A single gene controls leaf background color in caladium (Araceae) and is tightly linked to genes for leaf main vein color, spotting and rugosity

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Modern cultivated caladiums (Caladium × hortulanum) are grown for their long-lasting and colorful leaves. Understanding the mode of inheritance for caladium leaf characteristics is critical for plant breeders to select appropriate parents, predict progeny performance, estimate breeding population sizes needed, and increase breeding efficiencies. This study was conducted to determine the mode of inheritance of two leaf background colors (lemon and green) in caladium and to understand their relationships with four other important leaf characteristics including leaf shape, main vein color, spotting, and rugosity. Seven caladium cultivars and three breeding lines were used as parents in 19 crosses, and their progeny were phenotyped for segregation of leaf traits. Results showed that the two leaf background colors are controlled by a single nuclear locus, with two alleles, LEM and lem, which control the dominant lemon and the recessive green leaf background color, respectively. The lemon-colored cultivar ‘Miss Muffet’ and breeding lines UF-52 and UF-53 have a heterozygous genotype LEMlem. Chi-square tests showed that the leaf background color locus LEM is independent from the leaf shape locus F, but is tightly linked to three loci (S, V and RLF) controlling leaf spotting, main vein color, and rugosity in caladium. A linkage map that consists of four loci controlling major caladium leaf characteristics and extends ~ 15 cM was developed based on the observed recombination frequencies. This is the first report on the mode of inheritance of leaf background colors in caladium and in the Araceae family. The information gained in this study will be very useful for caladium breeding and study of the inheritance of leaf colors in other ornamental aroids, an important group of ornamental plants in the world.

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been a consistent interest in incorporating the lemon background color into new cultivars.

Information on the mode of inheritance for the leaf background color in caladium has been lacking; so has been in the whole Araceae family. Different modes of inheritance have been reported for leaf background colors in some other foliage plants. Roberts et al.9 reported that the leaf background color in Eastern redbud (Cercis canadensis) was controlled by a single locus with a dominant allele for the purple background color and a recessive allele for the green background color. The yellow and green leaf background colors in Sambucus nigra are controlled by a dominant and a recessive allele, respectively.10 The green leaf background in barberries (Berberis spp.) was controlled by a recessive allele while the red leaf background was regulated by a dominant allele for the purple background color and a recessive allele for the red background color. These cultivars and breeding lines were often used in caladium breeding programs to develop new caladium cultivars with enhanced aesthetical values, improved plant performance and abiotic and biotic tolerance. Their phenotypes and inferred genotypes for leaf background color. These cultivars and breeding lines were often used in caladium breeding programs to develop new caladium cultivars with enhanced aesthetical values, improved plant performance and biotic and abiotic tolerance. Their phenotypes and inferred genotypes for leaf background color were shown in Table 1.

Seed germination and progeny growing

Seeds were manually extracted from mature berries. Dried seeds were immediately sowed in 20-row germination trays filled by a commercial soilless substrate (Fafard Super Fine Germination Mix) and germinated in a growth chamber with a constant temperature of 25 °C and continuous light (cool fluorescent lights, 30 µmol·m−2·s−1). After one month, seedlings were individually transplanted to 128-cell trays filled with a commercial substrate (Fafad 38) and grown in a greenhouse. Young plants were irrigated by hand once a day and fertilized twice a week using a commercial water-soluble fertilizer containing 1.1% (w/w) ammonia nitrogen, 11.8% (w/w) nitrate nitrogen, 2.1% (w/w) urea nitrogen, 5% (w/w) phosphate (P2O5), and 15% potassium (K2O) (Peters Excel; Everis NA, Dublin, OH, USA). Between Apr. and May 2013, plants were transferred to raising beds at the GCREC experimental farm under a seepage irrigation system. Each plant was fed with 7.5 g of controlled-release fertilizer (Osmocote, 18N-2.6P-10K).

