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Inheritance of Leaf Spots and Their Genetic Relationships with Leaf Shape and Vein Color in Caladium

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Abstract. The ornamental value of caladium (*Caladium ×hortulanum* Birdsey) depends to a large extent on its foliar characteristics. Efficient genetic improvement of caladium foliar characteristics requires a good understanding of the inheritance of these traits, including leaf shape, color, and spots. This study was conducted to determine the inheritance of leaf spots in caladium and to understand their relationships with leaf shape and main vein color. Eighteen controlled crosses were made among eight commercial cultivars expressing red or no leaf spots, and progeny of these crosses were observed for segregation of leaf spots as well as leaf shape and vein color. A single locus with two alleles is shown to be responsible for the presence or absence of leaf spots in caladium, with the presence allele (*S*) dominant over the absence allele (*s*). The major spotted commercial cultivar Gingerland is heterozygous for this trait. Leaf spots are inherited independently from leaf shape, but they are closely linked with the color of the main leaf veins. The recombination frequencies between the leaf spot locus and the main vein color locus ranged from 0.0% to 8.9% with the crosses or the parental cultivars used, with an average of 4.4%. Leaf spots and vein colors represent the first linkage group of ornamental traits in caladium and possibly in other ornamental aroids. The knowledge gained in this study will be valuable when it comes to determine what crosses to make for development of new cultivars. It may be also useful to those interested in determining the inheritance of similar traits in other ornamental plants, including other ornamental aroids such as dieffenbachia (*Dieffenbachia* Schott).

Caladiums are ornamental aroids widely grown as pot plants or used in landscapes as accent or border plants. Commercial pot caladium plants are produced by forcing tubers, while dry tubers are available for garden or landscape planting (Evans et al., 1992). More than 95% of the caladium tubers used in the world for container forcing and dry sales are produced in Florida (Deng et al., 2005b). Pioneering breeding of caladium occurred in Europe in the 1860s, but since the beginning of the 20th century, breeding of this crop has been conducted primarily in Florida (Wilfret, 1993). It is generally believed that cultivated caladiums (*C. ×hortulanum*) resulted from intraspecific or interspecific hybridizations among several *Caladium* Vent. species, including *Caladium bicolor* (Aiton) Vent., *Caladium marmoratum* Mathieu, *Caladium picturatum* C. Koch, and *Caladium schomburgkii* Schott, which are native to the tropical regions of South America and Central America (Birdsey, 1951; Hayward, 1950; Wilfret, 1993). Caladiums are diploids with $2n = 2x = 30$ chromosomes (in Darlington and Wylie, 1955). They seem to be quite heterozygous genetically (Z. Deng, personal observation), which is expected as all commercial cultivars are asexually propagated through tuber division (Wilfret, 1993).

The ornamental value of caladium in the container or in the landscape depends, to a large extent, on its leaf characteristics, including leaf shape, color, and color pattern. Improving these characteristics or creating novel combinations of these characteristics has been one of the most important objectives in caladium breeding (Deng and Harbaugh, 2006; Wilfret, 1993). Often, more than 10 years are needed to develop a new caladium cultivar that is acceptable to both field growers engaged in large-scale commercial production of caladium tubers and to greenhouse growers producing pot caladium plants. To improve breeding efficiency and shorten this long breeding process, it has become increasingly important to have a good understanding of the mode of inheritance of major morphological and physiological traits that determine the ornamental and production values of caladium. Information of this kind can assist breeders in choosing appropriate parents and parent combinations, determining population sizes, and developing applicable screening or selection schemes.

In caladium, leaf shape has been shown to be controlled by one locus with two codominant alleles (Deng and Harbaugh, 2006; Wilfret, 1983, 1986) and main vein color by an independent locus with three alleles (Deng and Harbaugh, 2006; Wilfret, 1986). Leaf spots are another important trait involved in defining leaf color and coloration pattern. A number of major cultivars express leaf spots, resulting in intriguing coloration patterns on leaves with increase in ornamental and economic values. Tremendous efforts (at least in an aroid) have been made to understand the genetic control of leaf spots and their genetic relationship with other foliar traits. Based on the segregation of leaf spots and colors at the central leaf area in the progeny of a cross between two cultivars, Zettler and Abo El-Nil (1979) proposed that one locus controlled the vein color, vein pattern, and spotting in caladium and that 'Painter's Palette', a plant collected by W. Zettler from a homesite near Campville, FL (Gager, 1991), carried alleles *R* and *W* for its red and white spots, while

