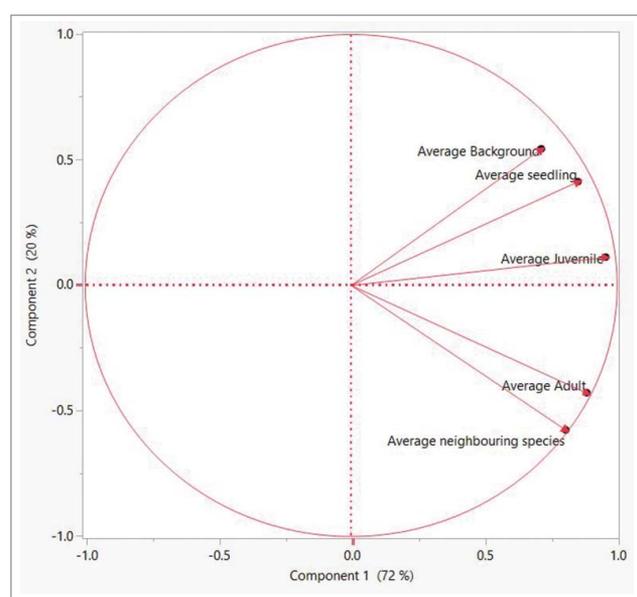


Figure 3. Principal components analyses results. PC1 and PC2 accounts for 92 % of the variation.

seedling were more closely related to each other than to the average juveniles.

Discussion

Although food and medicines sourced from *Amorphophallus* are widely used in East Asia, there is very little published information about this plant, especially on the defensive strategies against herbivores. Their subterranean tubers and inflorescences are valuable since their tubers can be made into different products and their inflorescences are visually impressive,

Table 1. Eigenvectors for PCA analysis.

	Principle component1	Principle component 2
<i>A. bufo</i> adult	0.46768	−0.43021
Other neighbouring species	0.42650	−0.57856
<i>A. bufo</i> juvenile	0.50514	0.11226
<i>A. bufo</i> seedlings	0.44971	0.41408
Background	0.37678	0.54417

combined with its carrion odor. *Amorphohallus bufo* is one of the little-known species growing in the Malaysian tropical rain forest.

The leaf spectral reflectance results were mainly focused on visible light (400 nm to 700 nm wavelength) and part of infrared light (700 nm to 750 nm wavelength). The leaf structure and composition determined the spectral reflectance patterns. Generally, the upper layer of leaves, which is called the palisade parenchyma, contains most of the chlorophyll and other pigments. They are responsible for absorbing the blue (400 nm to 500 nm) and red (600 nm to 750 nm) light. However, green light with wavelengths between 500 nm to 600 nm is weakly absorbed, which is why the majority of normal leaves are green based on human perception. The spectral reflectance curve of *A. bufo* and other seedling plants matched with this general green color pattern very well. Their pattern is more similar to each other than compared to others. Both curves started to rise around 500 nm wavelength, peaking at 550 nm and decreasing after 550 nm.

Our results suggest that the leaves of other neighboring seedling plant species and the adult *A. bufo* leaves both absorb blue and red light, but reflect most of green light, giving an appearance of normal green color. However, the spectral curve of *A. bufo* seedlings, the background (and *A. bufo* juveniles did not show any peak from wavelengths between 500 nm to 600 nm. All the three curves were almost similar and hardly distinguishable from each other. It can be inferred that *A. bufo* seedling and juvenile leaf colors are very similar to the background colors. Therefore, the seedlings and juveniles of *A. bufo* would remain inconspicuous. Another obvious pattern observed was the spectral curve above 700 nm wavelength. All the plant components showed a dramatic increase while the background curve did not. The near infrared light penetrates the palisade parenchyma and reaches the lower level of leaves (the spongy parenchyma). There are many irregular shaped cells inside this spongy parenchyma and extensive air spaces exist between those cells for gas circulation. Those air spaces randomly reflect any light above 700 nm wavelength.

