A BERRY COLOR DIMORPHISM IN A NEW SPECIES IN THE FAMILY *ERICACEAE*

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Abstract: The majority of plant color dimorphisms on record are floral dimorphisms, often with each morph having a different reproductive strategy. Fruit polymorphisms are very rare, but potentially important for the seed dispersal strategies of some species. In the páramo of Costa Rica, we found a previously unrecorded species of the family *Ericaceae*, temporarily named *Pernettya saelyeae*. The plant exhibited two berry color morphs, with either red or white mature berries. We recorded the locations of individual plants of both color morphs across seven 30 m x 30 m grids and measured mean mass per berry and mean seeds per berry of each plant. Each color morph was highly aggregated, and percent composition of white morphs was higher in sites with less ground cover. We found that red-berried plants had fewer seeds per berry and invested more berry mass per seed than in white-berried individuals.

Key Words: Pernettya saelyeae, Pernettya prostrata, *berry color dimorphism, Costa Rica, páramo, new species*

INTRODUCTION

Flower color polymorphisms have long been a subject of fascination for botanists. Many plants exhibit environmentally or genetically driven floral color dimorphisms, with fitness tradeoffs between resource allocation and pollinator preference (Jones and Reithel 2001). For example, several plants from the Heliconiaceae family have developed flower color dimorphisms, corresponding to male and female hummingbird nectar reward preferences and energetic requirements (Temeles and Kress 2003). Color polymorphisms can be maintained in plant populations through environmental heterogeneity (Warren and Mackenzie 2001) or by geographic isolation of conspecifics (Schemske and Bierzychudek 2001). While flower color dimorphisms have been extensively documented, dimorphisms of fruit color are rarely reported.

The color of a fruit is essential in its ability to attract effective seed-dispersers while inhibiting visitations from fauna who are poor seed-dispersers (Wheelwright and Janson 1985). Fruit pigmentation also has physiological effects, such as thermal regulation (Willson and Whelan 2001). Color polymorphisms in fruit are hypothesized to be maintained by environmental heterogeneity, with berry pigmentation often varying between stressed and non-stressed plant environments (Mandak and Pysek 1999).

In January of 2007, local conservationists Andrew and Satyia Saelye introduced us to a potential new species of plant in the family Ericaceae on the páramo in the San José province of Costa Rica, which they tentatively named *Pernettya saelyeae* (common name "banapple"). *Pernettya saelyeae* was previously thought to be of the species *P. prostrata*, a Central American shrub with purple berries poisonous to humans in all of its hybrids (Vindas, 2003). However, Andrew and Satyia asserted that the *P. saelyeae* berry was edible and therefore not *P. prostrata*. The authors consumed several hundred berries each and did not get sick, corroborating their assertion.

An interesting, salient characteristic of *Pernettya saelyeae* is that different individual plants exhibit either fully red or fully white berry pigmentations. We noticed immature green berries on both color morphs, and never found a plant that had both fully red and fully white berries on it. This provided evidence against the two colors being developmental stages of the same morphotype. We hypothesized that there was indeed a color dimorphism in *P. saelyeae*, and that the morphs differ in local distribution. Because fruit color polymorphs are often maintained by variation in environmental conditions, we expected individual plants with the same berry color morph to be aggregated in microhabitats. We predicted (1) that the morphs would be aggregated in patches by fruit color and (2) that there would be some difference in mass per seed and seeds per berry between individuals of the two berry morphs as it related to potential seed dispersers. We had previously observed that white berries appeared to be seedier, while red berries appeared to be sweeter, perhaps indicating some dichotomy in seed dispersal strategies.

METHODS

Study system.

Pernettya saelyeae is a dominant shrub in areas above treeline in the Talamanca mountain range of Costa Rica. Hence, the páramo region of Chirripó National Park in Costa Rica on 28-29 January 2007 (during the dry season) proved a good study site to record *P. saelyeae* dimorphic aggregations.

Field Methods.

We haphazardly chose a 30 m x 30 m quadrat in the páramo region of Chirripó National Park where *P. saelyeae* were present. We recorded the location of each *P. saelyeae* individual within this quadrat as a grid coordinate, noting berry pigmentation (red, white, or immature) of the plant, number of branches on the plant, and plant height (cm). For each of the 76 plants recorded within the 30 m x 30 m

grid, we collected ten representative berries and measured mass per berry (g) and counted seeds per berry to determine any differences between color morphs. For each plant, we calculated mean mass per berry and seeds per berry. We used these data to calculate mean berry mass per seed for each plant.

