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Morphological and molecular characterization of selected species belonging to the genus *Silphium*

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Abstract
This study seeks to characterize and compare three *Silphium* species — *S. perfoliatum*, *S. integrifolium* var. larvae, and *S. laciniatum* — employing both morphological and molecular markers. Distinctive features among the species were observed through morphological analysis, highlighting variations in leaf morphology, stem architecture, and inflorescence attributes. Molecular diversity was evaluated using Polymerase Chain Reaction (PCR) amplification with Directed Amplification of Minisatellites DNA (DAMD) and Start Codon Targeted (SCoT) primers, which generated reliable and polymorphic banding profiles. The profiles revealed genetic differences between species, matching their morphological variations. Molecular data confirmed their taxonomic separation and indicated moderate genetic divergence within the genus. Combining morphology and molecular analysis provided a thorough view of *Silphium* diversity and its relevance for future breeding and conservation efforts. These findings indicate that integrating phenotypic and molecular tools contributes to plant characterization and suggests that Silphium species may be suitable for research focused on perennial crop development and biodiversity conservation.

Keywords: genetic diversity, cup plant, molecular polymorphism, interspecific diversity, phenotypic traits

Introduction

The genus *Silphium* (Asteraceae) comprises perennial species valued for their adaptability, deep root systems, and substantial biomass production. In recent years, these plants have gained attention as models for developing perennial crops that support renewable energy and ecosystem restoration. Their agronomic and ecological traits make them relevant for studies linking phenotype, genotype, and sustainable productivity [26, 27].

Silphium perfoliatum (cup-plant) has been widely investigated for its bioenergetic potential and ecological resilience. Native to eastern North America, this diploid species (2n = 14) exhibits rapid growth, tolerance to moist soils, and high biomass yield, being considered a valuable candidate for bioenergy systems [9]. Comparative studies emphasize its role in sustainable agriculture and land restoration [11].

Silphium integrifolium (rosinweed) is regarded as a promising perennial oilseed crop due to its large seeds, drought tolerance, and wide adaptability. Recent genomic analyses have confirmed significant phenotypic variability and population structure, supporting selection and domestication efforts [20, 21, 23].

Silphium laciniatum (compass plant), native to North American prairies, is adapted to arid environments and represents an important model for studying ecological and genetic diversity. Compared with the first two species, it remains less investigated, justifying its inclusion in comparative analyses [15, 16].

Morphological and molecular characterization of these species is relevant for both agronomic and genetic perspectives. Perennial crops with deep roots improve soil stability, carbon sequestration, and long-term productivity, while maintaining high genetic variability useful for breeding and conservation [10, 26].

The present study aims to provide a comparative morphological and molecular characterization of *S. perfoliatum*, *S. integrifolium* (var. *laeve*), and *S. laciniatum*, with specific objectives to:

- Evaluate morphological variability among species (leaves, stems, inflorescences),
- Assess genetic diversity and similarity using SCoT and DAMD markers,
- Correlate phenotypic and molecular data to determine genotype relationships,
- Identify the potential for breeding and germplasm conservation within the genus *Silphium*.

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Materials and Method

Biological material

The biological material consisted of three *Silphium* species — *S. perfoliatum* L., *S. integrifolium* var. *laeve*, and *S. laciniatum* L. — selected for their agronomic and ecological relevance in studies of adaptability and genetic variability under the pedoclimatic conditions of western Romania [9, 11]. Plant material was obtained from experimental and greenhouse collections at the University of Life Sciences "King Mihai I" from Timișoara, cultivated under controlled conditions. Young, healthy leaves from uniformly developed plants were harvested at the optimal stage for DNA extraction and immediately processed to preserve genetic integrity [7].

Comparative morphological characterization of the studied species

Vegetative and reproductive descriptors characteristic of the Asteraceae family were analyzed: plant height (cm), number of fertile stems, leaf orientation and shape, leaf surface porosity, number and diameter of inflorescences, and root system.The selected traits are consistent with descriptors used in phenotypic and domestication studies within the genus *Silphium* [10, 11].

S. perfoliatum develops robust, quadrangular stems up to 3 m tall, with opposite perfoliate leaves that are lanceolate to triangular, dark green, and rough-textured [4]. *S. integrifolium* shows cylindrical, unbranched stems (0.4–2 m), opposite leaves at the base becoming alternate upwards, with entire margins and a firm texture, the lack of perfoliation distinguishes it from *S. perfoliatum* [11, 22].

