Independent Inheritance of Leaf Shape and Main Vein Color in Caladium

Zhnao Deng¹ and Brent K. Harbaugh

University of Florida, IFAS, Environmental Horticulture Department, Gulf Coast Research and Education Center, 14625 CR672, Wimauma, FL 33598

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ABSTRACT. The ornamental value of caladium (*Caladium xhortulanum* Birdsey) depends primarily on leaf characteristics, including leaf shape and main vein color. Caladium leaf shapes are closely associated with plant growth habit, stress tolerance, and tuber yield; leaf main vein colors are often used for cultivar identification. Thirty-eight crosses were made among 10 cultivars and two breeding lines; their progeny were analyzed to understand the inheritance of leaf shape and main vein color and to determine if there is a genetic linkage between these two traits. Results showed that a single locus with three alleles determined the main vein color in caladium. The locus was designated as *V*, with alleles *V^r*, *V^w*, and *V^g* for red, white, and green main veins, respectively. The white vein allele was dominant over the green vein allele, but it was recessive to the red vein allele, which was dominant over both white and green vein alleles; thus the dominance order of the alleles is *V^r* > *V^w* > *V^g*. Segregation data indicated that four major red-veined cultivars were heterozygous with the genotype *V^rV^g*, and that one white-veined cultivar was homozygous and one other white-veined cultivar and one breeding line were heterozygous. The observed segregation data confirmed that the three leaf shapes in caladium were controlled by two co-dominant alleles at one locus, designated as *F* and *f*, for fancy and strap leaves, respectively. The skewedness of leaf shape segregation in some of the crosses implied the existence of other factors that might contribute to the formation of leaf shape. Contingency chi-square tests for independence revealed that caladium leaf shape and main vein color were inherited independently. The chi-square tests for goodness-of-fit indicated that the five observed segregation patterns for leaf shape and main vein color fit well to the expected ratio assuming that two co-dominant and three dominant/recessive alleles control leaf shape and main vein color and they are inherited independently.

Caladiums are ornamental aroids grown for their long-lasting bright colorful foliage. They are often forced from tubers as container and hanging basket plants, or grown in garden beds as accent and border plants. Leaves of many modern caladium cultivars can rival many flowers in color and brightness (Hayward, 1950). Caladiums originated in the tropical or subtropical region of Central America and South America. Cytogenetically, they are diploids with $2n = 30$ chromosomes (in Darlington and Wylie, 1955). Generally, caladiums are asexually propagated by division of tubers. Florida is the leading producer and supplier of caladium tubers, providing more than 95% of the worldwide tuber demands (Bell et al., 1998). Early breeding efforts in caladium dated back to late 1800s (Hayward, 1950); and ≈ 100 cultivars are commercially propagated presently (Bell et al., 1998).

The ornamental value of caladiums in containers or in the landscape depends, to a great extent, on leaf characteristics, including shape, color, color pattern, and venation pattern. Compared to other ornamental aroids [e.g., *Aglaonema* Schott, *Alocasia* (Schott) G. Don, *Dieffenbachia* Schott, *Philodendron* Schott, *Syngonium* Schott, etc.], caladiums exhibit a remarkable level of diversity in these leaf characters (Henny, 1988, 2000; Wilfret, 1993). For example, the width and/or length of mature leaves can vary from several centimeters to over 20 cm among cultivars. Commercial caladium cultivars also possess very diverse leaf shapes. Broadly,

caladium leaves are classified into three shapes: fancy, lance, and strap (Fig. 1). Fancy-leaved caladiums have heart-shaped (triangular- or round-ovate) leaves, with three main veins on each leaf arranged in the form of an inverted letter Y, a peltate petiole attachment, and the two basal lobes are joined for more than one-fifth of their length and separated by a short narrow sinus.

Fig. 1. Typical leaf shapes and main vein colors expressed in caladium progeny (seedlings ≈ 3 months old). Top row from left to right: fancy leaves (heart-shaped with petioles attached to the back) with white, red, and green main veins; bottom row from left to right: lance leaves with white, red, and green main veins. Rightmost column: strap leaf with red main vein.

