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Research Article

Inheritance of Leaf Characters in Sweet Potato (*Ipomoea batatas* [L.] Lam.)

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Abstract: This study aimed to establish foundational knowledge regarding the inheritance patterns of two foliar traits (leaf morphology and midrib pigmentation) in *Ipomoea batatas*. To overcome the challenges associated with discretely classifying color and shape frequencies, five morphometric descriptors were employed. Two of these parameters addressed leaf shape (Circularity and Aspect Ratio), while three characterized the color of the central vein using the CIE L*a*b* color space. To elucidate the genetic control of these traits, parental genotypes exhibiting contrasting phenotypic attributes were selected, enabling the development of segregating populations. A total of 879 reciprocal crosses were performed, yielding 581 successful pollinations (63.87%). Incomplete dominance was observed for leaf morphology, with lobed leaves exhibiting dominance over the unlobed form. Regarding the circularity index, the highest frequency distribution (87.8%) fell within the 0.4 to 0.6 range. Segregation patterns for midrib color revealed a ratio of 4:1:4 among green, pink, and red phenotypes, respectively. Additionally, evidence of transgressive segregation was detected for both green and red pigmentation.

Keywords: Color, Crossing, Dominance, Shape, Sweet Potato

Introduction

The cultivated sweet potato (*Ipomoea batatas* [L.] Lam.) possesses a hexaploid genome, characterized by a somatic chromosome count of $2n = 6x = 90$ and a haploid number of $x = 15$ (King and Bamford, 1937). Determining whether its inheritance follows an allo- or autopolyploid pattern is essential for population genetics studies in this species. Recent molecular evidence suggests that sweet potato behaves as an autoallopolyploid, exhibiting partial preferential pairing during meiosis (Kriegner et al., 2003), while other studies support an autopolyploid nature (Mollinari et al., 2020).

Shiotani and Kawase (1987) suggested that the genomic formula of I. batatas is $B_1B_1B_2B_2B_2B_2$, where the B_1B_1 subgenome derives from a diploid ancestor and the $B_2B_2B_2B_2$ subgenome originates from a tetraploid ancestor. The tetraploid progenitor first appeared around 800,000 years ago. Subsequently, approximately 500,000 years ago, a cross occurred between this tetraploid form and a diploid parent, leading to the emergence of the sweet potato cultivars known today (Yang et al., 2017).

Evidence from genetic linkage mapping indicates that sweet potato exhibits polysomic inheritance patterns (Kriegner et al., 2003; Cervantes et al., 2008). Several inheritance models have been proposed for *I. batatas*, including disomic, tetrasomic, tetradisomic, and hexasomic patterns (Jones, 1967; Cervantes et al., 2008). In a diploid species with a single biallelic locus, three genotypic classes exist (AA, Aa, aa). In contrast, an autohexaploid can exhibit up to seven possible genotypic combinations: A_6, A_5a, A_4a_2, A_3a_3, A_2a_4, Aa_5, and a_6 (Shiotani, 1989). When allele frequencies fall between roughly $q = 0.2$ and $q = 0.8$, the heterozygosity level in hexaploid populations consistently exceeds 0.75 (Grüneberg et al., 2015).

Phenotypic segregation in *I. batatas* has been the subject of multiple investigations, with particular emphasis on leaf morphology (Rangaswami and Sampathkumar, 1978; Vimala et al., 2012), stem pigmentation (Hernandez, 1942; Harmon, 1960), tuberous root shape (Poole, 1955), and skin and flesh coloration (Arizio et al., 2009; Vimala et al., 2012; Morales et al., 2024).

Despite the numerous inheritance studies on leaf shape and color in sweet potato, inconsistencies persist regarding the genetic control of these traits. This is largely attributed to the absence of homozygous genotypes, a consequence of sporophytic multiallelic self-

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incompatibility (Morales et al., 2019; 2025c). Additionally, challenges in visually discriminating color frequencies (particularly between cream and yellow tones, as well as among varying intensities of red) have been documented (Harmon, 1960; Arizio, 2021; Vimala et al., 2012). To address these limitations, objective numerical color expression can be achieved using color spaces such as CIE L*a*b* (Morales et al., 2025a; 202b), where L represents luminosity, and a* and b* denote chromatic coordinates. Similarly, precise differentiation of leaf shapes can be accomplished using two morphometric variables (Circularity and Aspect Ratio) analyzed through professional digital image analysis software.