S. laciniatum reaches 1–3.5 m, with deeply lobed basal leaves and less dissected upper ones, conferring a distinctive divided-leaf appearance typical of prairie species [15, 16]. *S. perfoliatum* and *S. integrifolium* both develop extensive fibrous root systems ensuring anchorage and moderate drought tolerance [1, 17], while *S. laciniatum* forms a deep taproot adapted to arid prairie conditions [15].

S. integrifolium has compact inflorescences with numerous ligulate flowers, ensuring high reproductive efficiency [24]. *S. perfoliatum* displays variable capitulum number per plant, correlated with environmental and technological factors, and is noted for its high reproductive and biomass potential [9, 13]. *S. laciniatum* produces large capitula with bright yellow ligulate flowers and later flowering compared to the other two species, reflecting adaptation to prairie ecosystems [15, 27].

DNA Extraction, Amplification and Data Analysis

Genomic DNA was extracted from young, healthy leaves of *Silphium perfoliatum*, *S. integrifolium* var. *laeve*, and *S. laciniatum* using the CTAB method described by Doyle and Doyle (1987), with modifications including the addition of 3% PVP-40 and 3% β-mercaptoethanol to the extraction buffer, extended incubation at 65 °C, and a double chloroform:isoamyl alcohol purification step, to ensure high DNA purity in polyphenol-rich *Silphium* tissues [7]. DNA quality and concentration were assessed spectrophotometrically, and samples with an A260/A280 ratio between 1.8 and 2.0 were used for amplification.

PCR amplification was carried out using two marker systems: SCoT (Start Codon Targeted) [5] and DAMD (Directed Amplification of Minisatellite DNA) [28]. Five primers from each system (SCoT 3, 6, 24, 34, 35, DAMD 1, 6, 7, 8, 9) were selected for their ability to detect inter- and intra-specific genetic variability within Asteraceae. Reactions were performed in a thermocycler under standard ISSR-type conditions, optimized for clear and reproducible amplification patterns.

The primer sequences used in this study were as follows:

SCoT primers
SCoT 3 (CAACAATGGCTACCACCA),
SCoT 6 (CAACAATGGCTACCACGG),
SCoT 24 (CAACAATGGCTACCACGA),
SCoT 34 (CAACAATGGCTACCACGT),
SCoT 35 (CAACAATGGCTACCACGC).
DAMD primers
DAMD 1 (TACAAGGCGGGAATCATT),
DAMD 6 (CCTTCCCTCCTCCTCCTC),
DAMD 7 (AGGAGGAGGAGGAGGAGA),
DAMD 8 (GTTAGGGAGGAGGAGGA),
DAMD 9 (GGAGGAGGAGGAGGAGGA).

Amplified products were separated by agarose gel electrophoresis (1.8%) in 1× TAE buffer and visualized under UV transillumination. Gel images were analyzed using GelAnalyzer 23.1, and reproducible bands were scored in binary format (1 = presence, 0 = absence). The resulting matrix was used to calculate Jaccard's similarity coefficient [13] and to generate UPGMA dendrograms through the DendroUPGMA online platform [8, 25].

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The dendrograms obtained from SCoT and DAMD markers were compared to assess the degree of genetic similarity among the three *Silphium* species. Statistical analyses were conducted at a significance level of $p < 0.05$, and results were interpreted comparatively to establish correlations between molecular and morphological variability [5, 10, 11, 26]

Results and Discussion

Morphological analysis

The comparative morphological evaluation of the three *Silphium* species revealed significant interspecific variation in plant architecture, leaf morphology, inflorescence structure, and root system type. The results confirm the high phenotypic plasticity characteristic of the genus.

Silphium perfoliatum exhibited the greatest average height (160–183 cm), with robust, often quadrangular stems showing moderate apical branching. *S. integrifolium var. laeve* showed an intermediate height (141–172 cm), cylindrical stems, and reduced branching, features associated with a uniform vegetative structure favorable for the development of fertile inflorescences.