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¹To whom reprint requests should be addressed. E-mail address: zdeng@mail.ifas.ufl.edu.

Strap-leaved caladiums, on the other hand, have narrow linear (or ribbon-like) leaves, one main vein and no obvious basal lobes. Lance leaves are intermediate between fancy and strap types: leaf blades are broad sagittate to cordate-lanceolate, with basal lobes not obvious or broadly separated by a sinus, if present. The shape of caladium leaves directly affect the acceptance and marketing of caladium; in addition, it is closely associated with a number of other horticulturally important characteristics, such as plant growth habit, stress tolerance, tuber yield, etc. Generally, strap- or lance-leaved plants are much shorter in plant height, sprout more leaves from similarly-sized tubers, are more tolerant of sun and low temperatures, and produce smaller tubers than fancy-leaved plants (Z. Deng and B.K. Harbaugh, observation). The fancy leaf shape in current commercial cultivars seems to have been inherited from their parental species *C. bicolor* (Aiton) Vent., *C. marmoratum* Mathieu, and *C. picturatum* C. Koch, while the lance or strap leaf shape seems to have been inherited from *C. schomburgkii* Schott (Birdsey, 1951; Hayward, 1950).

Leaf color is another important characteristic of caladium. It is determined by the color of veins (main, secondary, and peripheral), interveinal areas, spots, and/or blotches. Leaf colors in many caladium cultivars are extremely diverse and intriguing. In some cultivars, leaf colors and colored areas can be quite variable on the same plant with changes in plant development or environmental conditions. Leaf color variation or instability may be undesirable for commercial production or propagation (Ahmed et al., 2004). However, the leaf main vein color seems to be an exception: it is quite stable under different environments, on different plants, or at different developmental stages. This stability of color expression in leaf main veins has been very useful for cultivar description and identification, besides its ornamental significance.

Information on the inheritance of leaf shape and main vein color, two important traits in ornamental plants, has been rather scant in caladium. Although breeding of caladium was once quite active by a number of hobbyists or professional horticulturists, their data on trait inheritance was not published and the information presumably had been lost. In recent years, efforts have been made to gain understanding of the inheritance of these characteristics for improved breeding efficiency. Wilfret (1983) investigated the inheritance of caladium main vein colors using three commercial cultivars ('White Queen', 'Candidum', and 'Candidum Jr.') and reported that a single dominant gene is responsible for the red main vein in caladium. Later, in published abstracts, Wilfret (1986) indicated that red vein is dominant to green, and white is dominant to both red and green. He also showed that the fancy leaf shape is controlled by a single gene, with one homozygous genotype producing the fancy leaf, the other homozygote developing a strap (ribbon) leaf, and the heterozygote having a lance leaf. Zettler and Abo El-Nil (1979) investigated segregation of leaf spots and colors at the central leaf area in various crosses between two cultivars and suggested that genes *R* and *W* control the red and white spots expressed in 'Painter's Palette', and that 'Poecile Anglais' has gene *R'* for the red center in a homozygous state.

Our work describes analysis of segregation of leaf shapes and main vein colors in the progeny of 38 caladium crosses. The segregation data were used to determine the inheritance of main vein color and leaf shape as well as the linkage relationship between these two characteristics. The segregation ratios were also used to determine the genotype of a number of major cultivars that are of significant value as breeding parents in caladium cultivar improvement.

PLANT MATERIAL. Ten commercial caladium cultivars and two breeding lines were used as parents in various crosses. Five cultivars ('Florida Irish Lace', 'Florida Moonlight', 'Florida Fantasy', 'Florida Red Ruffles', and 'Florida Sweetheart') were released in the last 15 years, and their immediate parents are known (Table 1). This information is also available for breeding lines BR-1 and BR-2. 'Aaron', 'Candidum', 'Candidum Jr.', 'Red Flash', and 'White Christmas' are major cultivars commercially propagated and grown presently (Bell et al., 1998), but information about their parentage is lacking in the literature. 'Candidum' was first produced by Alfred Bleu in mid-1800s in France (Hayward, 1950), and 'Candidum Jr.' might be a field sport of 'Candidum'. The phenotype and inferred genotype of each parent for leaf shape and main vein color are listed in Table 1. True strap-leaved plants were not available in commercial cultivars; when they appeared in breeding populations, they produced very few blooms. Thus, these types of plants were not used as parents.