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'Poecile Anglais', a commercial cultivar, had the allele *R′* in a homozygous state for its red center on the leaf. Subsequently, Wilfret (1983, 1986) showed that caladium leaf vein pattern and color were controlled by separate genetic systems. To resolve this discrepancy, Gager (1991) performed crosses between 'Painter's Palette' and 'Aaron' or 'Florida Cardinal', sib-mated their progeny, and analyzed the segregation of leaf spots, spot color, and vein pattern. The conclusion was that a single locus controlled the expression of spotting, with two codominant alleles, S_R for red spots and S_W for white spots, and a recessive allele *s* for no spots. It was believed that both progeny with pink spots and progeny with red and white spots had the same genotype (S_R/S_W), but the former resulted from the overlapping of red spots and white spots at the same locations on the leaf, while the latter was due to the expression of red and white spots at different locations on the leaf (Gager, 1991). Gager speculated that there is a separate gene that controls the location of spots (isolated, border touching, or overlapping). However, the observed segregation deviated from the expected ratios in 21 out of 45 crosses. This was thought to be caused by the presence of a factor with lethal effects on genotype S_R/s, especially on genotypes S_R/S_R, S_W/S_W, and S_R/S_W. To understand the genetic relationship between veins and spots, the joint segregation of these two traits were analyzed (Gager, 1991). The observed ratios did not fit to the expected 9:3:3:1 because one of the four phenotype classes (green-veined, no spots) was always missing in the progeny. Again, it was suspected that some form of lethality was involved and caused the deviation.

The objectives of this study were to 1) understand the inheritance of leaf spots, 2) determine the genetic relationship of spots with leaf shape and vein color, and 3) determine the leaf spot, shape, and vein color genotype of several important caladium cultivars.

Color spots are expressed also on the leaves of several other major ornamental aroids, such as aglaonema (*Aglaonema costatum* N.E. Br.) and calla lily (*Zantedeschia* Spreng.), and on the flowers of important cut flowers, flowering pot plants, or bedding plants, such as alstroemeria (*Alstroemeria* L.), lily (*Lilium* L.), orchid (Orchidaceae), and pansy (*Viola* ×*wittrockiana* Gams.)/viola (*Viola cornuta* L.). Information on the inheritance of the spots in these ornamental crops is not available or very limited as well.

Materials and Methods

Plant material. 'Painter's Palette' was not commercially available (Bell et al., 1998; Deng et al., 2005b). In this study, we chose another spotted cultivar, Gingerland, and seven non-spotted cultivars (Table 1) as parents to perform crosses and to conduct the inheritance study. These cultivars have been used frequently also as breeding parents for improving caladium's stress tolerance and disease and nematode resistance. Pedigree information for all cultivars, except 'Florida Blizzard', was not available in the literature. 'Candidum' was first produced by Alfred Bleu in mid-1800s in France (Hayward, 1950). 'Gingerland' is dwarf and possesses a high level of sun tolerance (Z. Deng, personal observation), and 'Candidum' and 'White Christmas' are resistant to fusarium tuber rot caused by *Fusarium solani* (Mart.) Saa. (Goktepe et al., 2007), pythium root rot caused by *Pythium myriotylum* Drechs. (Deng et al., 2005a), and root-knot nematodes [*Meloidogyne incognita* (Kofoid and White) Chitwood] (Dover et al., 2005; McSorley et al., 2004). The leaf spot, shape, and vein color phenotype and inferred genotype of each parent are shown in Table 1.

Flower induction. Flower induction was performed with GA_3 as described previously (Deng and Harbaugh, 2004; Harbaugh and Wilfret, 1979) in Aug. 2004. Jumbo-sized tubers (6.4–8.9 cm diameter) were soaked in a GA_3 solution (ProGibb T&O; Valent BioSciences, Libertyville, IL) at a concentration of 600 mg·L^{-1} for 16 h at room temperature and potted in 20-cm-diameter containers (3.5 L in volume) filled with a commercial container mix (VerGro container mix A; Verlite Co., Tampa, FL). Parental plants were grown in a shaded glasshouse with 20% to 30% light exclusion under a natural photoperiod in Bradenton, FL. The temperature inside the glasshouse ranged from 15 to 32 °C. A trickle irrigation system was provided to the containerized plants.