Phenotyping

While grown in the field, caladium progeny were phenotype for two leaf background colors (lemon or green), two leaf shapes (fancy or lance), leaf spotting (present or absent), three main vein colors (red, white or green), and leaf rugosity (present or absent) between Jun. and Sept. 2014. The phenotype of each progeny was examined at least four times and confirmed by at least two persons.

Data analysis

Segregation of leaf background color as well as leaf shape, main vein color, spotting, and rugosity in various caladium populations was examined by chi-square test for goodness of fit against expected Mendelian segregation ratios. Contingency chi-square tests were conducted for identification of possible independence or linkage between loci using the program developed by Preacher.15 To calculate the recombination frequency between traits, the number of recombinant progeny was divided by the total number of progeny in a population and multiplied by 100. Recombination frequencies were then converted to genetic distances in centiMorgan (cM) using the Kosambi’s mapping function {\[m = \frac{1}{2} \log_2 \left(1 + \frac{r^2}{2}\right)\]} × 100, where m represents genetic distance between loci and r is recombination frequency.

Table 1. Phenotypes and genotypes (inferred) of seven commercial caladium cultivars and three breeding lines used as parents for crosses performed in this study

| Cultivar/breeding line | Leaf spotting | Leaf shape | Main vein color | Leaf rugosity | Leaf background color |
|------------------------|---------------|------------|-----------------|---------------|----------------------|
|                        | Phenotype     | Genotypea | Phenotype       | Genotypea     | Phenotype             | Genotypeb | Phenotype | Genotypeb | Phenotype | Genotypeb |
| 'Aaron'                | No            | ss         | Fancy          | FF            | White                | v'v'v'    | No        | rfrfrf    | Green     | lemlem    |
| ‘Candidum’             | No            | ss         | Fancy          | FF            | Green                | v'v'v'    | No        | rfrfrf    | Green     | lemlem    |
| ‘Fairytale Princess’   | No            | ss         | Lance          | FF            | Red                  | v'v'v'    | No        | rfrfrf    | Green     | lemlem    |
| ‘Gingerland’           | Yes           | ss         | Lance          | FF            | White                | v'v'v'    | Yes       | RLfrfrf   | Green     | lemlem    |
| ‘Miss Muffet’          | Yes           | ss         | Fancy          | FF            | White                | v'v'v'    | No        | rfrfrf    | Lemon     | LEMlem    |
| ‘Fla. Moonlight’       | No            | ss         | Fancy          | FF            | Red                  | v'v'v'    | No        | rfrfrf    | Green     | lemlem    |
| ‘Red Flash’            | Yes           | ss         | Fancy          | FF            | White                | v'v'v'    | No        | rfrfrf    | Lemon     | LEMlem    |
| UF-52                  | No            | ss         | Fancy          | FF            | White                | v'v'v'    | No        | rfrfrf    | Lemon     | LEMlem    |
| UF-53                  | No            | ss         | Fancy          | FF            | White                | v'v'v'    | No        | rfrfrf    | Lemon     | LEMlem    |
| UF-317                 | Yes           | ss         | Fancy          | FF            | Green                | v'v'v'    | Yes       | RLfrfrf   | Green     | lemlem    |

aGenotypes of these cultivars or breeding lines for leaf shape, main vein color, leaf spotting, and leaf rugosity were determined previously,5–6 and they were reconfirmed in this study. bInferred in this study.
RESULTS

Inheritance of leaf background color in caladiums

When ‘Miss Muffet’ was selfed (Table 2; cross no. 1), progeny segregated in a ratio of 3 (lemon): 1 (green) \((P = 0.521)\). This segregation ratio suggests that the leaf background color is controlled by a single nuclear locus with a dominant allele for the lemon background color and a recessive allele for the green background color, and that ‘Miss Muffet’ should be heterozygous at this locus. When ‘Miss Muffet’ was crossed with ‘Gingerland’ or ‘Candidum’ (Table 2; cross no. 2–5), their progeny segregated in a ratio of 1 (lemon): 1 (green) \((P = 0.265–0.685)\). This segregation ratio was observed in crosses ‘Miss Muffet’ × ‘Red Flash’, ‘Aaron’ × ‘Miss Muffet’, ‘Fla. Moonlight’ × ‘Miss Muffet’ (Table 2; cross no. 5–7) \((P = 0.167–0.577)\). These results suggested that maternal factors were not involved in the inheritance of leaf background color.