The main objective of this study is to provide foundational knowledge regarding the inheritance pattern of two foliar traits.

Materials and Methods

Study Area

The controlled crossing experiment took place at the Tropical Viands Research Institute (INIVIT) in Santo Domingo, Villa Clara Province, Cuba (coordinates: 22° 35′ 00″ N, 80° 14′ 18″ W; elevation: 50 m above sea level). Conducted between August 2022 and March 2023 under open-air conditions, the trial was planted in a soft brown carbonated soil type (Hernández et al., 2015).

Crossing Blocks

A total of four parental lines, previously confirmed as cross-compatible, were chosen for this study. In the final week of August 2022, twenty stakes per parent were planted at 1 m intervals in both directions. Weather information was collected via the institution's automated meteorological station (network identifier: 78326; data accessible at: http://www.insmet.cu).

The controlled crossing procedure commenced in early December 2023. Female-designated flowers were emasculated during the afternoon of the day preceding pollination and subsequently covered with hollow sections cut from large absorbent straws (0.7 cm inner diameter, approximately 3 cm in length). Male flowers used as pollen donors received identical covers without undergoing emasculation. Pollen transfer was carried out the next morning between 07:00 and 10:00 h. After pollination, each flower received a label indicating the parental combination and was once again covered with a straw section. A daily log was kept to record all crossing activities. Irrigation was supplied as needed to maintain the plants in a moderately vigorous condition.

Botanical Seeds and Seedlings

Seeds were collected once the flower pedicels became necrotic, sorted by cross combination, cleaned, and stored in paper envelopes. Physical scarification was performed using nail clippers. One day prior to sowing, seeds were placed in Petri dishes with water to a depth of approximately 2 mm. In June 2023, seeds were sown in CRAS (Center for Accelerated Seed Reproduction) chambers at INIVIT, with a spacing of 5 cm between seedlings and 20 cm between rows, and grown for up to 50 days. From each F1 seedling, a 30 cm cutting was taken from the apical stem portion. Field planting was conducted in July 2023 at a spacing of 0.90 × 0.50 m. In November of the same year, seedlings were harvested, and foliage from each individual was placed separately in paper bags labeled with the corresponding family code.

Characters Investigated

To elucidate the inheritance pattern of leaf shape and central vein color, parents with contrasting phenotypic traits were selected to generate segregating populations. The selected parents and their phenotypic characteristics are summarized in Table 1.

Morphometric Variables

Five morphometric variables were employed (Table 2). Two variables pertained to leaf shape (Circularity and Aspect Ratio), while three variables characterized central vein color using the CIEL*a*b* color system established by the International Commission on Illumination (X-Rite, 2002). In this system, L* corresponds to brightness, a* indicates the red-green axis (positive readings reflect red tones, while negative values denote green tones), and b* represents the yellow-blue axis (positive values correspond to yellow hues and negative values to blue hues). A Canon EOS 600D camera was used to obtain RGB photographs from every sample.

Table 1: Selected parents and their contrasting phenotypic traits

Characters investigated	Parent 1	Phenotype	Parent 2	Phenotype
Leaf shape	CEMSA 74-228	Lobed leaf	INIVIT BM-90	Leaf without lobes
Central vein color	INIVIT BS-16	Red vein	INIVIT BM-8	Green vein

Table 2: Morphometric variables used in the study

Variables	Code	Formula
Circularity	C	$\frac{4\pi * (A)}{P^2}$
Aspect Ratio	AR	$\frac{Ema}{Eme}$
Luminosity	L*	-
a* coordinate	a*	-
b* coordinate	b*	-

Subsequent image processing was carried out with ImageJ version 1.46 (National Institutes of Health), a Java-based program designed for professional digital image analysis.

Prior to photography, leaves were washed and dried. Three measurements were taken from the central vein of each genotype. All measurements were conducted under controlled environmental conditions: temperature (20 ± 2°C), relative humidity (75 ± 5%), and illumination (500 lx).

