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Phylogenetic analysis of *Solanum macrocarpon*: the evolutionary relationships and species diversification

Original paper

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Abstract: *Solanum macrocarpon* L., commonly known as African eggplant, originates from Africa and is consumed worldwide for medicinal and culinary values. Despite its immense value, there is limited research about eggplant species diversity and evolutionary relationships. This study sought to investigate the evolutionary relationships and species diversification using molecular phylogenetic data of DNA sequences obtained from the rbcL gene of the plant species. Maximum Likelihood and Neighbour-Joining tree methods were employed to infer phylogeny using MEGA11 software. Results obtained inferred using branch lengths revealed the consensus; *S. macrocarpon* was slightly diverse than another identical species *MH722376.1_Solanum macrocarpon*; the only sample of *rbcL* region found on the NCBI database. The results also showed that OM965625.1_*Solanum violaceum*_subsp._*multiflorum*, OM965624.1_*Solanum violaceum* subsp._*violaceum*, and MK122638.1_*Solanum_pubescens* had relatively closer evolutionary relationship with *S. Macrocarpon.* This result provides information and resources about the evolutionary relationships and species diversity of *S. macrocarpon* which can be used for plant breeding, conservation biology, and biosystematics.

Keywords: Phylogenetic analysis, DNA barcoding, solanum, RBCL.

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Introduction

Solanum macrocarpon L. commonly known as the local garden egg, African eggplant is a plant of the Solanaceae family and the genus *Solanum*. *Solanum* is the largest genus in the family Solanaceae, comprising about 2000 species distributed in the subtropical and tropical regions of Africa, Australia, and parts of Asia, e.g., China, India, and Japan (Kaunda and Zhang, 2019). In Africa and adjacent islands, it is represented by at least 100 indigenous species; about 20 of these are recent introductions. *Solanum macrocarpon* has an African ancestry. Spiny wild forms are found throughout the tropical non-arid parts of Africa. the eggplant fruits still being gathered occasionally as a vegetable, constitute an important fruit and leaf vegetable, grown for the market and in home gardens. *S. macrocarpon* is a tropical perennial plant that is closely related to the eggplant (Oboh et al., 2005). *Solanum macrocarpon* is consumed in various regions around the world. The parts of the plant that are consumed are the fruits and its young leaves. While taste of both the leaves and the fruit is very bitter, they have a high nutrient yield. Eggplant has a rich content of phytochemicals, namely, saponins, alkaloids, and flavonoids as well as minerals, bioactive components that are associated with promoting health (Usunomena and Chinwe, 2016) Plant genomes hold the key to understanding the evolutionary history of plants. This phylogeny is both a record of present and past life serving as a powerful predictive tool for both basic and applied plant science (Soltis and Soltis, 2021). Phylogenies can guide our efforts to improve crop plants, discover new medicines, and develop effective conservation strategies.

Over the years, DNA markers have been employed to trace plant phylogeny, primarily derived not from the large and complex nuclear genome, but from the plastid genome (Soltis and Soltis, 2021). The renowned study of by Chase et al. (1993) on the phylogeny of seed plants demonstrated the value of the plastid *rbcL* (ribulose-1,5-bisphosphate carboxylase/oxygenase large) gene (which encodes the large subunit of the most abundant enzyme on earth, ribulose 1,5-bisphosphate carboxylase/oxygenase, RuBisCO) in plant phylogenetics. The plastid genome, beginning with *rbcL*-based studies and analyses of complete plastid genomes has provided a compelling view of plant phylogeny (Gitzendanner et al., 2018).

DNA barcoding is a species identification tool that uses a short section of the genome that provides a genetic signature of the species. The main advantage of this novel technique is that it requires a small sample of tissue (Trujillo-Argueta et al., 2022). In most animal groups, this technique is very effective. However, in plants, the recommended standard markers, such as *rbcL*a (ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit A gene) may not always work, and their efficacy remains to be tested in many plant groups (Trujillo-Argueta et al., 2022). Of the possible plant markers, *rbcL*a appears to be one of the best plant barcodes, because of its successful amplification and sequencing. Although far from perfect, the resolution of *rbcL*a was shown to be better than other markers such as *mat*K when tested both barcodes in wild arid plants in the United Arab Emirates (Maloukh *et al*., 2017) and when tested alone, in plants of Saudi Arabia (Bafeel *et al*., 2012). Also, *rbcL*a can be a valuable tool to identify species in conditions in which other methods are impractical. For instance, this marker was successfully used to study root diversity patterns in old-field communities in Ontario, Canada (Kesanakurti *et al*., 2011).

The use of molecular markers and DNA barcoding in eggplant diversity studies has thrown light into the taxonomic darkness of the plant (Aguoru et al., 2015). According to the limited published research, this study aims to assess the genetic diversity and examine the phylogeny of *Solanum macrocarpon* (garden eggplant) in African locales using *rbcL* markers.