Crossing. Hand pollination was conducted from 25 Oct. to 15 Nov. 2004 as described by Deng and Harbaugh (2004). Pollen was collected within several hours after being shed by the staminate flowers and stored in a refrigerator at 4 to 6 °C. Receptive pistillate flowers on the spadices were exposed by cutting off spathes with a scalpel and pollinated with pollen freshly collected or stored for 1–3 d, using clean camel-hair brushes. Pollinated flowers were tagged and bagged with nylon nets. Seeds were harvested at maturity (35–45 d after pollination).

Table 1. Phenotype and genotype (inferred) of eight commercial caladium cultivars used as parents for crosses performed in this study.

	Leaf spots		Leaf shape		Color of main vein	
Cultivar	Phenotype	Genotype[z]	Phenotype	Genotype[y]	Phenotype	Genotype[y]
Candidum	No	*ss*	Fancy	*FF*	Green	V^gV^g
Carolyn Whorton	No	*ss*	Fancy	*FF*	Red	V^rV^g
Fannie Munson	No	*ss*	Fancy	*FF*	Red	—[x]
Florida Blizzard	No	*ss*	Fancy	*FF*	White	V^wV^g
Frieda Hemple	No	*ss*	Fancy	*FF*	Red	V^rV^g
Gingerland	Yes	*Ss*	Lance	*Ff*	White	V^wV^g
Rosebud	No	*ss*	Fancy	*FF*	Red	V^rV^w
White Christmas	No	*ss*	Fancy	*FF*	Green	V^gV^g

[z]Inferred from this study.

[y]Genotypes of 'Candidum' and 'White Christmas' for leaf shape and vein color had been determined previously (Deng and Harbaugh, 2006), and they were confirmed again in this study. Genotypes for the rest of the cultivars (Carolyn Whorton, Fannie Munson, FL Blizzard, Frieda Hemple, Gingerland, and Rosebud) for leaf shape or vein color were inferred from this study.

[x]Fannie Munson seemed to behave somewhat differently in leaf main vein color from other cultivars, and its genotype information for vein color was not available.

Progeny growing. Seeds were sown 2 Dec. 2004 to 3 Jan. 2005 on the surface of the substrate (Verlite VerGrow container mix A) in 200-cell trays. Germination occurred at 21 °C inside a room under continuous light (cool fluorescent lights, 30 $\mu mol \cdot m^{-2} \cdot s^{-1}$). Seedlings were grown in the trays and under a mist system in a glasshouse until several true leaves formed. Plants were then individually transferred in early Mar. 2005 to six-pack plastic cells, which measured $3.5 \times 3.5 \times 5.5$ cm at top brim (≈45 mL in volume), and filled with the substrate (Verlite VerGrow container mix A) amended with 13N–6.4P–10.8K controlled-release fertilizer (Nutricote 13-13-13; The Scotts Co., Marysville, OH) at a rate of 7–9 granules/cell. Progeny were grown on the benches in a shaded glass greenhouse with 20% to 30% light exclusion, a *PPF* ranging from 600 to 800 $\mu mol \cdot m^{-2} \cdot s^{-1}$, under a natural photoperiod in Bradenton, FL. Irrigation was provided with an intermittent mist system, and the temperature was maintained in a range of 15 to 30 °C with cooling pads and fans.

Progeny in the six-pack cells were transplanted to raised field beds in mid to late June 2005. The soil was EauGallie fine sand with ≈1% organic matter and a pH of 6.2–6.8. The beds were fumigated with a mixture of methyl bromide and chloropicrin (67 : 33) at 196 $kg \cdot ha^{-1}$, mulched with white-on-black plastic, and irrigated with the seepage irrigation system (Geraldson et al., 1965). The beds were 91 cm wide and 20 cm high; caladium progeny were planted 25.4 cm apart in two rows on each bed. Fifteen grams of Osmocote controlled-release fertilizer (18N–2.6P–10K, 8–9 month; The Scotts Co.) was applied to each plant.