S. laciniatum displayed erect, rigid stems reaching 150–190 cm, with one or several flowering stems per plant, reflecting adaptation to open prairie habitats. The differences in average height among the three species were statistically significant (ANOVA, $p < 0.01$), confirming their distinct ecological adaptations and agronomic potential [9, 11]. Clear interspecific differences were observed in leaf conformation. *S. perfoliatum* has opposite, connate-perfoliate leaves forming a basal cup capable of retaining rainwater — a diagnostic trait unique to this species [4]. *S. integrifolium* shows opposite or alternate sessile leaves with entire or slightly toothed margins and firm texture. *S. laciniatum* possesses large, deeply pinnate basal leaves and smaller, less divided upper leaves. The mean number of leaves per plant varied between 29–32 in *S. perfoliatum*, 26–32 in *S. integrifolium*, and 17–21 in *S. laciniatum*, depending on plant age and cultivation density.

Inflorescences are of the capitulum type in all three species, consisting of peripheral ligulate and central tubular flowers, yet their size and architecture differ markedly. *S. perfoliatum* develops numerous medium-sized inflorescences (3–5 cm), richly arranged on terminal branches, conferring high ornamental value. *S. integrifolium* forms fewer but slightly larger capitula (3–6 cm), with broad yellow ligulate flowers . *S. laciniatum* develops large capitula (5–8 cm) that are solitary or in small groups, with a later flowering period (July–September) compared to the other two species (June–Septembre).

All species presented well-developed root systems with distinct structural differences. *S. perfoliatum* and *S. integrifolium* form fibrous roots with numerous lateral branches, contributing to drought tolerance and stability. *S. laciniatum* develops a deep taproot exceeding 2 m, an adaptation typical of prairie ecosystems.

The size of the achenes varied slightly among species, averaging 6.7 × 3.1 mm in *S. integrifolium*, 5.8 × 2.9 mm in *S. perfoliatum*, and 7.1 × 3.6 mm in *S. laciniatum*. Variations in achene dimensions reflect differences in reproductive strategies and degrees of adaptation within the genus.

Table 1. Main morphological characteristics of the analyzed *Silphium* species

Morphological character	*S. perfoliatum*	*S. integrifolium*	*S. laciniatum*
Plant height (cm)	160–183	141–172	150–190
Leaf shape	lanceolate–ovoid, perfoliate	lanceolate–ovate, entire	pinnatifid, deeply dissected
Leaf arrangement	opposite, connate at base	opposite at base, alternate upward	basal, pinnately divided
Leaf texture	rough, pubescent	firm, slightly pubescent	scabrid, sparsely pubescent
Root system	fibrous, with lateral roots	fibrous, vegetatively regenerative	taproot, deep-penetrating
Number of flower heads/plant	170–247	1–12	7–18
Capitulum diameter (cm)	3–5	3–6	5–8
Flowering period	June–September	June–September	July–September

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Morphological character	*S. perfoliatum*	*S. integrifolium*	*S. laciniatum*
Inflorescence type	numerous, terminally arranged	few, reproductively efficient	solitary or clustered
Achene size (mm)	5.8 × 2.9	6.7 × 3.1	7.1 × 3.6

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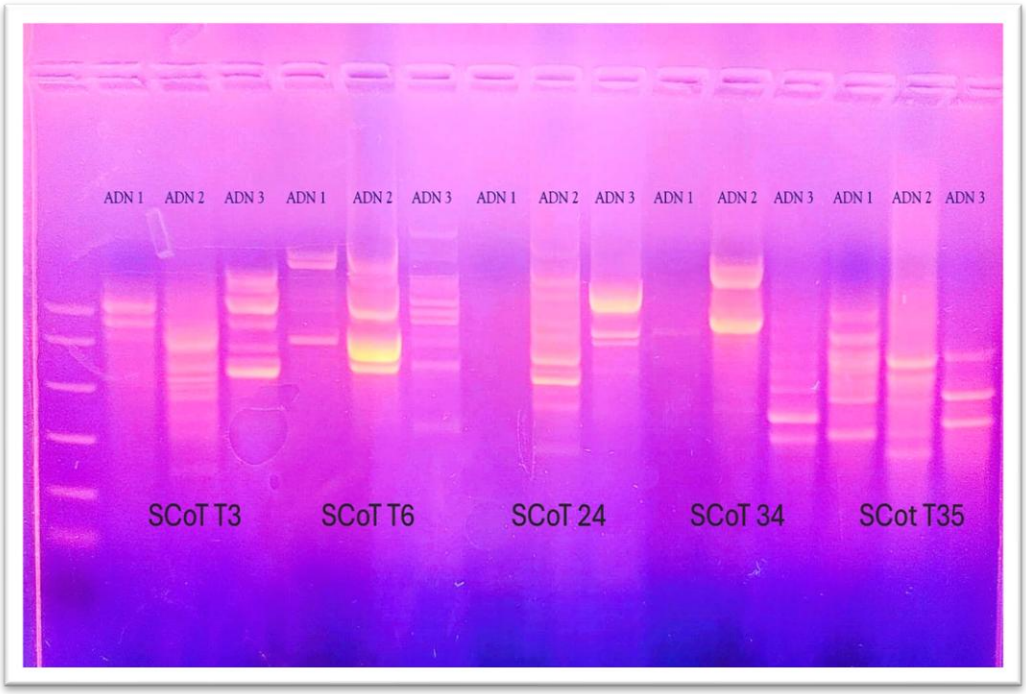
Table 1 summarizes the main morphological features observed among the three analyzed species, highlighting differences in vegetative and reproductive traits relevant for the interpretation of phenotypic variation and taxonomic delimitation. The comparative evaluation confirmed consistent interspecific differentiation in plant height, leaf shape, and inflorescence structure, supporting their distinct ecological adaptations.