Statistical Analysis and Visualization

The following formulas were used to estimate the genetic parameters:

$$\sigma_p^2 = \sigma_g^2 + \sigma_e^2 \qquad (1)$$

Where:

σ_p^2: Phenotypic variance
σ_g^2: Genotypic variance
σ_e^2: Environmental variance

$$\sigma_p^2 = \frac{\sum(Fi-m)^2}{n-1} \qquad (2)$$

Where:

Fi: Term of the data set
M: Medium
N: Number of observations

In the parents, it is inferred that phenotypic differences correspond to environmental differences: $\sigma_g^2 = 0$, $\sigma_p^2 = \sigma_e^2$. To determine the σ_p^2 y σ_g^2 of the progeny, it is taken as σ_e^2 the σ_p^2 of the parents.

Heritability in the broad sense:

$$H^2 = \frac{\sigma_g^2}{\sigma_p^2} * 100 \qquad (3)$$

Statistical differences among observed frequencies were assessed using the non-parametric Pearson chi-square (χ^2) goodness-of-fit test. Data processing, evaluation, and visualization were conducted using RStudio version 2023.03.1. Graphs were generated using the ggplot2 package (Wickham, 2016). Histograms were created with geom_histogram(), scatterplots with geom_jitter() and ggMarginal(), and density contour plots with geom_density_2d(). Color schemes were selected from ColorBrewer (Harrower and Brewer, 2003) and viridis (Garnier, 2017).

Results

Pollinations

A total of 879 reciprocal crosses were performed, of which 581 resulted in successful capsule formation (63.87%). A total of 678 botanical seeds were obtained, with an average of 1.26 seeds per capsule. The mean seed germination rate was 78.3%. Ultimately, 528 seedlings were produced, comprising 311 from the ISS-2301 family and 217 from the ISS-2304 family (Table 3).

Leaf Shape

The population derived from crossing a lobed-leaf parent (CEMSA 74-228; Circularity = 0.18) with an unlobed-leaf parent (INIVIT BM-90; Circularity = 0.58) consisted of 311 individuals and exhibited a mean circularity value of 0.49. The frequency distribution was left-skewed, with 87.8% of observations concentrated within the 0.4 to 0.6 range (moderately lobed leaves). Frequency dispersion decreased toward the extremes, with fewer individuals exhibiting either highly lobed or completely unlobed leaves. Circularity was selected as the primary morphometric descriptor due to its high sensitivity to leaf lobing, whereas other shape indices may yield proportional values irrespective of lobulation (Figure 1B).

Broad-sense heritability was estimated at 90.78%, indicating that the majority of phenotypic variation in leaf shape is attributable to genetic factors. The low genotypic variance observed among parents further suggests that environmental effects contributed minimally to the observed variation.

Segregation patterns for leaf shape within the full-sib family ISS-2301 were visualized using scatter plots of the two morphometric descriptors (Aspect Ratio × Circularity) (Figure 1A). The majority of the population exhibited Circularity values > 0.4 and Aspect Ratio values < 1.25, indicating a predominance of progeny with lobed leaves. Density contour plots (Figure 1C) revealed greater color intensity in the lower-right quadrant, consistent with the frequency distribution shown in the histogram. Observed segregation frequencies did not conform to Mendelian expectations (χ^2=105.26, $p<0.05$). These results support incomplete dominance for leaf shape inheritance, with the lobed leaf phenotype dominant over the unlobed type. The segregation ratio among lobed, moderately lobed, and unlobed leaves was 2:7:1, respectively.

Central Vein Color

The population (n = 217) derived from crossing a red-veined parent (INIVIT BS-16; L* = 23.14) with a green-veined parent (INIVIT BM-8; L* = 47.26) exhibited a mean luminosity value of 37.36. The frequency distribution was bimodal, with two peaks and a lower frequency observed in the central region (Figure 2B). Broad-sense heritability for central vein color was estimated at 97.80%, indicating that phenotypic variation is predominantly under genetic control.