Data taken. Progeny were examined for leaf spots (spotted or nonspotted), leaf shape (fancy, lance, or strap), and main vein color (red, white, or green) June to Nov. 2006. Each plant was examined multiple times during this period of time. Altogether, >1400 individuals from 18 populations were phenotyped.

Statistics. χ^2 tests for goodness-of-fit were performed to compare actual ratios to expected ratios, while contingency χ^2 tests were conducted to examine the possibility of independence or linkage between traits. Contingency χ^2 tests were preferred for test of independence between traits, because these tests make no prior assumptions about segregation ratios (Guner and Myers, 2001). In addition, χ^2 tests also were performed to examine the populations for homogeneity in the joint segregation of leaf spots and shape. Calculation of the χ^2 values for goodness-of-fit, independence, and homogeneity, and their probabilities was conducted using the program Calculation for the Chi-Square Test developed by Preacher (2005). To calculate the recombination frequency between leaf spots and vein color, the recombinant progeny were identified and the number of these progeny was divided by the total number of progeny (recombinant + parental type progeny) in a population and multiplied by 100.

Results and Discussion

Inheritance of leaf spots. 'Candidum', 'Frieda Hemple', and 'Rosebud' have different leaf colors (white, red, and pink, respectively), but are all nonspotted (Table 1). Progeny from selfing of 'Candidum' did not show any spots; neither did progeny from 'Frieda Hemple' × 'Rosebud' (Table 2). These results suggest that nonspots were recessive and that these cultivars were homozygous. The inheritance of nonspotting was further examined in a different genetic background: nonspotted but blotched cultivars. 'White Christmas' and 'Florida Blizzard' show white blotches on leaves, while 'Carolyn Whorton' has pink blotches on leaves. They do not express leaf spots. None of their progeny (175 individuals) from selfing exhibited any spots on their leaves and neither did the progeny (131 individuals) from crosses between them ('Florida Blizzard' × 'Carolyn Whorton' and 'White Christmas' × 'Carolyn Whorton') (Table 2). Additionally, 128 individuals from the cross between 'Candidum' and 'White Christmas' and from the cross between 'White Christmas' and 'Rosebud' did not

Table 2. Segregation for leaf spots in progeny of 18 caladium crosses (crosses made in 2004; progeny phenotyped in 2006).

Cross	Progeny (no.)			Chi-square	
Seed parent (genotype) × pollen parent (genotype)	Spotted (*S_*)[z]	Nonspotted (*ss*)[z]	Expected ratio[y]	χ^2	*P*
Candidum (*ss*) ⊗	0	76	0:1		
Frieda Hemple (*ss*) × Rosebud (*ss*)	0	29	0:1		
Carolyn Whorton (*ss*) ⊗	0	48	0:1		
Florida Blizzard (*ss*) ⊗	0	86	0:1		
White Christmas (*ss*) ⊗	0	41	0:1		
Candidum (*ss*) × White Christmas (*ss*)	0	61	0:1		
Florida Blizzard (*ss*) × Carolyn Whorton (*ss*)	0	61	0:1		
White Christmas (*ss*) × Carolyn Whorton (*ss*)	0	70	0:1		
White Christmas (*ss*) × Rosebud (*ss*)	0	67	0:1		
Gingerland (*Ss*) ⊗	56	24	3:1	1.067	0.302
Candidum (*ss*) × Gingerland (*Ss*)	37	47	1:1	1.190	0.275
Gingerland (*Ss*) × Candidum (*ss*)	44	46	1:1	0.044	0.833
Carolyn Whorton (*ss*) × Gingerland (*Ss*)	29	19	1:1	2.083	0.149
Fannie Munson (*ss*) × Gingerland (*Ss*)	40	48	1:1	0.727	0.394
Gingerland (*Ss*) × Fannie Munson (*ss*)	37	50	1:1	1.943	0.163
Florida Blizzard (*ss*) × Gingerland (*Ss*)	53	39	1:1	2.130	0.144
Gingerland (*Ss*) × White Christmas (*ss*)	46	41	1:1	0.287	0.592
White Christmas (*ss*) × Gingerland (*Ss*)	47	47	1:1	0.000	1.000

[z]Genotype for each of the two phenotypes: spotted or nonspotted. There were two possible genotypes (*SS* or *Ss*, as indicated by *S_*) for the spotted progeny but only one genotype (*ss*) for the nonspotted progeny.
[y]Segregation ratios expected for traits controlled by single dominant nuclear genes.

express any spots. These results agreed with the previous observation of leaf-spot expression in progeny of 'Aaron' and 'Florida Cardinal' (Gager, 1991) and confirmed that nonspotting is recessive and that the above-mentioned cultivars are homozygous. Therefore, they could serve as parents for test crosses for an inheritance study of leaf spots.