The majority of the leaves from other neighboring plants were green in color due to chlorophyll and other pigments maximizing the efficiency of photosynthesis. Therefore, red colored leaves in some plants may be considered as a handicap. Red pigments exert extra production costs to the plant while reducing the efficiency of photosynthesis. The red color in the leaves is usually derived from two components, anthocyanins and betalains. Betalains only exist in certain plant species of the order Caryophyllales while anthocyanins can be found in almost all the flowering plants.²⁷

There are various hypotheses explaining why plants produce anthocyanin pigments. The commonly discussed hypothesis is the photoprotective role of anthocyanins: it helps plants to reduce photoinhibition and photobleaching.^{30,20} Photoinhibition is a phenomenon where the efficiency of photosynthesis declines when there is excess of light. Anthocyanins, considered as a sunscreen, reduce the penetration of sunlight radiation into the leaves, which prevents over-excitation.²⁷ However, experimental results were inconclusive. Photoinhibition experiments on green versus red color varieties showed that red leaf varieties, containing anthocyanins in their upper epidermis, were less damaged by UV radiation than green leaf varieties, which

suggested that anthocyanins were protective.² However, Krause et al.¹⁹ suggested that the xanthophyll cycle pigments, rather than anthocyanins, were responsible for helping young leaves to protect the photosynthetic apparatus in tropical forests. Furthermore, experiment on juvenile leaves of *Syzygium* showed that the isolated anthocyanins absorbed little UV radiation, which suggested that anthocyanin does not provide a photoprotective function.³⁴ Manetas²⁷ also suggested that the optical properties of anthocyanins may not be suitable for sunscreen protective function.

A. bufo is a relatively short plant that grows in the understory of tropical forest. Since the light intensity is quite low at the understory level of tropical forests, the necessity of an understory plant to protect its leaves from excessive light may not be high. However, Gould et al.¹⁰ claimed that understory leaves in low light intensity areas have enriched the photosynthetic apparatus (PSII), which are more vulnerable to photoinhibition and may be more easily damaged by brief flecks of sunlight. The ratio of green leaves against red leaves plant species does not support this hypothesis since the majority of understory plant species leaves are green. Furthermore, the adult *A. bufo* leaves change from dark red to green while still remaining an understory species. If the red pigment functions as sunscreen to prevent sunflecks from damaging the photosynthetic apparatus, adult leaves should remain red throughout their ontogeny.

Apart from the theory of photoprotective function, another hypothesis about anthocyanins is aposematism. Bright (red) color may serve as a warning signal to herbivores and plants' bright coloration may signify that that part of the plant is not palatable.^{21,23,25} Hamilton and Brown²¹ proposed that autumn trees' bright coloration, which is made of costly pigments, serves as a handicap signal so that individual trees can exhibit a defensive commitment against colonizing aphids. Furuta⁹ found that the female maple aphid (*Periphyllus californiensis* Shinji) prefers to colonize on orange-yellow leaves but lays fewer eggs on red colored leaves. This phenomenon was also observed in other tree species. An increased autumn coloration in the mountain birch (*Betula pubescens*) is correlated with a decreased insect damage.¹²

In tropical rainforests, young leaves of a few *Shorea* species (Family: Diptocarpaceae) are red or purple. The colors fully change to green when the leaf is fully extended. This mechanism is called delayed-greening. Numata et al.²⁹ found that delayed-green leaves suffered less insect damage than normal green leaves. Manetas²⁷ argued that this may come from the co-evolution between chlorophyllous leaves and folivorous insects since chlorophyll is the major pigments absorbing blue and red color but reflects green color. Hence, insect vision is more tuned towards green color. Most insects lack the long wavelength (red) photoreceptors in their eyes making them less aware of the red color.¹⁷ Therefore, red leaves may hardly be distinguishable by insects.²⁷ The existence of anthocyanins is always associated with phenolics which can deter many kinds of general herbivores since they are bitter and bad for digestion.²⁹ Karagergou and Manetas²⁷ found that the high level of phenolics in the young leaves of *Quercus coccifera* is correlated with high concentration of anthocyanins and green leaves suffered greater damage by herbivores compared to red leaves. Furthermore, it was also hypothesized that red colored leaves

can disrupt green colored insect's camouflage causing them to be easily captured by their predators.²⁶