When green-colored parents, including ‘Gingerland’, ‘Candidum’, ‘Red Flash’, ‘Fla. Moonlight’, ‘Fairytale Princess’, ‘Aaron’ and UF-317, were crossed (Table 2; cross no. 9–16), their progeny all exhibited green leaves, suggesting that these parents are homozygous recessive for leaf background color.

Two breeding lines (UF-52 and UF-53) also exhibited lemon-colored leaves; they were selected to produce additional segregating populations to validate the above inferred mode of inheritance for leaf background color. Progeny of crosses UF-52 × UF-317 and UF-53 × ‘Gingerland’ (Table 2; cross no. 17 and 18) segregated in 1 (lemon): 1 (green) \((P = 0.325–0.435)\). When UF-52 and ‘Miss Muffet’ were crossed (Table 2; cross no. 19), their progeny segregated in an anticipated ratio of 3 (lemon): 1 (green) \((P = 0.611)\). These results support the above inference that a single nuclear locus controls leaf background color and also suggest that UF-52 and UF-53 have a heterozygous genotype at the leaf background color locus.

We propose \textit{LEM} as the gene symbol for the dominant allele controlling the lemon background color and \textit{lem} for the recessive allele controlling the green leaf background color. Therefore, ‘Miss Muffet’, UF-52, and UF-53 have a heterozygous genotype of \textit{LEMlem}, while ‘Aaron’, ‘Candidum’, ‘Fairytale Princess’, ‘Gingerland’, ‘Fla. Moonlight’, ‘Red Flash’, and UF-317 possess a recessive genotype of \textit{lemlem}.

Figure 1. Typical leaves of ‘Miss Muffet’ (a: fancy, rugose, spotted, white-veined, and lemon background color), ‘Candidum’ (b: fancy, non-rugose, non-spotted, green-veined, and green background color), and three progeny ([c: fancy, rugose, spotted, green-veined, and green background color], [d: fancy, non-rugose, spotted, white-veined, and green background color], and [e: fancy, non-rugose, non-spotted, white-veined, and lemon background color]) from the crosses between ‘Miss Muffet’ and ‘Gingerland’.
leaves. Previous studies showed that leaf spotting in caladium is controlled by a single locus with two co-dominant alleles, F and f, which form three genotypes FF, Ff, and ff conferring fancy, lance, and strap leaves, respectively. The lance-leaved 'Gingerland' has the FF genotype and fancy-leaved 'Miss Muffet' and UF-52 has a FF genotype. In this study, progeny of the cross between 'Gingerland' and 'Miss Muffet' (Table 3; cross no. 2 and 3) showed a segregation of 3:1 (spotted, lemon): 3 (spotted, green): 1 (green veined, lemon): 1 (green veined, green), as expected for independent inheritance of leaf background color and leaf main vein color. Progeny of two pseudo BC1 crosses, their progeny did not segregate in 3:1 (white veined, lemon): 3 (white veined, green), as expected for two loci under independent assortment. Progeny of two pseudo BC1 crosses, 'Miss Muffet' and 'Candidum' (Table 5; cross no. 4 and 5), also did not segregate in 1:1 (white veined, lemon): 1 (green veined, green), as expected for independent inheritance of leaf background color and leaf main vein color (P < 0.001). Neither did the segregation in the cross UF-52×UF-317 (Table 5; cross no. 17) (P < 0.001). These results indicated a genetic relationship between leaf background color and leaf main vein color.
Table 3. Joint segregation of leaf shape (fancy or lance) and leaf background color (lemon or green) in progeny of three caladium crosses