'Gingerland' (Fig. 1A) was used as the primary parent for crosses in this study, because it exhibits white veins, brick-red spots, and lance leaves and could provide an opportunity to understand the inheritance of leaf spots as well as the relationships among these foliar traits. Progeny (80 individuals) of 'Gingerland' selfing did not segregate obviously in spot color but did segregate in the presence or absence of spots. The 3 : 1 segregation ratio between spotted and nonspotted individuals suggests the possibility of a single dominant nuclear gene controlling leaf spots in this cultivar (Table 2; $\chi^2 = 1.067$, $P = 0.302$). To confirm this, two test crosses were made using 'Candidum' (Fig. 1A) as the recessive homozygous parent. Progeny segregated in a 1:1 ratio in the cross 'Gingerland' × 'Candidum' ($\chi^2 = 0.044$, $P = 0.833$), but the segregation was slightly skewed toward nonspotted progeny (37 spotted : 50 nonspotted) in the reciprocal cross 'Candidum' × 'Gingerland' ($\chi^2 = 1.943$, $P = 0.163$). To determine if there was any possible maternal effects on spotting from nonspotted seed parents, 'Gingerland' was crossed both as a male and as a female, with two other nonspotted cultivars (with different leaf colors): 'White Christmas' and 'Fannie Munson.' Among progeny from these four crosses, segregation between spotted and nonspotted progeny seemed to fit a 1 : 1 ratio, as expected for a single dominant gene controlling the spots ($\chi^2 = 0.000$ to 1.943, $P = 1$ to 0.163). No maternal effects were detected. Additionally, two more nonspotted cultivars Florida Blizzard and Carolyn Whorton were used as maternal parents to make test crosses with 'Gingerland'. Segregation between spotted and nonspotted progeny in these crosses fit a 1:1 ratio ($\chi^2 \approx 2.100$, $P \approx 0.145$), although the probability values were low compared with the above-mentioned crosses and more spotted progeny than nonspotted progeny.