Table 3: Results of controlled pollinations among selected parents

Parental	Family	No. of pollinations	No. of capsules	% positive pollinations	No. of seeds	No. of seeds/capsule	% seed germination	No. *seedlings*
CEMSA 74-228 x INIVIT BM-90	ISS-2301	556	400	71.88	408	1.02	76.3	311
INIVIT BS-16 x INIVIT BM-8	ISS-2304	323	181	55.86	270	1.5	80.3	217
Average		-	-	63.87	-	1.26	78.3	-
Total		879	581	-	678	-	-	528

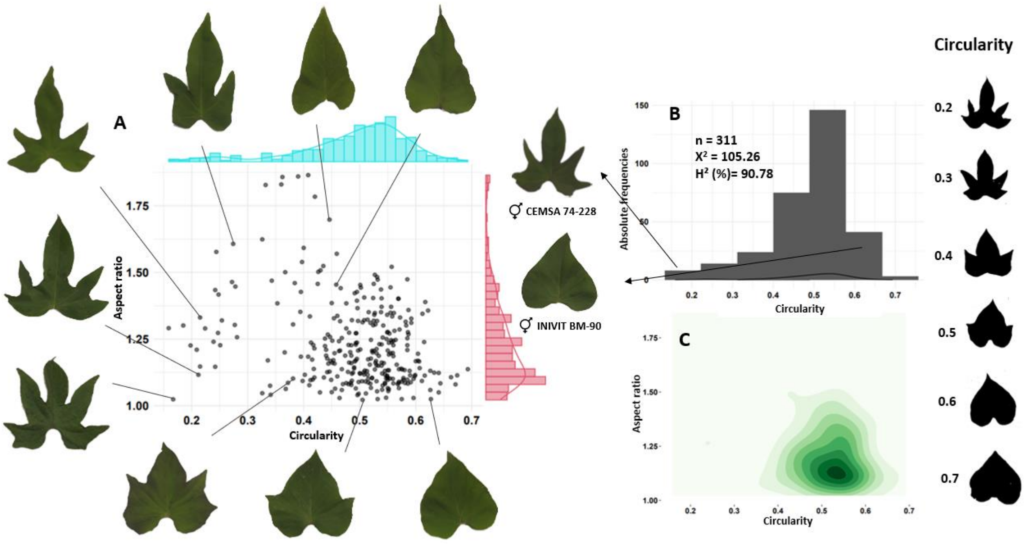

Fig. 1: Morphometric analysis of leaf shape. (A) Scatter plot of Aspect Ratio versus Circularity; (B) absolute frequency histogram for Circularity; (C) density contour plot for Aspect Ratio versus Circularity

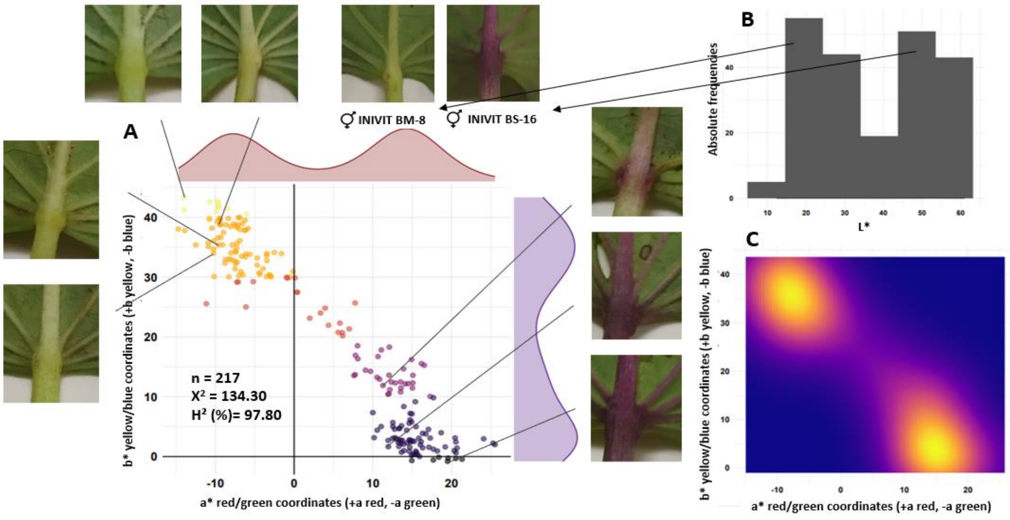

Fig. 2: Color analysis of the central vein using the CIE L*a*b* color space. (A) Scatter plot of a* versus b* coordinates; (B) absolute frequency histogram for L* (luminosity); (C) density contour plot for a* versus b* coordinates