Materials and Methods

Materials collection

Two accessions of African eggplant NGB00247 and NG/MR/MAY/09/007 were used in the study. The seeds were collected from the National Center for Genetic Resources and Biotechnology (NACGRAB), Ibadan. The seeds were planted with each accession planted in three replicates.

DNA extraction

Young leaf samples of *S. macrocarpon* were used. A Qiagen DNeasy Plant Mini Kit was used for DNA isolation. Amplification and sequencing assays were carried out for the extracted DNA. The experiments were carried out in the Molecular Laboratory of the Department of Plant Biology, University of Ilorin, Ilorin, Kwara State.

Amplification and sequencing of RBCL

PCR amplification was performed with the primer as shown in Supplementary Table 1. The PCR was carried out with a total reaction volume of 30µl in a thermocycler (Eppendorf, Germany). Template preparation and optimum concentration for cycle sequencing reactions are shown in Supplementary Table 2. The reaction mixture consisted of 20-50 ng of genomic DNA, 10 X PCR buffer, 2.5 µM dNTPs, 5 pmol primer and 1 unit of Taq DNA polymerase (Genet.Bio. Korea). The thermocycler condition included an initial denaturation of 95 °C for 5 min followed by 35 cycles of denaturation at 95 °C for 30secs. Annealing was at 55 °C for 30s and extension was at 72 °C for 1 min. The final extension was at 72 °C for 5mins (Supplementary Table 3). The amplicon was purified with EZ-10 Spin Column PCR product purification Kit (Bio Basic Inc. Ontario, Canada). The PCR setup for cycle sequencing reaction was done in a total reaction volume of 10µl and PCR condition included an initial denaturation of 96 °C for 1 min in 1 cycle, denaturation at 96 °C for 10s, and 30 cycles of annealing at 50 °C for 5s. Extension for the reaction was at 60 °C for 4 min and the final extension was done at 60 °C for 7 mins (Supplementary Table 4). The DNA sample to be sequenced was combined with rbcl primer, DNA polymerase, and DNA nucleotides (dATP, dTTP,dGTP, and dCTP). The four dye-labeled,chain-terminating dideoxynucleotides were added as well. The mixture was first heated to denature the template DNA (separate the strands) for 1 min, then cooled so the primers could bind to the single-stranded template (Abdulkareem et al., 2023). When the primer bounded, the temperature was raised again, allowing DNA polymerase to synthesize new DNA starting from the primer. No further nucleotides can be added, the strand ended with the dideoxy. This process was repeated in several cycles. The dideoxynucleotide was incorporated at every single position of the target DNA in at least one reaction (Abdulkareem et al., 2023). The various alleles were sequenced using 3130xl Genetic analyser (Applied Biosystems, CA, USA). The obtained sequences were edited by Sequence Scanner software v1.0 Applied Biosystems, CA, USA), and the full-length sequences were assembled using a local alignment algorithm CodonCode Aligner version 4.24 (Codon Code Corporation).

Data analysis

The obtained forward and reverse sequences were grouped using the SeqTrace 9.0 tool and were submitted to the NCBI (National Center for Biotechnology Information) for BLAST (Basic Local Alignment Search Tool) analysis. The query cover of the sequences was identified considering E value a<10 and maximum hits (99 or 100%) with species in the reference database of the NCBI. Evolutionary analysis was conducted in MEGA11 (Tamura et al., 2021). In the phylogenetic analysis, DNA sequences were aligned using the MUSCLE (MUltiple Sequence Comparison by Log-Expectation) algorithm for sequence alignment, The alignment process considered gaps and mismatches to maximize sequence similarity (Edgar, 2004). Genetic distances were calculated using the Tamura-Nei model, which accounts for different rates of nucleotide substitution and varying GC content among sequences.(Tamura and Nei, 1993). Phylogenetic trees were constructed using Maximum Likelihood (Kumar et al., 2018) and Neighbor-Joining (Saitou and Nei, 1987) methods. Bootstrap analysis was conducted with 1000 replicates to assess the reliability of the phylogenetic trees (Felsenstein, 1985). Cophenetic matrix and mantel tests were carried out to determine the best-fit tree using RStudio software version 4.4.1.

The evolutionary history was inferred by using the Maximum Likelihood method and Tamura-Nei model (Tamura and Nei, 1993). Initial tree(s) for the heuristic search were obtained automatically by applying Neighbor-Join and BioNJ algorithms to a matrix of pairwise distances estimated using the Tamura-Nei model, and then selecting the topology with superior log likelihood value.