To examine aggregations and abundances of *P. saelyeae* berry color morphotypes across the páramo, we haphazardly chose six additional 30 m x 30 m quadrats where we recorded the location and berry pigmentation of each fruiting *P. saelyeae*. For each quadrat, we observationally recorded vegetative ground cover. Each quadrat was considered to have uniform vegetative cover (dense cover, medium cover, or clear). We defined quadrats with dense cover as those which were overgrown with woody tussock grasses, while medium cover areas were covered only by small herbaceous plants, and clear areas were composed of either human-made trails or large areas of open earth. In one quadrat with a very clear human-made trail (quadrat 7), we also measured the distance from each plant to the trail. We created X-Y plots for each quadrat using the coordinates of each *P. saelyeae* plant sampled, distinguishing plants of each berry morphotype. We sampled 513 total plants in all 7 quadrats, and calculated the relative abundance of each berry morph on the páramo. During this process, we dug holes around what appeared to be several individual plants to be certain that there were no roots connecting multiple individuals.

We also collected 50 mature berries of each color for human taste preference trials conducted at La Estación Biología at Cerro de la Muerte on 30 January 2007. Fifteen volunteer subjects blindly sampled two berries (one red, one white), and then stated their taste preference. We conducted two trials per individual, flipping a coin to determine the color sequence in each trial.

Statistical analysis.

We visually assessed the data from our 7 quadrats to determine whether the berries were obviously spatially aggregated by color. We performed a chi-squared test on the number of red-berried and white-berried individuals in grids with each level of vegetative ground cover to determine if ground cover influenced percent composition of red-berried and white-berried plants. To look at plant morphotype distribution on a smaller scale as it relates to vegetative ground cover, we used a two-tailed t-test to analyze the distance of each individual from a man-made trail in grid number seven. Ground cover decreased as one approached the trail. Analysis of all seven quadrats examined berry morphotype aggregation by ground cover across the páramo, while

analysis of quadrat 7 took a detailed look at the gradient of ground cover in a small section of the páramo.

We used a MANOVA to test whether there was a difference in mean berry mass, mean seeds per berry and mean berry mass per seed between the two berry color morphs. The model was statistically significant, which allowed us to use two-tailed t-tests (assuming unequal variance) to individually compare the mean berry mass, mean seeds per berry and mean berry mass per seed between the two berry color morphs. We used a chi-squared test to analyze taste preference of berry color of the 15 experimental subjects.

RESULTS

We found 407 (79% of total individuals) red-berried and 92 (18%) white-berried *P. saelyeae* individuals in our seven 30 m x 30 m grids on the páramo, with 14 (3%) additional individuals with pre-mature berries.

It is visually apparent that the color morphs of *P. saelyeae* aggregate into distinct clusters (Fig. 1). We found that there was a greater proportion of white-berried individuals in quadrats with less ground cover ($X^2_{4,507}$=46.493, P<.0001, Fig. 2). This lends more support to the idea of microhabitat segregation, suggesting that the white berries are relatively more common in clear areas. In quadrat 7, which had a high density of *P. saelyeae* plants as well as a trail transecting it, we found that white plants were, on average, 35% closer to the trail than the red plants (t_{151}=3.69, P=0.0003). White plants were on average 6.24 meters from the trail, while red plants were on average 9.54 meters from the trail.