| Cross (cross no.) | Progeny (no.) | Expect. ratio | χ² (P) |
|-------------------|---------------|---------------|--------|
|                   | Fancy (FF)    |                |        |
|                   | Lemon (LEM₂) | Green (lemlem) |        |
| 'Miss Muffet' (FF LEMlem) × 'Gingerland' (FF lemlem) [2] | 64 | 79 | 60 | 63 | 1:1:1:1 | 3.26 (0.35) |
| 'Gingerland' (FF lemlem) × 'Miss Muffet' (FF LEMlem) [3] | 89 | 87 | 76 | 95 | 1:1:1:1 | 2.18 (0.53) |
| UF-53 (FF LEMlem) × 'Gingerland' (FF lemlem) [4] | 21 | 18 | 16 | 11 | 1:1:1:1 | 3.21 (0.36) |

*Segregation ratio expected for independent inheritance between leaf shape and leaf background color. bTwo possible genotypes (LEMLEM or LEMlem, generalized as LEM₂ here) produce the lemon background color, and only the recessive genotype (lemlem) produces the green background color.

Table 4. Joint segregation of leaf spotting (present or absent) and leaf background color (lemon or green) in progeny of five caladium crosses

| Cross (cross no.) | Caladium progeny (no.) | Expect. ratio | χ² (P) | Recombination (%) |
|-------------------|-------------------------|---------------|--------|-------------------|
|                   | Spotted (S₁)            | Non-spotted (ss) |     |                   |
|                   | Lemon (LEM₂) | Green (lemlem) | Lemon (LEM₂) | Green (lemlem) |     |                   |
| 'Miss Muffet' (S lem//s LEM) × 'Gingerland' (S lem//s lem) [2] | 70 | 130 | 54 | 12 | 3:3:1:1 | 47.618 (P < 0.001) | 9.02 |
| 'Gingerland' (S lem//s lem) × 'Miss Muffet' (S lem//s LEM) [3] | 103 | 172 | 62 | 10 | 3:3:1:1 | 65.903 (P < 0.001) | 5.76 |
| 'Miss Muffet' (S lem//s LEM) × 'Candidum' (S lem//s lem) [4] | 6 | 294 | 293 | 15 | 1:1:1:1 | 527.171 (P < 0.001) | 3.45 |
| 'Candidum' (S lem//s lem) × 'Miss Muffet' (S lem//s LEM) [5] | 17 | 323 | 307 | 12 | 1:1:1:1 | 548.958 (P < 0.001) | 4.40 |
| 'Fla. Moonlight' (s lem//s lem) × 'Miss Muffet' (S lem//s LEM) [15] | 2 | 38 | 50 | 1 | 1:1:1:1 | 82.582 (P < 0.001) | 3.30 |
| 'Aaron' (s lem//s lem) × 'Miss Muffet' 2 (S lem//s LEM) [16] | 4 | 83 | 96 | 8 | 1:1:1:1 | 153.286 (P < 0.001) | 6.28 |

Average 5.37 (±2.15)

*Two possible genotypes (LEMLEM or LEMlem, generalized as LEM₂ here) produce the lemon background color, and only the recessive genotype (lemlem) produces the green background color. Two possible genotypes (SS or Ss, generalized as S₁ here) produce the spotted progeny, and only the recessive genotype (ss) produces non-spotted progeny. *Segregation ratio expected for independent inheritance between leaf spotting and leaf background color. *Recombination frequencies in these populations were calculated as follows: [(no. of non-spotted and green progeny/total no. of progeny) × 2] × 100. *Recombination frequencies in these pseudo BC₁ populations were calculated as follows: [(no. of spotted and lemon progeny + no. of non-spotted and green progeny)/total no. of progeny] × 100.
Table 5. Joint segregation of leaf background color (lemon or green) and main vein color (white or green) in progeny of four caladium crosses