The coloration of *Amorphophallus bufo* seedlings is likely to conform to the camouflage hypothesis. Cryptic red/ dark colored leaves are less discernible to some invertebrate herbivores due to the lack of red photoreceptors in their eyes.⁵ The dull coloration of *A. bufo* leaves, likely caused by anthocyanins and chlorophyll, are similar to the drab colored young leaves in some Malaysia palms.³¹ *Macaranga* plants, which are usually found within the vicinity of *A. bufo*, protect themselves with the help of ants (myrmecophyte).¹⁴ However, one particular species, (*M. bancana*) also use camouflage as defensive strategy during the seedling stage in which no ant could establish a colony to provide protection.⁸ *Corydalis benecincta*, an alpine plant in Yunnan, China also shows a cryptic strategy. The grey colored leaf variety showed less herbivory compared to the green colored variety. It was shown that their main herbivore, (*Parnassius* butterflies) can hardly distinguish grey-colored leaves against the alpine grey background.²⁸ Since the coloration of seedling leaves of *A. bufo* resembles the coloration of the background of soil and debris, we hypothesize that they use cryptic coloration to avoid herbivores during the seedling stage. There are also several other hypotheses concerning anthocyanins function. For example, anthocyanin can protect young leaves from damage by fungi.⁵ It can also protect leaves from ultraviolet radiation and a good source of antioxidants (Gound,^{11,27} These hypotheses might also apply to *A. bufo*, but further experiments are needed in the future.

After *A. bufo* has reached the adult stage, their leaves are about 30 cm above the ground. The adult leaves change to a normal green color similar to other neighboring plants. During this stage, the protective strategies of *A. bufo* are still unknown. However, the numerous tiny black spots on the petiole and rachises (Fig. 4a, b) suggest a unique form of mimicry. We propose that the black spots on the surface of petiole and rachises are an ant-mimicry pattern, which serves as a warning signal to deter herbivores. Mimicry is very common in the animal kingdom, however, it is often neglected in the plant kingdom. Dafni⁴ discussed how certain species of flowers of orchids that mimic female insect and thereby attract male insects. Such mimicry is termed as pseudocopulation. Nevertheless, Lev-Yadun and Inbar²⁴ argued that the plant may mimic animals to deter herbivores. For example, black spots on the stem and branches of *Xanthium trumarium* (Asteraceae) resemble ants swarming on the plants.²⁴ Flowers of many *Passiflora* species also express many dark spots and short strips, which serve as a type of Bastesian ant mimicry to prevent herbivores from eating the flowers.²² This mimetic strategy may either reduce the chance of colonization by herbivore insects or deter feeding behaviour of megaherbivores.²⁴

Although similar hypotheses have never been proposed for a tropical plant species, here we propose that the black spots on *A. bufo* may serve a similar function. The appearance of a swarm of ants climbing might be able to deter herbivores from eating the plant. Butterfly egg mimicry on *Passiflora* leaves suggested that the mimicry may reduce the eggs laid by butterflies.³³ The black spots of *A. bufo* are mainly located underneath the leaves. Large bodied herbivores would be less likely to notice the black spots. We noticed there were many other myrmecophyte plants



Figure 4. 4a: Numerous black spots on the petiole of an adult *A. bufo*. **Figure 4b:** Black spots of the rachis of an adult *A. bufo*. **Figure 4c:** The folded rachis of the *A. bufo* seedling in the plant house. The second clump of rachis opened up a little, but the leaves remained pointed upwards and did not fully extend as compared to the ones in the natural forest condition. **Figure 4d:** The picture of the same plant a few months afterwards. The second clump of the rachis did not fully open, while still retaining the transitional dark from juvenile to adult color.

(*Macaranga* and a few species of rattan plants) growing near *A. bufo*. Some of them were colonized by aggressive ants. Large herbivores may have experience of being attacked by ants when they are foraging in this area. In this case, pretending to be swarmed with ants while growing in an area with ant defended plants may be very advantageous for *A. bufo*.

Although *A. bufo* grows in abundance in the wild, transplanting them in the green house proved to be very tricky. Only a single individual managed to thrive in our greenhouse and this particular plant underwent a drastic change in its growth pattern (Fig. 4c, d). This *A. bufo* grew very fast and did not expand its rachises or leaves, although the seedling leaf colors remain dark (Fig. 4c). All the rachises were pointing up so that all black spots could easily be seen. It only started to expand its leaves after the leaves were green in color and its reached the adult height. By this strategy, the *A. bufo* may reach the adult stage in a short time and display the most warning signals during the vulnerable seedling and juvenile stage. It can be inferred that *A. bufo* may choose different growth strategies as the environment changes. However, our observation currently remains anecdotal as we lack the number of plants to verify this. We are currently recreating the transplanting experiment.