Segregation patterns for central vein color within the full-sib family ISS-2304 were visualized using scatter plots (Figure 2A). The population was nearly equally distributed between red and green color phenotypes. Density contour plots (Figure 2C) showed similar intensity toward both color extremes, suggesting incomplete dominance in the inheritance of red and green pigmentation. Observed segregation frequencies did not conform to Mendelian expectations ($\chi^2 = 134.30$, $p<0.05$). The segregation ratio among green, pink, and red phenotypes was 4:1:4, respectively. Additionally, transgressive segregation was observed for both green and red color phenotypes, indicating the presence of progeny exhibiting more extreme expression than either parent.

Discussion

Pollinations

None of the crossing combinations achieved 100% successful pollinations. This outcome can be attributed to multiple factors, including variations in pollen fertility, environmental conditions at the time of crossing, and inherent biological constraints (Morales et al., 2023; 2024). Furthermore, lower gametic fertility is linked to meiotic irregularities frequently found in hexaploid sweet potato, as aberrant chromosome pairing during meiosis can impair the formation of functional gametes (Reynoso et al., 1998; Morales et al., 2025c).

The frequency of successful capsule formation following controlled pollinations in sweet potato varies considerably across studies. Reported values range from 30% to 75% (Arizio, 2021), 63.21% (Kambale et al., 2018), and 35% to 87% (Lestari et al., 2019). Similarly, seed set per capsule has been documented as 1.2 (Arizio et al., 2009), between 1.10 and 1.68 (Rukarwa et al., 2013), and less than 2 (Lestari et al., 2019). The values obtained in the present study (63.87% successful pollinations and 1.26 seeds per capsule) are consistent with these previously reported ranges, confirming that the crossing methodology employed was effective and yielded results comparable to those in the literature.

Inheritance of Leaf Shape

The inheritance pattern observed for leaf shape in this study supports incomplete dominance, with the lobed leaf phenotype exhibiting dominance over the unlobed form. This finding is consistent with earlier reports by Harmon (1960); Rangaswami and Sampathkumar (1978), who also described incomplete dominance of deeply lobed leaves. However, it contrasts with the conclusions of Poole (1955), who reported incomplete dominance of the unlobed leaf over the lobed type. Similarly, Vimala et al. (2012), in a large-scale study involving 1,630 seedlings from controlled crosses, observed a predominance of unlobed leaves and noted that deeply lobed forms occurred at low frequencies (1.66%).

These discrepancies in reported inheritance patterns may be explained by several factors inherent to the genetic architecture of sweet potato. As a hexaploid species, sweet potato exhibits complex polysomic inheritance, where multiple alleles at each locus and dosage effects can significantly influence phenotypic expression (Jones, 1967; Cervantes et al., 2008). According to Franklin and Jones (1986), segregation ratios in sweet potato crosses are often complex, although simple Mendelian ratios may occasionally be observed when a single dominant allele is present. However, the presence of homozygosity at certain loci can distort simple ratios, leading to continuous rather than discrete segregation patterns. When dosage effects are operative, trait expression becomes quantitative, and clear-cut Mendelian ratios are unlikely to occur, even in cases where a single genetic locus largely controls the trait. The majority of agronomically relevant characteristics in sweet potato, leaf shape included, seem to follow quantitative inheritance patterns, which aligns with the continuous variation observed in our experimental populations.

The elevated broad-sense heritability value (90.78%) recorded for leaf morphology reinforces the notion that genetic factors predominantly govern this trait, while environmental effects play a minor role. The observed segregation ratio of 2:7:1 (lobed:moderately lobed:unlobed) deviated significantly from simple Mendelian expectations, reflecting the underlying hexaploid inheritance pattern. The absence of discrete classes and the continuous distribution of circularity values are consistent with a polygenic model or a single locus with dosage effects in a hexaploid background.