Molecular Results – SCoT markers



DNA 1 - *S. laciniatum*
DNA 2 - *S.integrifolium*
DNA 3 - *S. perfoliatum*

Figure 1. Agarose gel electrophoresis profile generated by five SCoT primers in *Silphium* species

The molecular analysis performed with SCoT markers revealed a high level of polymorphism among the three *Silphium* species. The amplified fragments ranged from 200 to 2000 bp, demonstrating the efficiency of SCoT primers in differentiating related genotypes within the genus [5, 11].

A total of 16 amplification products were obtained, of which 15 (93.75%) were polymorphic, indicating a considerable degree of genetic variability. The calculated genetic parameters were as follows: He_mean = 0.129, Rp = 7.35, EMR = 15, MI = 1.94. These values confirm the high discriminatory capacity of the SCoT primers, comparable to those reported for other perennial Asteraceae [5, 23].

The similarity coefficients (Jaccard) were consistent with the literature, confirming a high level of both intra- and interspecific diversity.

Table 2. Jaccard similarity coefficients and genetic distances (1–J) among *Silphium* species (SCoT markers

Compared pair	Similarity coefficient (J)	Genetic distance (1–J)
S. perfoliatum – S. integrifolium	0.081	0.919
S. perfoliatum – S. laciniatum	0.200	0.800
S. integrifolium – S. laciniatum	0.286	0.714

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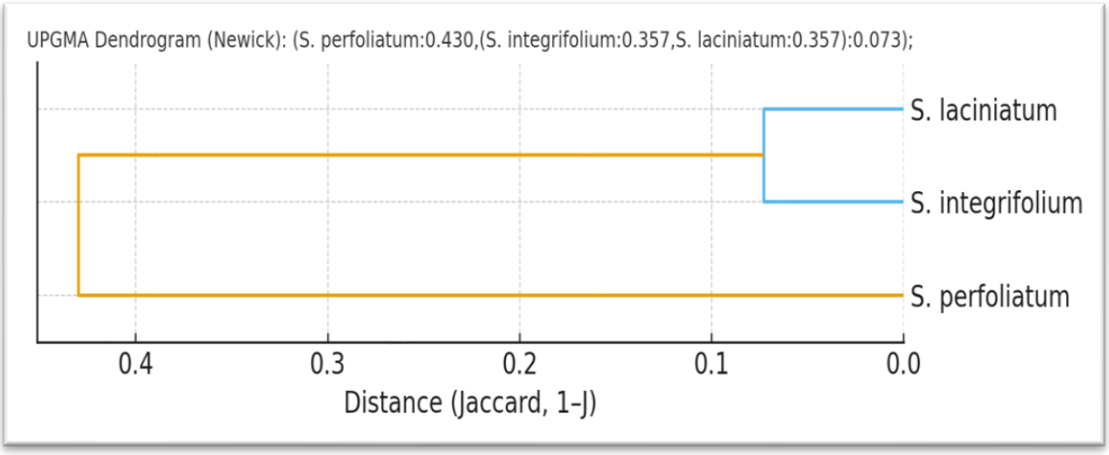
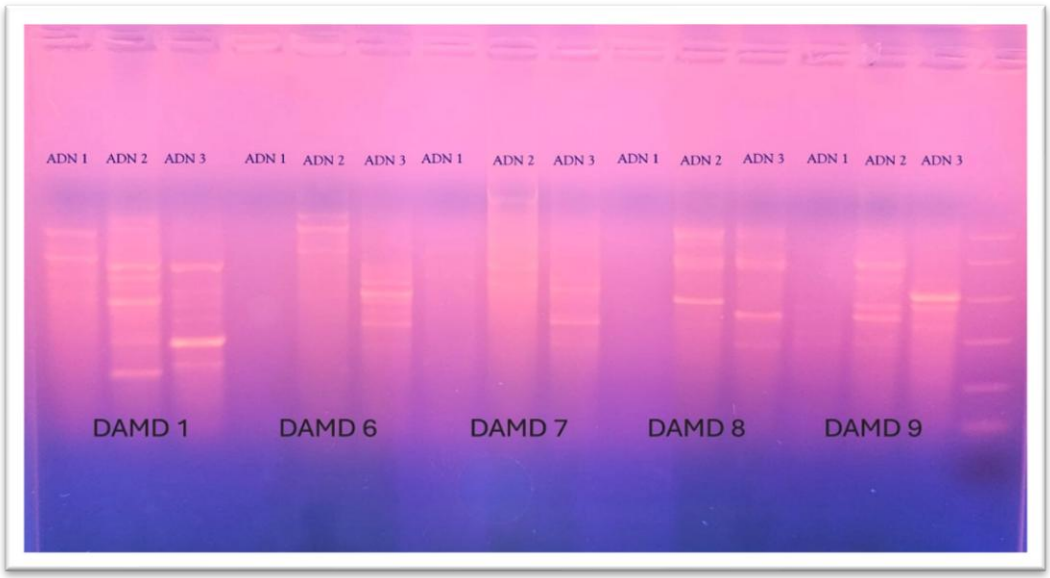