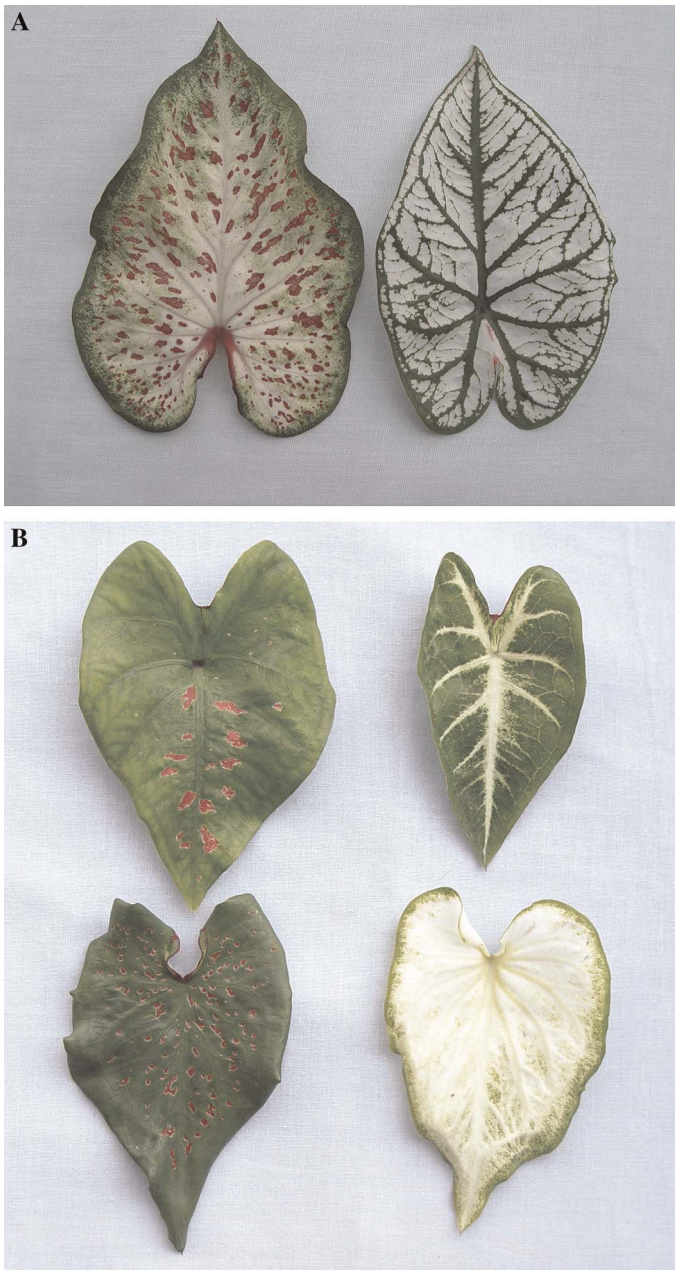

Fig. 1. (**A**) Leaf of two parental cultivars, Gingerland (left) and Candidum (right). 'Gingerland' is spotted, lance-shaped, white-veined, while 'Candidum' is nonspotted, fancy- or heart-shaped, and green-veined. (**B**) Leaf of the four major types of progeny from 'Gingerland' × 'Candidum' to show the genetic relationship among spotting, color of main vein, and leaf shape. Because of the close genetic linkage between the color of main leaf vein and spotting, spots were frequently observed on leaves with green main veins (left column) but rarely on leaves with white main veins (right column). Spots appeared at similar frequencies on fancy-shaped (top row) or lance-shaped (bottom row) leaves, as spots and leaf shapes segregated independently.

These results showed that spotting in 'Gingerland' is controlled by a single dominant nuclear gene with two alleles. Segregation between the two alleles seemed to behave normally in all the crosses, without significant deviation from expected ratios, in contrast to what was observed in 'Painter's Palette'. We intended to cross 'Gingerland' with 'Painter's Palette' and to determine the relationship between the leaf spot locus in 'Gingerland' and the S_R or S_W alleles in 'Painter's Palette', but the unavailability of 'Painter's Palette' prevented us from doing so. To be consistent with the previous report by Gager (1991), we designated the 'Gingerland' leaf spot locus as *S*, with alleles *S* and *s* for spots and nonspots, respectively.

Genetic relationship between leaf spots and shape. In 'Gingerland' × self progeny, leaf shape segregated in a 1 : 2 : 1 (fancy : lance : strap) ratio (data not shown), indicating that the genetic control of leaf shape in 'Gingerland' follows the model previously proposed (Deng and Harbaugh, 2006) and that 'Gingerland' is heterozygous in leaf shape with a genotype *Ff*.

Six types of progeny were therefore expected from 'Gingerland' × self: fancy spotted and nonspotted, lance spotted and nonspotted, and strap spotted and nonspotted (Table 3). These six types segregated in a 3 : 1 : 6 : 2 : 3 : 1 ratio ($\chi^2 = 4.233$, $P = 0.516$), as expected for two independently inherited loci. To confirm this relationship between leaf shape and spots, a forward and a reciprocal cross were made between 'Gingerland' and 'White Christmas'. The observation that the four phenotypes segregated in a 1 : 1 : 1 : 1 ratio in the crosses supports the model with two independent loci controlling the two traits. The same was observed in crosses 'Gingerland' × 'Candidum', 'Florida Blizzard' × 'Gingerland', and 'Gingerland' × 'Fannie Munson'. Data were pooled from all

Table 3. Joint segregation of leaf shape (fancy and lance) and spots (present and absent) in progeny of 18 caladium crosses.