FLOWER INDUCTION. Flower induction was performed as described previously (Deng and Harbaugh, 2004; Harbaugh and Wilfret, 1979). Jumbo-sized tubers (6.4–8.9 cm diameter) were soaked in a GA₃ solution (ProGibb T&O; Valent BioSciences, Libertyville, Ill.) at a concentration of 600 mg·L⁻¹ for 16 h at room temperature and potted in 20-cm-diameter containers (3.5 L volume) filled with a commercial container mix (VerGro container mix A; Verlite Co., Tampa, Fla.). Parental plants were grown in a shaded glasshouse with 20% to 30% light exclusion under a natural photoperiod at Bradenton, Fla. The temperature inside the glasshouse ranged from 21 to 32 °C. A trickle irrigation system was provided to the containerized plants.

CROSSING. Controlled crosses between the parents were made from May to July in 2003 and 2004 as described by Hartman et al. (1972). Pollen was collected within several hours after being shed by the staminate flowers and stored in a refrigerator at 4 to 6 °C (Deng and Harbaugh, 2004). Receptive pistillate flowers on the spadixes were exposed by cutting off spathes with a scalpel and pollinated with pollen freshly collected or stored for 1 to 3 d, using clean camel-hair brushes. Pollinated flowers were tagged and bagged with nylon nets.

PROGENY GROWING. Seeds were harvested at maturity (30 to 35 d after pollination in summer) and sown immediately. They were germinated on the surface of the substrate (Verlite VerGrow container mix A) in 10-cm-diameter pots at 25 °C inside a room under continuous light (cool fluorescent lights, 30 μmol·m⁻²·s⁻¹). Seedlings were grown in the pots and under a mist system in a glasshouse until two true leaves formed. Plants were then individually transferred from the pots to 128-cell trays filled with commercial container mix (Verlite VerGrow container mix A) and grown on benches in a glasshouse under a mist system. Plants were fertilized with a liquid fertilizer solution containing 50 to 250 mg·L⁻¹ N twice per week. The glasshouse had 20% to 30% light exclusion.

DATA TAKEN. Progeny was examined for phenotypes in leaf shape and main vein color when seedlings were ≈3 months old and had developed about eight leaves. Progeny individuals were classified into one of the nine possible groups [three leaf shapes (fancy, lance, and strap) by three leaf main vein colors (white, red, and green)], and the number of progeny in each group was recorded for each population and used for segregation analysis. Altogether, more than 2600 progeny individuals from 38 popu-

lations were examined for phenotypes in leaf shape and main vein color.

STATISTICS. Chi-square tests for goodness-of-fit were performed to examine the segregation ratios of leaf shapes or main vein colors in progeny against expected ratios for the two individual traits, while contingency chi-square tests were conducted to examine the possibility of independence or linkage between the two traits. Contingency chi-square tests were preferred for test of independence between traits, since it makes no prior assumptions about segregation ratios (Guner and Myers, 2001). In addition, chi-square tests also were performed to examine populations' homogeneity in leaf shape segregation. Calculation of the chi-square values for goodness-of-fit, independency and homogeneity and their probabilities was conducted using a program developed by Preacher (2003).