Figure 2. UPGMA dendrogram based on Jaccard distances derived from SCoT marker data in *Silphium* species

The UPGMA dendrogram based on SCoT data grouped *S. integrifolium* and *S. laciniatum* in one cluster, while *S. perfoliatum* formed a separate branch, confirming its distinct genetic profile and greater evolutionary divergence. This structure aligns with morphological differentiation, particularly leaf fusion and stem architecture.

Molecular Results – DAMD markers



ADN 1- *S.laciniatum*
AND 2- *S.integrifolium*
AND 3- *S. perfoliatum*

Figure 3. Amplification profiles generated with DAMD markers for the three *Silphium* species

The DAMD marker system generated clear and reproducible amplification profiles, with 12–18 bands per primer and a polymorphism rate above 85%. The high density of polymorphic fragments, especially for primers DAMD 6 and DAMD 8, confirmed the system's sensitivity in detecting interspecific genetic diversity.

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Table 3. Jaccard similarity coefficients and genetic distances (1–J) among *Silphium* species (DAMD markers)

Compared pair	Similarity coefficient (J)	Genetic distance (1–J)
S. laciniatum – S. integrifolium	0.103	0.897
S. laciniatum – S. perfoliatum	0.040	0.960
S. integrifolium – S. perfoliatum	0.375	0.625

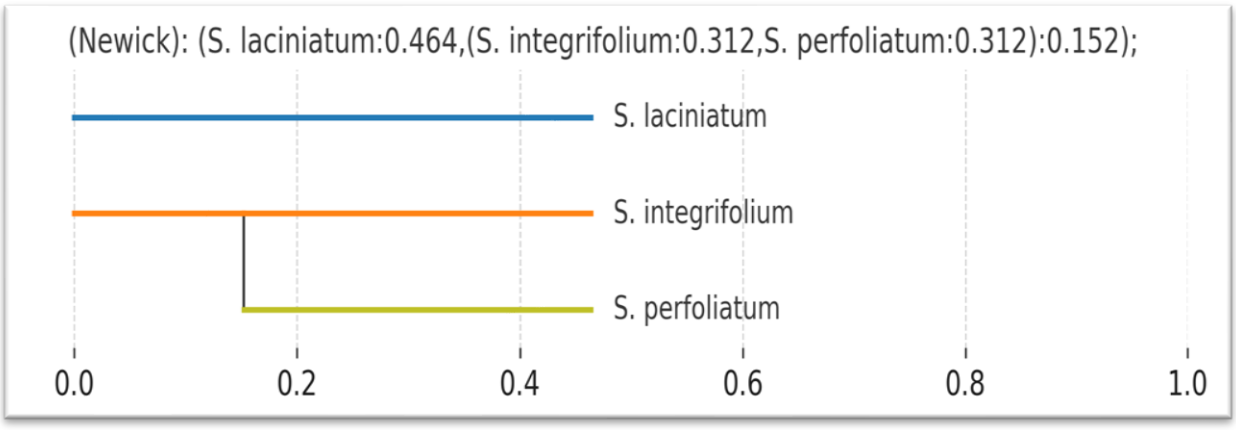

Figure 4. UPGMA dendrogram of *Silphium* species based on DAMD markers (1–Jaccard distances)