During our observations, we did not find any herbivores consuming *A. bufo*. There was little damage on the surface of the leaves, which may have been caused by insect herbivores.

Currently, very little is known about *A. bufo*, and we acknowledged that there may be other simultaneous defensive strategies that could be used by this species. Future studies may focus on the cost of red color pigment production, and photosynthesis performance.

Conflict-of-interest and financial disclosure statements

All the authors hereby state that we have no conflict of interest. This project is funded by USM RU grant 1001/PBIOLOGI/811329 and 1001/PBIOLOGI/811330.

Acknowledgment

This project is funded by USM RU grant 1001/PBIOLOGI/811329 and 1001/PBIOLOGI/811330. We thank Syed Ahmad Edzham for helping with the sample collection. We would like to thank Prof Simcha Lev-yadun for his comments in improving the manuscript.

ORCID

Nik Fadzly  <http://orcid.org/0000-0002-6282-8423>

Asyraf Mansor  <http://orcid.org/0000-0003-1255-7239>

References

1. Beath DD. Pollination of *Amorphophallus johnsonii* (Araceae) by carrion beetles (*Phaechroux amplus*) in a Ghanaian rain forest. *J Trop Ecol.* 1996;12:409–418. doi:10.1017/S0266467400009603.
2. Burger J, Edwards GE. Photosynthetic efficiency, and photodamage by UV and visible radiation, in red versus green leaf coleus varieties. *Plant Cell Physiol.* 1996;37:395–399. doi:10.1093/oxfordjournals.pcp.a028959.
3. Chua M, Baldwin TC, Hocking TJ, Chan K. Traditional uses and potential health benefits of *Amorphophallus konjac* K. Koch ex NE Br. *J Ethnopharmacol.* 2010;128:268–278. doi:10.1016/j.jep.2010.01.021.
4. Dafni A. Mimicry and deception in pollination. *Annu Rev Ecol Syst.* 1984;15:259–278. doi:10.1146/annurev.es.15.110184.001355.
5. Dominy NJ, Lucas PW, Ramsden LW, Riba–Hernandez P, Stoner KE, Turner IM. Why are young leaves red? *Oikos.* 2002;98:163–176. doi:10.1034/j.1600-0706.2002.980117.x.
6. Fadzly N, Burns KC. Hiding from the ghost of herbivory past: evidence for crypsis in an insular tree species. *Int J Plant Sci.* 2010;171:828–833. doi:10.1086/654850.
7. Fadzly N, Jack C, Schaefer HM, Burns KC. Ontogenetic colour changes in an insular tree species: signalling to extinct browsing birds? *New Phytol.* 2009;184:495–501. doi:10.1111/j.1469-8137.2009.02926.x.
8. Fadzly N, Zuharah WF, Mansor A, Zakaria R. Cryptic coloration of *Macaranga bancana* seedlings: A unique strategy for a pioneer species. *Plant Signal Behav.* 2016;11:e1197466. doi:10.1080/15592324.2016.1197466.
9. Furuta K. Host preference and population dynamics in an autumnal population of the maple aphid, *Periphyllus californiensis* Shinji (Homoptera, Aphididae). *J Appl Entomol.* 1986;102:93–100. doi:10.1111/j.1439-0418.1986.tb00896.x.
10. Gould KS, Kuhn DN, Lee DW, Oberbauer SF. Why leaves are sometimes red. *Nature.* 1995;378:241–242. doi:10.1038/378241b0.
11. Gould KS. Nature's Swiss army knife: the diverse protective roles of anthocyanins in leaves. *BioMed Res Int.* 2004;5:314–320.
12. Hagen SB, Folstad I, Jakobsen SW. Autumn colouration and herbivore resistance in mountain birch (*Betula pubescens*). *Ecol Lett.* 2003;6:807–811. doi:10.1046/j.1461-0248.2003.00496.x.
13. Hetterscheid WLA, Ittenbach S. Everything you always wanted to know about *Amorphophallus*, but were afraid to stick your nose into. *Aroideana.* 1996;19:7–131.
14. Itioka T. Diversity of anti-herbivore defenses in *Macaranga*. In: Roubik D, Sakai S, Hamid Abg A, editors. *Pollination Ecology and the Rain Forest.* New York, NY: Springer; 2005. pp. 158–171.