Results and Discussion

INHERITANCE OF LEAF MAIN VEIN COLOR. The main vein of 'Candidum' and 'Candidum Jr.' is green. Progeny from selfing of 'Candidum' (cross no. 1; Table 2) and crossing between 'Candidum' x 'Candidum Jr.' (cross no. 2; Table 2) expressed green main veins, consistent with a previous report (Wilfret, 1983) and indicating the homozygosity status of their vein color. Previously, Wilfret (1983, 1986) showed that the green vein color was recessive to both red and white main vein colors. Therefore, 'Candidum' and 'Candidum Jr.' should both contain homozygous recessive alleles for their green vein color. Being homozygous recessive, these two cultivars would be excellent parents for testcrosses, and therefore, they were used in several such crosses to determine the genotype of four cultivars ('Florida Fantasy', 'Florida Red

Table 1. Phenotype and genotype (inferred) of 10 commercial caladium cultivars and two breeding lines that were used as parents.

Name	Parentage	Leaf shape		Color of main vein	
		Phenotype	Genotype	Phenotype	Genotype
Aaron	Unknown	Fancy	<i>FF</i>	White	V^wV^w
BR-1	Aaron x Candidum Jr.	Fancy	<i>FF</i>	White	V^wV^g
BR-2	Florida White Ruffles x Florida Sweetheart	Lance	<i>Ff</i>	Red	V^rV^g
Candidum	Unknown	Fancy	<i>FF</i>	Green	V^gV^g
Candidum Jr.	Unknown	Fancy	<i>FF</i>	Green	V^gV^g
Florida Fantasy	Candidum Jr. x Red Frill	Fancy	<i>FF</i>	Red	V^rV^g
Florida Irish Lace	(Candidum Jr. x Red Frill) x (Candidum Jr. x Red Frill)	Lance	<i>Ff</i>	Green	V^gV^g
Florida Moonlight	Aaron x Candidum Jr.	Fancy	<i>FF</i>	White	V^wV^g
Florida Red Ruffles	(Red Frill x Candidum Jr.) x Red Frill	Lance	<i>Ff</i>	Red	V^rV^g
Florida Sweetheart	Candidum Jr. x Red Frill	Lance	<i>Ff</i>	Red	V^rV^g
Red Flash	Unknown	Fancy	<i>FF</i>	Red	V^rV^g
White Christmas	Unknown	Fancy	<i>FF</i>	Green	V^gV^g

Table 2. Segregation for color of the main vein in leaves of progeny from 20 crosses in caladium.

Crosses ² [cross no.]	Color of main vein			Expected ratio	χ^2	<i>P</i>
	White (V^wV^w or V^wV^g)	Red (V^rV^g)	Green (V^gV^g)			
Candidum (V^gV^g) x Candidum (V^gV^g) [1]	0	0	11	0:0:1	0	1
Candidum (V^gV^g) x Candidum Jr. (V^gV^g) [2]	0	0	31	0:0:1	0	1
Candidum Jr. (V^gV^g) x Fantasy (V^rV^g) [3]	0	18	14	0:1:1	0.5	0.48
Fantasy (V^rV^g) x Candidum Jr. (V^gV^g) [4]	0	35	34	0:1:1	0.01	0.91
White Christmas (V^gV^g) x Fantasy (V^rV^g) [5]	0	51	39	0:1:1	1.16	0.28
Red Ruffles (V^rV^g) x Candidum (V^gV^g) [6]	0	16	19	0:1:1	0.26	0.61
Red Ruffles (V^rV^g) x Candidum Jr. (V^gV^g) [7]	0	17	15	0:1:1	0.13	0.72
Sweetheart (V^rV^g) x Candidum (V^gV^g) [8]	0	11	17	0:1:1	1.29	0.26
Sweetheart (V^rV^g) x Candidum Jr. (V^gV^g) [9]	0	14	17	0:1:1	0.29	0.59
Candidum Jr. (V^gV^g) x Sweetheart (V^rV^g) [10]	0	18	16	0:1:1	0.12	0.73
Candidum (V^gV^g) x Red Flash (V^rV^g) [11]	0	18	16	0:1:1	0.12	0.73
Red Flash (V^rV^g) x Red Flash (V^rV^g) [12]	0	28	6	0:3:1	0.98	0.32
Fantasy (V^rV^g) x Red Flash (V^rV^g) [13]	0	93	28	0:3:1	0.22	0.64
Moonlight (V^wV^g) x Moonlight (V^wV^g) [14]	18	0	5	3:0:1	0.13	0.72
Moonlight (V^wV^g) x Fantasy (V^rV^g) [15]	7	19	7	1:2:1	0.76	0.68
Moonlight (V^wV^g) x Red Flash (V^rV^g) [16]	5	15	12	1:2:1	3.12	0.20
Sweetheart (V^rV^g) x Moonlight (V^wV^g) [17]	8	16	11	1:2:1	0.77	0.68
BR-1 (V^wV^g) x Fantasy (V^rV^g) [18]	31	48	28	1:2:1	1.28	0.53
Aaron (V^wV^w) x Red Flash (V^rV^g) [19]	45	34	0	1:1:0	1.53	0.22
Red Flash (V^rV^g) x Aaron (V^wV^w) [20]	55	41	0	1:1:0	2.04	0.15