Cross: Seed parent (genotype) × pollen parent (genotype)	Total	Progeny (no.) Fancy (*FF*)[z] S (*S*_)[y]	Fancy (*FF*)[z] N (*ss*)[y]	Lance (*Ff*)[z] S (*S*_)[y]	Lance (*Ff*)[z] N (*ss*)[y]	Strap (*ff*)[z] S (*S*_)[y]	Strap (*ff*)[z] N (*ss*)[y]	Expected ratio[x]	Chi-square χ^2	Chi-square *P*
Gingerland (*Ff Ss*) ⊗ Gingerland (*Ff Ss*) × White Christmas (*FF ss*)	80	18	7	29	12	9	5	3:1:6:2:3:1	4.233	0.516
White Christmas (*FF ss*) × Gingerland (*Ff Ss*)	87	20	27	26	14			1:1:1:1	5.000	0.172
Gingerland (*Ff Ss*) × Candidum (*FF ss*)	87	25	19	22	21			1:1:1:1	0.862	0.835
Candidum (*FF ss*) × Gingerland (*Ff Ss*)	91	17	29	27	18			1:1:1:1	4.956	0.175
Gingerland (*Ff Ss*) × Fannie Munson (*FF ss*)	94	21	28	16	29			1:1:1:1	4.809	0.186
Florida Blizzard (*FF ss*) × Gingerland (*Ff Ss*)	87	21	19	16	31			1:1:1:1	5.828	0.120
Total	91	26	17	26	22			1:1:1:1	2.407	0.492
	537	130	139	133	135			1:1:1:1	0.318	0.957

[z]Phenotype and genotype (in parentheses) for leaf shape.
[y]Phenotype and genotype (in parentheses) for leaf spotting. There were two possible genotypes (*SS* or *Ss*, as indicated by *S*_) for spotted (S) progeny but one only genotype (*ss*) for nonspotted (N) progeny.
[x]Segregation ratios expected for two independently inherited traits.

these crosses, and the ratio among the four leaf shape and spotting types fit nicely to a 1 : 1 : 1 : 1 ratio (χ^2 = 0.318, *P* = 0.957).

Genetic relationship between leaf spots and vein color. Previously, the color of the main vein in caladium was shown to be controlled by one multiallelic locus (red vein allele V^r > white vein allele V^w > green vein allele V^g) (Deng and Harbaugh, 2006; Wilfret, 1983, 1986). Progeny from 'Gingerland' × self segregated 3 white vein : 1 green vein (data not shown; χ^2 = 0.444, *P* = 0.505), indicating that 'Gingerland' is heterozygous, with genotype V^wV^g for vein color. Therefore, four types of progeny (V^w_*S*_ : V^w_*ss* : V^gV^g*S*_ : V^gV^g*ss*) were expected from 'Gingerland' × self. However, only three types of progeny were observed, with the green-veined, nonspotted type (double recessive, V^gV^g*ss*) absent. This deviated from the expected 9 : 3 : 3 : 1 ratio for independent inheritance of spotting and vein color (χ^2 = 11.625, *P* = 0.009), indicating a possible genetic linkage between the two traits and a genotype $V^ws//V^gS$ for 'Gingerland'. This linkage was suggested also by the significant deviation from independent inheritance in the other six crosses in which leaf spots and vein color were segregating (Table 4).

Table 4. Joint segregation of leaf spots (present and absent) and main vein color in progeny of 18 caladium crosses.

Cross: Seed parent (genotype) × pollen parent (genotype)	Total	Progeny (no.) White (V^w_)[z] S (*S*_)[y]	White (V^w_)[z] N (*ss*)[y]	Green (V^gV^g)[z] S (*S*_)[y]	Green (V^gV^g)[z] N (*ss*)[y]	Expected ratio[x]	Chi-square χ^2	Chi-square *P*	Recombination (%)
Gingerland ($V^ws//V^gS$) × Gingerland ($V^ws//V^gS$)	78	36	24	18	0	9:3:3:1	13.077	0.004	—[w]
Gingerland ($V^ws//V^gS$) × Candidum ($V^gs//V^gs$)	91	1	47	43	0	1:1:1:1	85.182	<0.001	1.1[v]
Candidum ($V^gs//V^gs$) × Gingerland ($V^ws//V^gS$)	84	0	47	37	0	1:1:1:1	86.381	<0.001	0.0[v]
Gingerland ($V^ws//V^gS$) × White Christmas ($V^gs//V^gs$)	87	2	40	44	1	1:1:1:1	75.805	<0.001	3.4[v]
White Christmas ($V^gs//V^gs$) × Gingerland ($V^ws//V^gS$)	94	1	40	46	7	1:1:1:1	41.161	<0.001	8.5[v]
Florida Blizzard ($V^ws//V^gs$) × Gingerland ($V^ws//V^gS$)	90	30	36	22	2	3:3:1:1	18.444	<0.001	8.9[u]