The resulting dendrogram formed two clusters:
- Cluster I: *S. integrifolium* and *S. perfoliatum*, showing high genomic proximity (J = 0.375),
- Cluster II: *S. laciniatum*, clearly distinct, with the largest genetic distance (0.960).

The topology corresponds with the observed morphological data — *S. laciniatum* exhibits deeply dissected leaves and a strong taproot, while *S. integrifolium* and *S. perfoliatum* share similar vegetative traits and overlapping flowering periods [4, 11, 15].

Comparative interpretation between SCoT and DAMD markers

Comparing the dendrograms obtained with SCoT and DAMD markers revealed minor topological differences, explained by the distinct genomic regions targeted by each system. SCoT markers, oriented toward coding sequences, reflect functional genetic variation, whereas DAMD markers, anchored in minisatellite regions, reveal neutral polymorphism [5, 28].

Both systems generated over 85–90% polymorphic bands, confirming a high degree of genetic diversity within *Silphium*. Their combined use provides complementary insights into the species' genetic structure, enabling a more robust phylogenetic interpretation.

Table 4. Comparison of similarity coefficients obtained with SCoT and DAMD markers

Compared pair	SCoT similarity	DAMD similarity	General trend
S. integrifolium – S. perfoliatum	0.286	0.375	High similarity
S. integrifolium – S. laciniatum	0.286	0.103	Intermediate
S. perfoliatum – S. laciniatum	0.200	0.040	Large distance

The close genetic relationship between *S. integrifolium* and *S. perfoliatum* reflects potential common ancestry or convergent adaptation to similar ecological conditions. Conversely, *S. laciniatum* shows marked genomic divergence, consistent with its morphological specialization for arid environments.

The dendrograms obtained from both marker systems were consistent with morphological observations. The association between *S. integrifolium* and *S. perfoliatum* corresponded to their shared traits — similar leaf morphology, robust stems, and overlapping flowering periods — whereas *S. laciniatum* was clearly isolated both morphologically and genetically.

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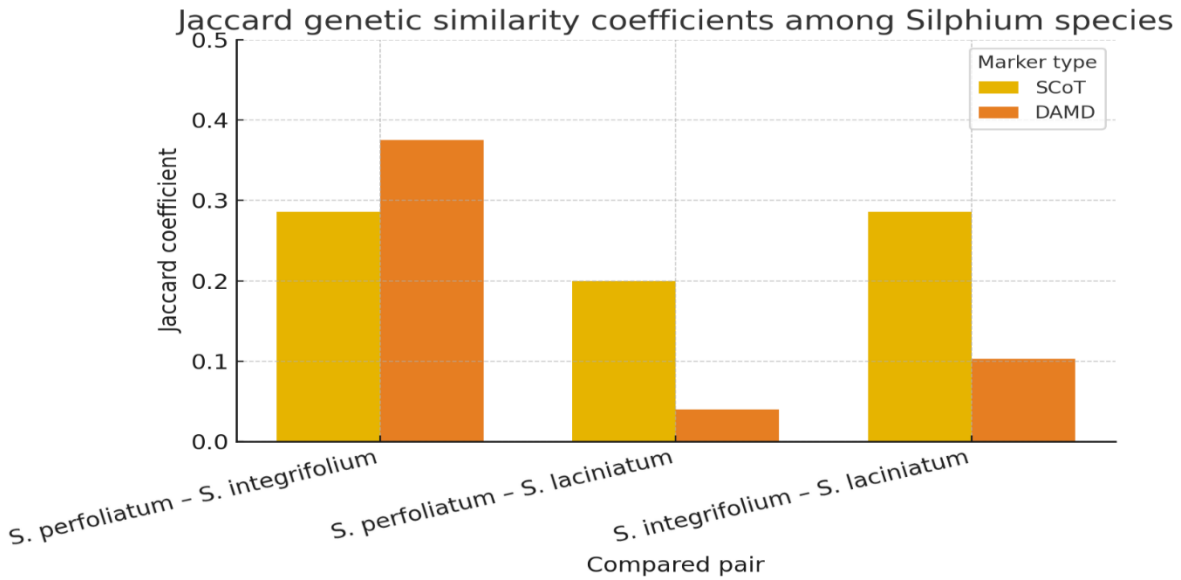