²Listed in the parenthesis is the inferred genotype for the color of the leaf main vein.

Ruffles', 'Florida Sweetheart', and 'Red Flash') that develop red main veins. Two types of vein colors, red and green, were observed in the progeny of reciprocal crosses between 'Candidum Jr.' and 'Florida Fantasy', and they segregated in a 1:1 ratio (cross no. 3 and 4; Table 2), indicating that 'Florida Fantasy' is heterozygous. To confirm this, 'Florida Fantasy' was crossed with another green-veined cultivar, 'White Christmas', and a 1:1 ratio between red- and green-veined progeny was again observed (cross no. 5; Table 2). 'Florida Red Ruffles' was tested using both 'Candidum' and 'Candidum Jr.'; their testercross progeny exhibited a 1:1 segregation of red- and green-veined individuals (cross no. 6 and 7), indicating that 'Florida Red Ruffles' is heterozygous at the locus determining the leaf main vein color. Three crosses were made to test 'Florida Sweetheart', including reciprocal crosses with 'Candidum Jr.' (cross no. 9 and 10) and a cross with 'Candidum' (cross no. 8). The 1:1 ratio between red- and green-veined progeny indicated that 'Florida Sweetheart' is heterozygous as well. The 1:1 segregation of red and green vein colors in the progeny of the cross between 'Candidum' x 'Red Flash' (cross no. 11) revealed that 'Red Flash' also is heterozygous. This was confirmed by a self pollination (cross no. 12) and a cross with 'Florida Fantasy' (cross no. 13). Since both parents were heterozygous in these two crosses, a segregation ratio of 3 red : 1 green was expected, and the data had an acceptable fit (Table 2).

Previously, Wilfret (1986) indicated that white main vein was dominant to both red and green veins, but details of the crosses and the segregation data in their progeny were not available. To further the understanding of the relationship of white veins over red and green veins, two cultivars ('Aaron' and 'Florida Moonlight') and one breeding line (BR-1) that express white main veins (Table 1) were chosen, and they were selfed or crossed with some of the above characterized cultivars. Progeny of selfed 'Florida Moonlight' (cross no. 14) exhibited segregation of white and green main veins in a 3:1 ratio (Table 2), which indicated that 'Florida Moonlight' is heterozygous and that white is dominant to green. 'Florida Moonlight' was then crossed separately to three heterozygous red-veined cultivars ('Florida Fantasy', 'Red Flash', and 'Florida Sweetheart') to confirm the reported dominance of white main veins over red veins. Three types of individuals (white, red, and green-veined) were observed in the progeny of these crosses; they segregated in a 1:2:1 ratio (Table 2). This segregation did not fit the previously reported model in which white was supposed to be dominant over red (where a ratio of 2 white : 1 red : 1 green would be expected in these crosses). Rather, the data better fit a model in which red is dominant over white and green, and white is dominant over green, with chi-square values ranging from 0.76 to 3.12 and probabilities from 0.68 to 0.20. When white-veined breeding line BR-1 was crossed with 'Florida Fantasy' (heterozygous red-veined), a similar segregation of vein colors (1 white : 2 red : 1 green) was observed in their progeny (Table 2), which supports the new model. Progeny of reciprocal crosses between 'Aaron' and 'Red Flash' segregated two main vein colors, white and red, in a 1:1 ratio (Table 2). This segregation again supported the above proposed dominance of red over white, and also indicated that 'Aaron' is homozygous white-veined, different from 'Florida Moonlight'.