From a breeding perspective, leaf shape has practical implications for crop management. Cultivars with moderately lobed or unlobed leaves tend to achieve faster soil coverage, thereby reducing weed pressure and associated labor costs. Therefore, selecting parents with unlobed or moderately lobed leaves may facilitate the development of cultivars with improved early vigor and competitive ability against weeds.

Inheritance of Central Vein Color

To our knowledge, no prior studies have specifically addressed the inheritance pattern of central vein color in sweet potato. Therefore, our results are discussed in the context of stem pigmentation inheritance, which is likely controlled by similar genetic mechanisms due to the shared anthocyanin biosynthetic pathway.

Poole (1955), studying a population of 452 self-fertilized seedlings, proposed that a major pair of alleles governs red versus green pigmentation in stems and leaves, reporting a 3:1 (red:green) segregation ratio. However, Poole also noted the difficulty of discretely classifying color phenotypes due to overlapping intensities of red pigmentation, a challenge that we circumvented in the present study by employing the objective CIE L*a*b* color space.

Subsequent investigations have yielded contrasting results. Wada (1935), as cited by Poole (1955), reported partial dominance of green stem over red, also with a 3:1 ratio. Hernandez (1942) suggested that stem color inheritance is more complex, likely involving gene interactions and multiple loci. Harmon (1960) further proposed that purple stem pigmentation may be controlled by recessive genes, with quantitative expression and cumulative effects. Additionally, complementary gene action has been suggested as a potential mechanism influencing stem color (Harmon, 1960).

Collins (1992) examined the inheritance of nectary coloration (yellow vs. green) in *Ipomoea trifida*, a wild species closely related to sweet potato, and determined that this trait is governed by a minimum of one gene, wherein green exhibits monogenic dominance over yellow.

In the present study, the segregation pattern observed for central vein color 4:1:4 (green:pink:red) deviated significantly from simple Mendelian expectations ($\chi^2 = 134.30$, $p<0.05$) and did not conform to previously reported ratios. The bimodal distribution and the presence of pink intermediates suggest incomplete dominance, while the near-equal distribution between green and red phenotypes indicates that both parental alleles contribute substantially to the progeny. The estimated broad-sense heritability (97.80%) reflects strong genetic control with minimal environmental influence.

Notably, we observed transgressive segregation for both green and red color phenotypes, indicating the presence of progeny exhibiting more extreme pigmentation than either parent. This phenomenon is often attributed to the segregation of complementary alleles or the accumulation of favorable alleles at multiple loci in a polygenic system (Hernandez, 1942). In the context of hexaploid sweet potato, transgressive segregation may also arise from dosage effects, where different allelic combinations at multiple homologous loci produce additive or synergistic effects on pigment accumulation.

The ratio of 4:1:4 observed in this study (with equal proportions of green and red phenotypes and a smaller intermediate pink class) suggests a genetic model involving multiple loci with dosage sensitivity, consistent with the hexaploid nature of sweet potato. Future studies employing molecular markers and Quantitative Trait Locus (QTL) mapping will be necessary to elucidate the specific genetic architecture underlying central vein color inheritance.

Conclusion

The application of five morphometric variables enabled objective characterization of leaf shape and central vein color in sweet potato, overcoming the limitations of visual classification. High broad-sense heritability estimates (90.78% for leaf shape and 97.80% for central vein color) confirmed that phenotypic variation is primarily under genetic control. Incomplete dominance was observed for both traits: lobed leaf over unlobed type for leaf morphology, and red and green pigmentation with intermediate pink phenotypes for central vein color, exhibiting a segregation ratio of 4:1:4 (green:pink:red). Additionally, transgressive segregation was detected for both green and red pigmentation, suggesting complementary allele accumulation or dosage effects in this hexaploid species. These findings provide a foundation for sweet potato breeding programs targeting leaf architecture and pigmentation traits.

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Author's Contributions

Alfredo Morales and Dania Rodríguez : Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration: A. Morales, Resources, Software, Supervision, Validation, Visualization, Write original draft, Write review and edited.

Ethics

The corresponding author hereby declares that all co-authors have reviewed and endorsed the final version of this manuscript, and that no ethical concerns arise from this study.

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