| Cross [cross no.] | Caladium progeny (no.) | Expect. ratio | χ² (P) | Recombination (%) |
|-------------------|------------------------|--------------|--------|-------------------|
|                   | White veined (Vw_ b)   |              |        |                   |
|                   | Lemon (LEM_ b)         | Green (lemlem) |          |                   |
| 'Miss Muffet' (Vw LEN/Vg lem) × 'Gingerland' (Vw lem/Vg lem) [2] | 116 | 78 | 8 | 64 | 3:3:1:1 | 55.003 (P < 0.001) | 6.02 c |
| 'Gingerland' (Vw lem/Vg lem) × 'Miss Muffet' (Vw LEN/Vg lem) [3] | 147 | 99 | 18 | 83 | 3:3:1:1 | 83.906 (P < 0.001) | 10.37 c |
| 'Miss Muffet' (Vw LEN/Vg lem) × 'Candidum' (Vg lem/Vg lem) [4] | 293 | 14 | 6 | 295 | 1:1:1:1 | 530.855 (P < 0.001) | 3.29 d |
| 'Candidum' (Vg lem/Vg lem) × 'Miss Muffet' (Vw LEN/Vg lem) [5] | 310 | 11 | 14 | 324 | 1:1:1:1 | 563.416 (P < 0.001) | 3.79 d |
| UF-52 (Vw LEN/Vg lem) × UF-317 (Vg lem/Vg lem) [17] | 64 | 5 | 3 | 73 | 1:1:1:1 | 115.685 (P < 0.001) | 5.51 d |
| Average | 5.80 (± 2.80) |

Two possible genotypes (VwVw and VwVg, generalized as Vw_ here) in these crosses produce white-veined progeny, and the recessive genotype (VgVg) produces green-veined progeny. Two possible genotypes (LEMLEM or LEMlem, generalized as LEM_ here) produce the lemon background color, and the recessive genotype (lemlem) produces the green background color. Segregation ratio expected for independent inheritance between leaf main vein color and leaf background color. Recombination frequencies in these populations were calculated as follows: [(no. of green-veined and lemon progeny/total no. of progeny) × 2] × 100.

Table 6. Joint segregation of leaf background color (lemon or green) and leaf rugosity (rugose or flat) in progeny of four caladium crosses

| Cross [cross no.] | Caladium progeny (no.) | Expect. Ratio | χ² (P) | Recombination (%) |
|-------------------|------------------------|--------------|--------|-------------------|
|                   | Rugose (RLF_ b)        |              |        |                   |
|                   | Lemon (LEM_ b)         | Green (lemlem) |          |                   |
| 'Miss Muffet' (LEM rlf/lem RLF) × 'Gingerland' (lem RLF/lem rlf) [2] | 41 | 94 | 40 | 15 | 3:3:1:1 | 69.832 (P < 0.001) | 15.79 c |
| 'Gingerland' (lem RLF/lem rlf) × 'Miss Muffet' (LEM rlf/lem RLF) [3] | 69 | 106 | 43 | 17 | 3:3:1:1 | 73.681 (P < 0.001) | 14.47 c |
| 'Miss Muffet' (LEM rlf/lem RLF) × 'Candidum' (lem rlf/lem rlf) [4] | 29 | 272 | 270 | 37 | 1:1:1:1 | 372.882 (P < 0.001) | 10.86 d |
| 'Candidum' (lem rlf/lem rlf) × 'Miss Muffet' (LEM rlf/lem RLF) [5] | 62 | 295 | 262 | 40 | 1:1:1:1 | 318.924 (P < 0.001) | 15.48 d |
| Average | 14.15 (± 2.26) |

Two possible genotypes (RLFRLF and RLFrlf, generalized as RLF_ here) produce rugose progeny, and the recessive genotype (rlfrlf) produces the non-rugose progeny. Two possible genotypes (LEMLEM or LEMlem, generalized as LEM_ here) produce the lemon background color, and the recessive genotype (lemlem) produces green background color. Segregation ratio expected for independent inheritance between leaf rugosity and leaf background color. Recombination frequencies in these populations were calculated as follows: [(no. of non-rugose and green progeny/total no. of progeny) × 2] × 100. Recombination frequencies in these pseudo BC1 populations were calculated as follows: [(no. of white-veined and green progeny + no. of green-veined and lemon progeny)/total no. of progeny] × 100.
genetic linkage between leaf main vein color and leaf background color.