In summary, the above segregation data supported previous observations (Wilfret, 1983, 1986) that the green main vein phenotype is controlled by a recessive allele, and that red main vein is dominant over the green main vein. They revealed that four of the major red-veined commercial cultivars are heterozygous, containing both the red and green vein alleles. These data con-

firmed the dominance of white main veins over the green main veins, but revealed a different relationship between red and white main veins. White is not dominant to red, rather red is dominant to white. It seems that caladium has evolved several alleles for the main vein color. We propose the locus determining the main vein color be named V , with V^r , V^w , and V^g designated as the alleles for red, white, and green main veins, respectively. The dominance order of these alleles is $V^r > V^w > V^g$. Accordingly, the genotype for the main vein color was inferred from the above-mentioned segregation data and shown in Table 2. 'Candidum' and 'Candidum Jr.' have the V^gV^g genotype; 'Florida Fantasy', 'Florida Red Ruffles', 'Florida Sweetheart', and 'Red Flash' shared the V^rV^g genotype. The genotype of 'Aaron' for main vein color is V^wV^w , while that of 'Florida Moonlight' and BR-1 is V^wV^g .

INHERITANCE OF LEAF SHAPES. Among the 38 crosses, 16 were fancy x fancy, 7 fancy x lance, 13 lance x fancy, and 2 lance x lance, respectively. All progeny (859 individuals) of fancy x fancy crosses exhibited fancy leaves (Table 3). Two leaf types (fancy and lance) were observed in the progeny of each of the fancy x lance crosses; their segregation ratio in each population fit 1:1, with a probability ranging from 0.12 to 0.92 (Table 3). Chi-square tests showed that the seven populations were homogeneous in the segregation of leaf shapes (data not shown). When the segregation data were pooled together from the seven crosses, 329 and 298 individuals were fancy- and lance-leaved, respectively. In 10 of the 13 lance x fancy crosses, the segregation between fancy and lance leaf types fit a ratio of 1:1 with a probability from 0.11 to 1.00 (Table 3). The 10 populations were homogeneous in leaf shape segregation as well (data not shown). However, the segregation in the progeny of three of the crosses was skewed toward more fancy leaf type individuals. This skewedness was most obvious in one cross ('Florida Red Ruffles' x 'Candidum Jr.'), and the observed segregation in this cross did not fit a 1:1 ratio (probability of fit was 0.002; Table 3). Although the probability of fit to a 1:1 ratio in the other two crosses ('Florida Sweetheart' x 'White Christmas' and 'Florida Red Ruffles' x 'Florida Fantasy') was >0.05 (0.054 to 0.09), skewedness was obvious when the segregation data were combined (Table 3). The cause(s) of this skewed segregation remains to be elucidated. Both 'Florida Red Ruffles' and 'Florida Fantasy' were developed from crosses between 'Candidum Jr.' and 'Red Frill' (Table 1); therefore, these four cultivars are very closely related, and crossing between them may lead to inbreeding and exposure of potential lethal alleles. The segregation of three leaf types in the progeny of two lance x lance crosses fit well to a ratio of 1 fancy : 2 lance : 1 strap, with a probability of 0.52 and 0.98, respectively (Table 3).

In summary, the above segregation data from four types of crosses indicated that the three leaf shapes in caladium are controlled by two co-dominant alleles at one locus, which supports a previous report (Wilfret, 1986). We propose that the two alleles be named F and f , for fancy and strap leaves, respectively. Therefore, the genotype of fancy-, lance-, and strap-leaved caladiums would be FF , Ff , and ff , respectively. The skewedness of leaf shape segregation in some of the crosses indicates that other factors might contribute to the development of leaf shapes.