15. Karageorgou P, Manetas Y. The importance of being red when young: anthocyanins and the protection of young leaves of *Quercus coccifera* from insect herbivory and excess light. *Tree Physiol.* 2006;26:613–621. doi:10.1093/treephys/26.5.613.
16. Kavanagh PH, Shaw RC, Burns KC. Potential aposematism in an insular tree species: are signals dishonest early in ontogeny? *Biol J Linnean Soc.* 2016;118:951–958. doi:10.1111/bij.12785.
17. Kelber A, Vorobyev M, Osorio D. Animal colour vision–behavioural tests and physiological concepts. *Bio Rev.* 2003;78:81–118. doi:10.1017/S1464793102005985.
18. Kite GC, Hetterscheid WL. Inflorescence odours of *Amorphophallus* and *Pseudodracontium* (Araceae). *Phytochemistry.* 1997;46:71–75. doi:10.1016/S0031-9422(97)00221-5.
19. Krause GH, Virgo A, Winter K. High susceptibility to photoinhibition of young leaves of tropical forest trees. *Planta.* 1995;197:583–591. doi:10.1007/BF00191564.
20. Lee DW, Gould KS. Why leaves turn red. *American Scientist.* 2002;90:524. doi:10.1511/2002.39.794.
21. Lev-Yadun S. Aposematic (warning) coloration associated with thorns in higher plants. *J Theor Biol.* 2001;210:385–388. doi:10.1006/jtbi.2001.2315.
22. Lev-Yadun S. Ant mimicry by *Passiflora* flowers. *Isr J entomol.* 2010;39:159–163.
23. Lev-Yadun S. Aposematic (warning) coloration in plants. In: *Plant-environment interactions. From sensory biology to active plant behavior.* Baluska F, editor. Berlin: Springer-Verlag; 2009. pp. 167–202.
24. Lev-Yadun S, Inbar M. Defensive ant, aphid and caterpillar mimicry in plants? *Biol J Linnean Soc.* 2002;77:393–398. doi:10.1046/j.1095-8312.2002.00132.x.
25. Lev-Yadun S, Inbar M, Izhaki I, Dafni A. Colour patterns in vegetative parts of plants deserve more research attention. *Trends Plant Sci.* 2002;7:59–60. doi:10.1016/S1360-1385(01)02190-2.
26. Lev-Yadun S, Dafni A, Flaishman MA, Inbar M, Izhaki I, Katzir G, Ne'eman G. Plant coloration undermines herbivorous insect camouflage. *BioEssays.* 2004;26:1126–1130. doi:10.1002/bies.20112.
27. Manetas Y. Why some leaves are anthocyanic and why most anthocyanic leaves are red? *Flora-.* 2006;201:163–177. doi:10.1016/j.flora.2005.06.010.
28. Niu Y, Chen G, Peng DL, Song B, Yang Y, Li ZM, Sun H. Grey leaves in an alpine plant: a cryptic colouration to avoid attack? *New Phytologist.* 2014;203:953–963. doi:10.1111/nph.12834.
29. Numata S, Kachi N, Okuda T, Manokaran N. Delayed greening, leaf expansion, and damage to sympatric *Shorea* species in a lowland rain forest. *J Plant Res.* 2004;117:19–25. doi:10.1007/s10265-003-0126-2.
30. Steyn WJ, Wand SJE, Holcroft DM, Jacobs G. Anthocyanins in vegetative tissues: a proposed unified function in photoprotection. *New Phytologist.* 2002;155:349–361. doi:10.1046/j.1469-8137.2002.00482.x.
31. Stone BC. Protective coloration of young leaves in certain Malaysian palms. *Biotropica.* 1979;11:126–126. doi:10.2307/2387788.
32. Strauss SY, Cacho NI, Schwartz MW, Schwartz AC, Burns KC. Apparency revisited. *Entomologia Experimentalis et Applicata.* 2015;157:74–85. doi:10.1111/eea.12347.
33. Williams KS, Gilbert LE. Insects as selective agents on plant vegetative morphology: egg mimicry reduces egg laying by butterflies. *Science.* 1981;212:467–469. doi:10.1126/science.212.4493.467. PMID:17802547.
34. Woodall GS, Stewart GR. Do anthocyanins play a role in UV protection of the red juvenile leaves of *Syzygium*? *J Exp Bot.* 1998;49:1447–1450.