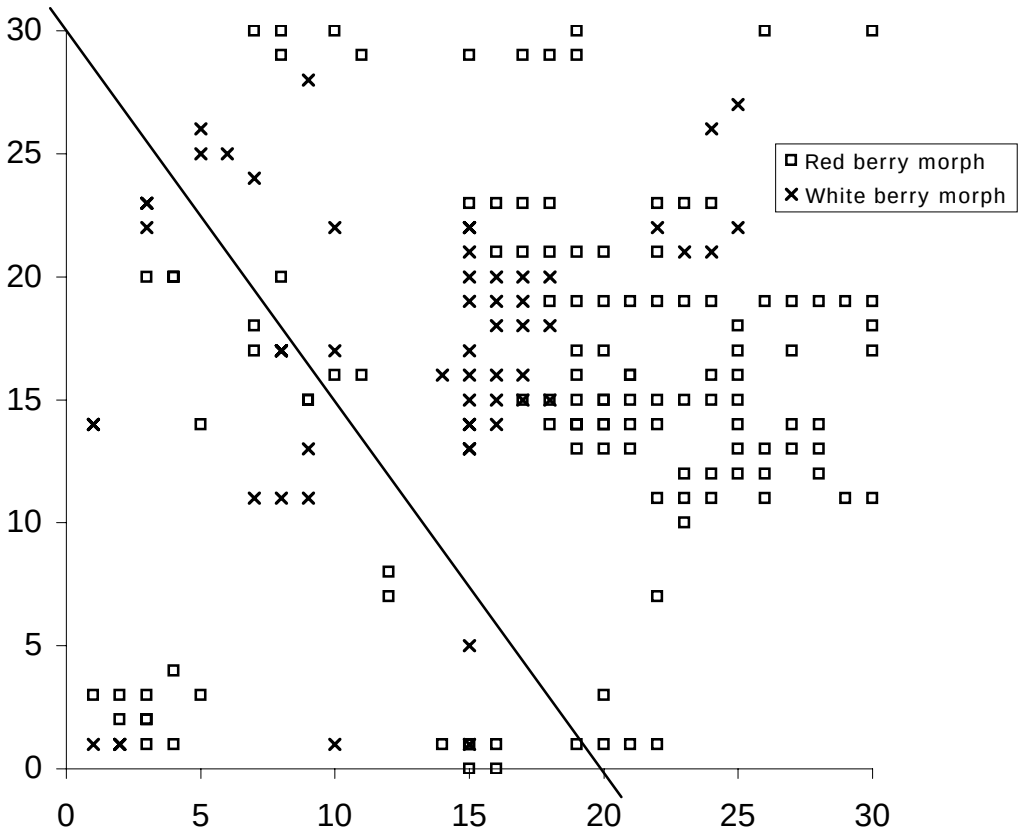

Figure 1. Distribution of *Pernettya saelyeae* berry color morphotypes (red and white) in a 30 by 30 meter grid. The solid line in this figure represents the man made path running through quadrat 7. The number of white morphs and red morphs present are N=57 and N=99, respectively. Bold squares represent two data points.

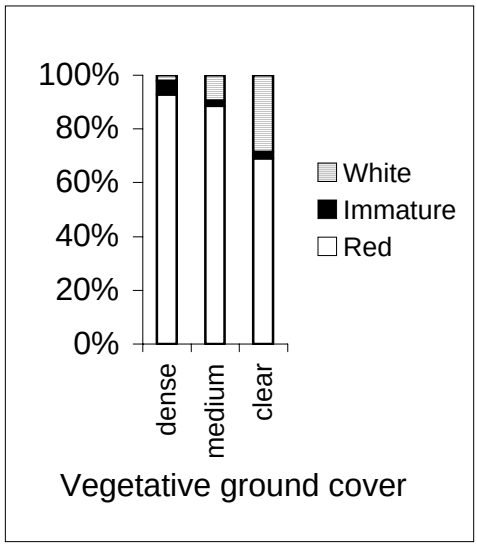

Figure 2. Percentage of *Pernettya saelyeae* berry color morphotypes and individuals with immature berries (white, red, and immature) in seven quadrats at different levels of vegetative ground cover (dense, medium, and clear). As the vegetative ground cover level decreased, the relative percentage of white plants to red plants increased. Total sample size of plant individuals was N=516.

We found significant differences in berry mass, seeds per berry, and berry mass per seed between the two berry morphs (MANOVA: $F_{3, 36}$=1.12, P<.0001). We found no significant difference between the mass of white berries (mean ± 1 SE=0.77 ± 0.078 grams) and red berries (mean ± 1 SE=0.78 grams ± 0.078) ($t_{26.85}$=0.46, P=0.65). However, the standard deviation of the masses of red berries (.43 grams) was nearly twice that of the masses of white berries (.23 grams) ($F_{1,38}$=.935, P=.0041). We found that the white berries contained 23% more seeds than red berries ($t_{33.36}$=4.51, P<0.0001); red berries contained a mean of 29.10 ± 1.57 seeds, while white berries contained a mean of 37.61 ± 1.06 seeds. Furthermore, red berries had 35% more berry mass per seed than white berries ($t_{27.65}$=5.59, P<0.0001). Red berries contained a mean of 0.004276 ± 0.00017 grams of berry per seed, while white berries contained a mean of 0.003191 ± 0.00009 grams of berry per seed.