INDEPENDENT INHERITANCE BETWEEN LEAF SHAPE AND MAIN VEIN COLOR. Both leaf shape and main vein color segregated in the progeny of 16 crosses. Five patterns of segregation were observed (Table 4). Contingency chi-square tests for independency were first performed on the segregation data. This test offers several advantages compared to other tests for this purpose (Guner and Myers, 2001). Results showed that the chi-square value for

Table 3. Segregation for leaf shape in the progeny of 38 caladium crosses (2003 and 2004).

Type of cross	Crosses (no.)	Leaf shape types (no. progeny)			Expected ratio	χ^2	<i>P</i>
		Fancy (<i>FF</i>)	Lance (<i>Ff</i>)	Strap (<i>ff</i>)			
Fancy x fancy	16	859 ^z	0 ^z	0 ^z	1:0:0	0 ^y	1 ^y
Fancy x lance	7	329	298	0	1:1:0	0.01~2.45	0.92~0.12
Lance x fancy	10	375	330	0	1:1:0	0~2.61	1~0.11
Lance x fancy	2 ^x	111	76	0	1:1:0	2.84, 3.72	0.09, 0.05
Lance x fancy	1 ^w	23	9	0	1:1:0	6.13	0.002
Lance x lance	2	47	101	45	1:2:1	0.04~1.30	0.98, 0.52

^zTotal number of progeny from crosses of a specific cross type.^yRange of χ^2 and *P* values for all the crosses of the cross type. The χ^2 and *P* values for each individual cross were not shown.^xThe two crosses were 'Florida Red Ruffles' x 'Florida Fantasy' and 'Florida Sweetheart' x 'White Christmas'.^wThe cross was 'Florida Red Ruffles' x 'Candidum Jr.'.

Table 4. Segregation for leaf shapes and main vein colors in the progeny of 16 caladium crosses.

Crosses ^z [cross no.]	Leaf shape and color of the leaf main vein (no. progeny)									Expected ratio	χ^2 (<i>P</i>)
	Fancy			Lance			Strap				
	W ^y	R	G	W	R	G	W	R	G		
Aaron (<i>FF V^wV^w</i>) x Sweetheart (<i>Ff V^rV^g</i>) [21]	21 ^x	24		24	27					1:1:1:1	0.75 (0.86)
Sweetheart (<i>Ff V^rV^g</i>) x Aaron (<i>FF V^wV^w</i>) [22]	20	18		18	13					1:1:1:1	1.55 (0.67)
Sweetheart (<i>Ff V^rV^g</i>) x White Christmas (<i>FF V^gV^g</i>) [23]		30	28		17	22				1:1:1:1	4.32 (0.23)
White Christmas (<i>FF V^gV^g</i>) x Sweetheart (<i>Ff V^rV^g</i>) [24]		17	31		23	26				1:1:1:1	4.24 (0.24)
Irish Lace (<i>Ff V^gV^g</i>) x Fantasy (<i>FF V^rV^g</i>) [25]		58	52		49	48				1:1:1:1	1.17 (0.76)
Candidum (<i>FF V^gV^g</i>) x Sweetheart (<i>Ff V^rV^g</i>) [26]		24	23		15	18				1:1:1:1	2.70 (0.44)
Red Flash (<i>FF V^rV^g</i>) x Sweetheart (<i>Ff V^rV^g</i>) [27]		44	11		33	10				3:1:3:1	2.35 (0.50)
Red Flash (<i>FF V^rV^g</i>) x Sweetheart (<i>Ff V^rV^g</i>) [28]		36	14		30	15				3:1:3:1	2.09 (0.55)
Red Ruffles (<i>Ff V^rV^g</i>) x Fantasy (<i>FF V^rV^g</i>) [29]		42	11		28	9				3:1:3:1	3.45 (0.33)
Red Ruffles (<i>Ff V^rV^g</i>) x Moonlight (<i>FF V^wV^g</i>) [30]	14	22	15	10	25	10				1:2:1:1:2:1	3.45 (0.33)
Red Ruffles (<i>Ff V^rV^g</i>) x BR-1 (<i>FF V^wV^g</i>) [31]	14	27	12	14	27	14				1:2:1:1:2:1	0.22 (1.00)
BR-1 (<i>FF V^wV^g</i>) x Red Ruffles (<i>Ff V^rV^g</i>) [32]	19	36	16	14	29	15				1:2:1:1:2:1	1.63 (0.90)
BR-1 (<i>FF V^wV^g</i>) x Sweetheart (<i>Ff V^rV^g</i>) [33]	10	26	7	9	29	12				1:2:1:1:2:1	4.43 (0.49)
Sweetheart (<i>Ff V^rV^g</i>) x Moonlight (<i>FF V^wV^g</i>) [34]	4	9	5	5	7	6				1:2:1:1:2:1	1.11 (0.95)
Irish Lace (<i>Ff V^gV^g</i>) x BR-2 (<i>Ff V^rV^g</i>) [35]		14	10		30	16	10	14		1:1:2:2:1:1	5.57 (0.35)
Irish Lace (<i>Ff V^gV^g</i>) x Red Ruffles (<i>Ff V^rV^g</i>) [36]		10	13		29	26	8	13		1:1:2:2:1:1	2.86 (0.72)