[z]Phenotype and genotype (in parentheses) for the color of leaf main veins. There were two phenotypes for vein color, white and green; there were two possible genotypes (V^wV^w or V^wV^g, as indicated by V^w_) for white-veined progeny, but only one genotype (V^gV^g) for green-veined progeny.
[y]Phenotype and genotype (in parentheses) for leaf spotting. There were two possible genotypes (*SS* or *Ss*, as indicated by *S*_) for spotted (S) progeny but only one genotype (*ss*) for nonspotted (N) progeny.
[x]Segregation ratios expected with independent inheritance between leaf spotting and main vein color assumed.
[w]Calculation of the recombination frequency was not possible due to the lack of double-recessive progeny (green-veined, nonspotted) among the progeny.
[v]In these crosses, 'Candidum' or 'White Christmas' were double recessive (green-veined, nonspotted), and both types of progeny (white-veined and spotted, and green-veined, nonspotted) resulted from recombination events between the vein color and leaf spot loci. Therefore, the recombination frequency = (no. of white-veined, spotted progeny + no. of green-veined, nonspotted progeny) ÷ total no. of progeny × 100.
[u]In this cross, one (V^wS) of the two types of recombinant gametes would not be recognized in the progeny due to the presence of V^w allele in 'Florida Blizzard', and only half of the recombinant events would appear. Therefore, the recombination frequency = [no. double-recessive (green-veined, nonspotted) progeny × 2] ÷ total no. of progeny × 100.

Due to the lack of double-recessive recombinants (green, nonspotted) in the progeny of 'Gingerland' × self and the dominant nature of red vein or white vein over green vein, it was not possible to estimate the recombination frequency between the two traits in this cross. To overcome this difficulty, 'Gingerland' was crossed with 'Candidum' and 'White Christmas', two double-recessive cultivars with the genotype $V^{g}s//V^{g}s$, in both forward and reciprocal directions. One recombinant (white-vein, spotted) individual was observed among the 91 progeny from 'Gingerland' × 'Candidum' (Fig. 1B), while no recombinants were identified among 84 progeny from the reciprocal cross. More recombinants were observed among progeny of the cross 'Gingerland' × 'White Christmas' (3 of 87) and the reciprocal cross (8 of 94). Thus, the recombination frequency varied from 0.0% ('Candidum' × 'Gingerland') to 8.9% ('Florida Blizzard' × 'Gingerland') among the five test crosses, and the average recombination frequency across the crosses was 4.4%.

Foliar characteristics are important to the value of many ornamental aroids (Henny, 2000). Understanding the mode of inheritance of major foliar traits has been a priority in genetic studies of these plants. Although the genetic control of the foliar variegation in aglaonema and diffenbachia (Henny, 1982, 1983, 1986a, 1986b) and the genetic control of leaf shape and main vein color in caladium (Deng and Harbaugh, 2006; Wilfret, 1983, 1986) seem to be well understood, the genetic relationships among these traits in ornamental aroids are much less known. To the authors' knowledge, there have been only two reports on these relationships: Henny (1983) showed a linkage between the white foliar midrib and the foliar variegation in dieffenbachia, and Deng and Harbaugh (2006) described an independent inheritance between leaf shape and vein color in caladium. This current study represents the first report in caladium showing a tight genetic linkage between two foliar traits with their recombination frequency estimated.

There are a number of breeding objectives in caladium cultivar development, including transferring the sun tolerance from some lance or strap-leaved cultivars into the fancy-leaved type, moving the high tuber yield and disease or pest resistance from some fancy-leaved cultivars into the lance type and generating new coloration patterns, such as dense bright-colored spots in various leaf types. Knowledge of the number of gene loci, allelic and interallelic relationships, and recombination frequencies for the traits of interest will help us choose parental combinations, population sizes, and screening/selection strategies. Additional studies are underway to further understand the genetic relationship of leaf spots, shape, and vein color with leaf growth and development and tuber yield.

Caladium and certain other ornamental aroids such as aglaonema and dieffenbachia that are widely grown in the worldwide foliage industry may inherit certain morphological and physiological characteristics similarly (Henny, 2000). Therefore, genetic information gained in caladium may be useful to those starting genetic studies on aroids and other cut flowers, pot plants, or bedding plants that express color spots on leaves or on flowers.

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