Finally, in the human berry preference test, red was preferred in 81% of the trials, while white was preferred in 19% of the trials (X^2_1= 9.85, P=.002). In 23 out of 28 trials, the red berry was preferred, while white berries were preferred in only 5 trials.

DISCUSSION

Fruit color polymorphisms are not yet well understood. While dimorphic flowers are commonplace, distinct fruit phenotypic differences in conspecifics are not. Our observation that white and red berries never co-occur on the same individual plant and that immature green fruit are on both plants supported the possibility of a berry color polymorph. Both morphotypes transition though a pinkish pre-mature phase; berries turn their mature color starting from the side opposite their stipule, where their flower dropped from their inferior ovary. These morphotype-specific development observations suggest that there is a color dimorphism in the fruits of *P. saelyeae.* The lack of knowledge about this dimorphic fruit exists in more than just the biological community. Satyia Saelye stated that even local people in the area were unaware that this berry was edible, and confused it with its poisonous relative, *P. prostrata*, also present in the páramo zone.

In our visual analysis of our grid data, we found distinctly segregated clumps of red and white-berried plants, supporting our prediction that the plants would be spatially aggregated by color. This suggests that there are factors such as different microenvironments or

local dispersal patterns that favor the different color morphs. Interestingly, there was a much greater abundance of red-berried morphs than white, even in areas clear of vegetative cover, where white-berries were found in greatest abundance.

The distinctive traits of the two berry morphs may illuminate reasons for this difference in berry color morph abundance. We found a high density of approximately 130 *P. saelyeae* seeds in a single pellet of excrement of a grey junco bird, indicating that birds are an important disperser for this fruit. Although tropical birds vary in their visual preferences for fruit pigmentation, an overwhelming number of studies have found that red is the most common color for bird-dispersed fruits in neotropical regions (e.g., Wheelright and Janson 1985, Janzen 1983). This may mean that the red berries are more likely to be dispersed and possibly that red individuals have higher reproductive success. However, Willson *et al.* (1990) showed that when frugivorous birds are presented with fruits of equivalent nutritional value, they did not show a strong preference for red fruit over other colors. Therefore, color alone may not predict preference and subsequent dispersal rates between the two morphs.

From a disperser perspective, mass of the fruit's mesocarp should be important in foraging preference. Although the mean mass of mature berries between the two berry color morphs were equal, red berries had 35% more berry mass per seed than white berries. This red coloring is therefore probably an honest signal of rewards to a potential seed disperser, and the larger mesocarp in the red morph should create a frugivorous bird preference for red berries over white berries.

Although local dispersal patterns could predict berry color morph aggregations in space, it does not explain why relatively more white-berried individuals are found in areas with less vegetative cover. While some fruiting plant species always produce white fruits, other species produce white fruits only when the plant is under stress (Mandak and Psyek 1999). Stress-induced white pigmentation of fruits has previously been studied in apple cultivars, specifically involving light-stress. This bleaching has been hypothesized to be a result of decreased anthocyanin production. Typically, anthocyanin functions to sequester light energy internally, protecting fruit tissues from high light intensities (Merzlyak *et al.* 2003). At an altitude above 11,000 feet, plants in the páramo have a number of adaptations for the sun. Many plants have rosette formations for indirect deflection of heat. Others have white sheens acting as a "sunscreen," providing protection from intense sunlight. The red berry

morphs of *P. saelyeae* may be a similar adaptation for the high light intensity. Sun-protective anthocyanin production may only be available in areas of high soil nutrient content, which may explain why red berry morphs are found in areas with denser vegetative cover.

It is also possible that genetics plays a role in the berry color morph distribution of *P. saelyeae*. If this is case, anthropogenic factors could contribute to the high aggregation of white-berried individuals in areas with low ground cover such as near the main trail. We found that our volunteers greatly preferred red berries, and thus, human consumption of these red berries along the trail may lead to unsuccessful red berry dispersal in this area. With many tour groups visiting the páramo every week, it seems likely that anthropogenic factors play a role in the distribution of this common fruiting plant.

Our study was not able to determine whether *P. saelyeae* berry color morphotypes are environmentally induced, heritable, or both. To augment our study, future experiments could include growing *P. saelyeae* under different light intensities as well as cross-breeding individuals to look for Mendelian or more complex genetic patterns involved in determining berry morphotype. Knowledge of this newly described plant could contribute to the relatively new field of research on the adaptability and evolution of fruit color morphisms.

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