^zListed in the parenthesis is the inferred genotype for each parent.^yColor of the leaf main vein: W = white, R = red, and G = green.^xNumber of progeny showing the specific combination of leaf shape and main vein color characteristics.

independence between leaf shape and main vein color in the 16 crosses ranged from 0.001 to 3.59 (*P* = 0.97 to 0.17) (data for each individual cross not shown), indicating that two leaf traits assort independently.

Based on this independence between the two traits and the above-proposed mode of inheritance for three leaf shapes and three main vein colors, expected ratios of segregation could be derived for progeny of each of the crosses (Table 4). Chi-square tests were then performed for goodness-of-fit of the observed segregation ratios to these expected ratios. Four types of individuals (fancy white, fancy red, lance white, and lance red) appeared in the progeny of two crosses (cross no. 21 and 22; reciprocal crosses of 'Aaron' and 'Florida Sweetheart') in a ratio of 1:1:1:1. This ratio was also observed in another four crosses (cross no. 23, 24, 25, and 26) among four different types of individuals (fancy red, fancy green, lance red, and lance green). In three crosses (cross no. 27, 28, and 29), these four types of progeny segregated in a 3:1:3:1 ratio. The progeny of five crosses (cross no. 30, 31, 32, 33, and 34) showed six types of individuals, fancy white, red and green, and lance white, red and green, in a ratio of 1:2:1:1:2:1,

respectively. Six types of progeny (fancy red and green, lance red and green, and strap red and green) were observed in two crosses (cross no. 35 and 36), in a ratio of 1:1:2:2:1:1. The probability of fit in the above crosses ranged from 0.23 to 1.00 (Table 4), indicating that the actual segregations were in a good agreement with the expected ratios.

A number of breeding objectives have been sought in caladium genetic improvement, including transferring the sun tolerance of lance or strap type caladiums into the fancy type and the high tuber yield of the fancy type into the lance type, breeding new colors or color patterns in various leaf types, etc. Some of these traits targeted by breeding seem to be associated with leaf types or colors. A better understanding of the genetic relationship (allelism and linkage) between caladium characteristics will help to improve crossing and/or selection plans. The present study examined the segregation of two important leaf traits, singly or in combination, in numerous crosses (or against a diverse genetic background), and revealed genetic information of the traits and between them, which has been lacking or insufficient. Analyses of these traits' association or independence with other leaf or tuber

characteristics are under way. As a member of Araceae, caladium may share similar modes of inheritance in some leaf characteristics with other ornamental aroids that are grown as major crops in the worldwide foliage plant industry (Henny, 2000). Therefore, genetic information gained in caladium might also facilitate elucidation of modes of inheritance in these aroids.

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