In three pseudo BC₁ populations (Table 5; cross no. 4, 5 and 17), significantly more progeny with white vein and lemon leaf background or with green vein and green leaf background were observed than expected, indicating a repulsion phase between white veined allele (V<sup>g</sup>) and green leaf background allele (lem).

In cross no. 2 and 3 (Table 5), only one type of recombinants could be identified and they showed green veins and lemon background color. The recombination frequencies between V and LEM loci were estimated to be between 6.02 and 10.37%. In the three pseudo BC₁ populations (Table 5; cross no. 4, 5 and 17), two types of recombinants were present, white-veined progeny with green leaf background color, and green-veined progeny with lemon color. The recombination frequencies between V and LEM loci in these crosses varied from 3.29 to 5.51%. The average recombination frequency from these crosses was 5.80% (Table 5).

Genetic relationship between leaf background color and leaf rugosity

Both rugose leaf and leaf background color segregated in the progeny of four crosses (Table 6). A previous study has shown that leaf rugosity in ‘Miss Muffet’ and ‘Candidum’ and other caladium cultivars is controlled by a single nuclear locus with a dominant rugose leaf allele (RLF) and a recessive non-rugose leaf allele (rlf). The genotype of ‘Miss Muffet’ (rugose) and ‘Candidum’ (non-rugose) for the leaf rugosity locus is heterozygous (RLFrlf) and homozygous recessive (rlfrlf), respectively.6

Progeny of the crosses between ‘Miss Muffet’ and ‘Gingerland’ (Table 6; cross no. 2 and 3) did not segregate in 3 (rugose, lemon): 1 (non-rugose, lemon): 1 (non-rugose, green), as expected for two independently inherited loci (P < 0.001). Similarly, the segregation of rugose leaf and leaf background color in the progeny of pseudo BC₁ populations of ‘Miss Muffet’ and ‘Candidum’ (Table 6; cross no. 4 and 5) deviated from 1 (rugose, lemon): 1 (rugose, green): 1 (non-rugose, lemon): 1 (non-rugose, green), as expected for two independently inherited loci (P < 0.001).

In cross no. 2 and 3 (Table 6), one type of recombinants was identified, and they were non-rugose and had the green leaf background color. The recombination frequencies in these crosses were estimated to be 14.47 to 15.79% (Table 6). In two pseudo BC₁ populations (Table 5; cross no. 4 and 5), two types of recombinants were identified: rugose and lemon progeny, and non-rugose and green progeny. The recombination frequencies in these two BC₁ crosses were 10.86 to 15.48%. The average recombination frequency between the rugose leaf and the leaf background color loci in these populations was 14.15% (Table 6).

Genetic distance and gene order among main vein color, leaf spotting, rugose leaf, and leaf background color

Progeny of the crosses between ‘Miss Muffet’ and ‘Candidum’ segregated for four characters, main vein color, leaf spotting, rugose leaf, and leaf background color.

Table 7. Joint segregation of four foliar traits, main vein color, spotting, rugosity and background color in progeny of ‘Miss Muffet’ (V<sup>g</sup> s lem RLF) and ‘Candidum’ (V<sup>y</sup> s lem rlf //Vg s lem rlf)