Figure 5. Jaccard genetic similarity coefficients among Silphium species based on SCoT and DAMD markers

The high Jaccard distances (0.714–0.960) confirmed the genetic divergence of *S. laciniatum*, supporting its position as an ecologically specialized taxon within the genus. These findings emphasize the reliability of the combined SCoT–DAMD approach in distinguishing closely related taxa and in reflecting evolutionary differentiation within *Silphium*.

Both SCoT and DAMD markers proved efficient and complementary in detecting interspecific polymorphism. SCoT markers, targeting regions adjacent to the start codon (ATG), revealed variation in coding sequences and functional genes, providing insights into expressed genetic diversity. Conversely, DAMD markers, anchored in minisatellite sequences, highlighted structural differences in non-coding regions of the genome.

The convergence of the results obtained with both systems validates the robustness of the methodology and supports their combined use in genetic studies of perennial crops. The dual-marker approach improves resolution and enables accurate assessment of genomic relationships, even in species with complex evolutionary histories [23, 26].

The close genetic association between *S. integrifolium* and *S. perfoliatum* suggests that these species may serve as complementary genetic resources in breeding programs for perennial bioenergy crops. *S. integrifolium* occupies an intermediate phylogenetic position, acting as a bridge species that links divergent taxa within the genus.

In contrast, *S. laciniatum* exhibits marked genetic divergence and distinct morphological traits — deeply dissected leaves, a tall stature, and a strong taproot — supporting its recognition as a separate evolutionary lineage adapted to arid habitats. These findings align with recent research describing *Silphium* as a genetically diverse and dynamically evolving genus [11, 26].

The combined morphological and molecular analyses confirm a positive correlation between phenotypic and genetic variation, validating the use of SCoT and DAMD markers in the phylogenetic and taxonomic assessment of *Silphium* species.

The integrative morpho-molecular evaluation highlights the specific agronomic potential of each studied species.

-*S. integrifolium* demonstrates versatility and adaptability, making it suitable as a genetic base for crop improvement, bioenergy applications, and the ecological rehabilitation of marginal lands.

-*S. perfoliatum*, characterized by high biomass productivity and tolerance to moist soils, is best suited for cultivation in humid and temperate environments.

-*S. laciniatum*, with its deep taproot and drought tolerance, is ideal for arid areas and prairie restoration programs.

Future research should focus on expanding the molecular and phenotypic analyses to include a wider range of natural and cultivated populations, integrating next-generation sequencing (NGS) and transcriptomic

approaches to identify functional genes associated with agronomic traits. Multi-location field trials are also essential to evaluate the performance of selected genotypes under diverse environmental conditions.

Conclusions

The study revealed significant morphological and genetic variability among the three analyzed *Silphium* species — *S. perfoliatum*, *S. integrifolium* var. *laeve*, and *S. laciniatum* — confirming their high potential for agronomic, ecological, and biotechnological applications.

Morphological characterization emphasized clear interspecific differences in plant architecture, leaf morphology, root system type, and inflorescence structure, traits that can be effectively utilized in breeding and selection programs.

The molecular analyses performed with SCoT and DAMD markers confirmed these differences, showing a strong correlation between genetic and phenotypic variability. In both marker systems, *S. integrifolium* and *S. perfoliatum* displayed close genetic affinity, while *S. laciniatum* was clearly distinct, confirming its divergent position within the genus.

The high level of polymorphism (over 90%) and the calculated genetic indices (He = 0.129, MI = 1.94) demonstrated the efficiency of the marker systems and validated the methodological relevance of combining SCoT and DAMD approaches for assessing genetic diversity in perennial crops [5, 28].

This research contributes to strengthening the understanding of the genetic structure of the *Silphium* genus and provides a solid scientific foundation for breeding, conservation, and biotechnological valorization programs.

The integrated analysis highlights the importance of combining morphological and molecular approaches to identify genotypes with superior agronomic potential and to promote the sustainable utilization and preservation of perennial plant resources adapted to diverse agroecological conditions.

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