| Type of progeny | Parental types | Single crossover I (between RLF and S) | Single crossover II (between S and V<sup>r</sup>) | Single crossover III (between LEM and V<sup>r</sup>) | Double crossover I (between RLF and S, and between S and V<sup>r</sup>) | Double crossover II (between S and V<sup>r</sup>, and between V<sup>r</sup> and LEM) | Double crossover III (between RLF and S, and between LEM and V<sup>r</sup>) | Triple crossover (between RLF and S, between S and V<sup>r</sup>, and between V<sup>r</sup> and LEM) |
|----------------|----------------|----------------------------------------|----------------------------------------|----------------------------------------|------------------------------------------------|------------------------------------------------|------------------------------------------------|------------------------------------------------|
| No. of progeny | 1267           | 563                                    | 528                                    | 4                                      | 21                                           | 0                                           | 0                                           | 0                                           |
| Main vein color | Green (V<sup>y</sup>) | White (V<sup>y</sup>) | Green (V<sup>y</sup>) | Green (V<sup>y</sup>) | White (V<sup>y</sup>) | White (V<sup>y</sup>) | Green (V<sup>y</sup>) | White (V<sup>y</sup>) |
| Leaf spotting | Spotted (5s) | Non-spotted (ss) | Spotted (5s) | Non-spotted (ss) | Spotted (5s) | Non-spotted (ss) | Spotted (5s) | Non-spotted (ss) |
| Leaf background color | Green (lemlem) | Lemon (LEMlem) | Green (lemlem) | Lemon (LEMlem) | Green (lemlem) | Lemon (LEMlem) | Green (lemlem) | Lemon (LEMlem) |
| Leaf rugosity | Rugose (RLFrlf) | Non-rugose (rlfrlf) | Non-rugose (rlfrlf) | Non-rugose (rlfrlf) | Rugose (RLFrlf) | Non-rugose (rlfrlf) | Rugose (RLFrlf) | Non-rugose (rlfrlf) |

*Recombination frequency between RLF (leaf rugosity) and S (leaf spotting) was calculated using the following formula: (no. of progeny from single crossover I + no. of progeny from double crossover I + no. of progeny from double crossover III + no. of progeny from triple crossover)/total number of progeny × 100.6

**Recombination frequency between S (leaf spotting) and V<sup>r</sup> (rugosity) was calculated using the following formula: (no. of progeny from single crossover II + no. of progeny from double crossover II + no. of progeny from double crossover III + no. of progeny from triple crossover)/total number of progeny × 100.6

Recombination frequency between V<sup>r</sup> and LEM (leaf background color) was calculated using the following formula: (no. of progeny from single crossover III + no. of progeny from double crossover III + no. of progeny from triple crossover)/total number of progeny × 100.6

Recombination frequency between RLF and S + recombination frequency between S and V<sup>r</sup> + recombination frequency between RLF and LEM = 14.84% in 1267 progeny.
Leaf background color is an important characteristic in many ornamental aroids. In *Aglaonema*, *Colocasia*, and *Dieffenbachia*, green, lemon, yellow, and black leaves have been observed in many cultivars.\(^{16,17}\) However, knowledge on the mode of inheritance for leaf background colors in these aroids has been lacking. Previous inheritance studies have shown that caladium and other aroids seem to share similar modes of inheritance for foliage characters.\(^{3,18,19}\) Knowledge gained on the mode of inheritance of leaf background color in caladium may be useful for study of the inheritance of leaf background colors in other aroids.

So far, a number of genes for leaf background colors have been mapped in several plant species.\(^{20}\) A single dominant gene *Pr*, encoding a R2R3 MYB transcription factor, controls anthocyanin accumulation patterns and purple leaves in *Brassica*.\(^{21}\) The yellow leaf trait in *rice* (*Oryza sativa*) is controlled by a recessive gene *leaf 8* (*yl8*), which reduces the content of total chlorophyll in rice leaves.\(^{22}\) Guan *et al*.\(^{23}\) showed that the yellow leaf trait in maize (*Zea mays*) is controlled by recessive gene *leaf-1* (*yl1-1*) that causes an abnormal chloroplast development in maize. These studies will be very useful for genetic mapping, molecular cloning, and functional analysis of the *LEM* gene that controls the leaf background color in caladium.

**CONFLICT OF INTEREST**

The authors declare no conflict of interest.

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Supplementary Information for this article can be found on the Horticulture Research website (http://www.nature.com/hortres)

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