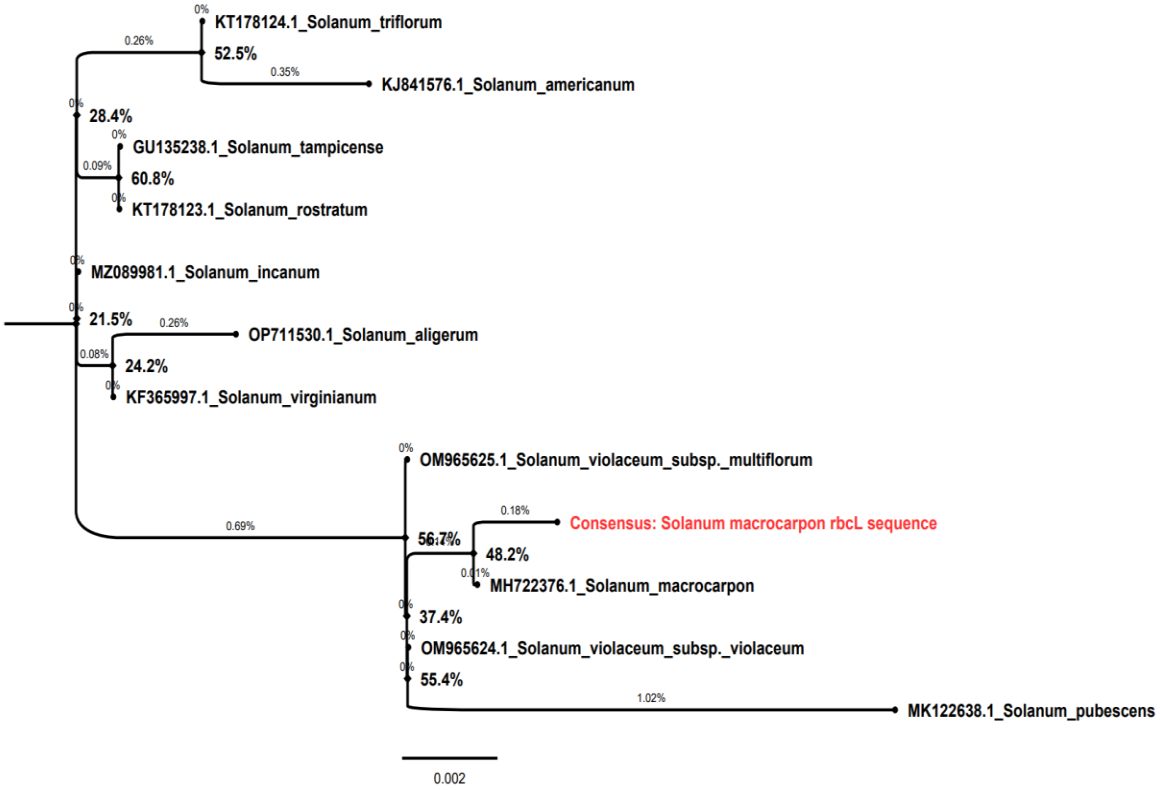

Figure 1. Phylogenetic analysis of *Solanum macrocarpon rbcL* sequences by Maximum Likelihood method.

Results

rbcL gene isolation

The DNA which was extracted from *Solanum macrocarpon* was sequenced for the *rbcL* (Ribulose 1,5 biphosphate carboxylase/oxygenase large subunit) gene. The length of the consensus sequence was 569 bp. The DNA sequences are provided in the supplementary material (see Supplementary Figure 1).

Evolutionary analysis

In this study Maximum Likelihood and Neighbour Joining trees were initially constructed, However, cophenetic matrices for each tree and Mantel tests were conducted to compare these matrices. The Mantel test results indicated that the ML and NJ trees had a very high correlation (Mantel statistic r = 0.78, p = 0.001), suggesting that these methods provided the most consistent representation of the genetic distances among represented taxa. Therefore, the ML tree was selected as the best-fit tree for our analysis due to its statistical value (Figure 1).

The phylogenetic analysis revealed that the Consensus: *Solanum macrocarpon* rbcL sequence clustered with *MH722376.1_Solanum macrocarpon*; an identical species as the consensus, forming a monophyletic group with a bootstrap support value of 48.2%. however, the branch length of Consensus: *Solanum macrocarpon* rbcL sequence is relatively longer than that of *MH722376.1_Solanum macrocarpon* with branch length values of 0.18% and 0.01% respectively thus inferring some degree of evolutionary divergence between the identical species. Also, Consensus: *Solanum macrocarpon* rbcL sequence belongs to a clade attached to a node with bootstrap support value of 56.7% containing four other members belonging to the Solanum genus including OM965625.1_*Solanum violaceum_subsp._multiflorum*, OM965624.1_*Solanum violaceum_ subsp._violaceum*, *and*

MK122638.1_Solanum_pubescens. Concerning the branch lengths within the clade containing the consensus species, the results revealed that *MK122638.1_Solanum_pubescens* is the most genetically evolved species from the last most recent common ancestor (MRCA) in the group with branch length value of 1.02%; a value relatively higher than that of the consensus. Results also revealed that there was no genetic divergence between OM965625.1_*Solanum violaceum_subsp._multiflorum* and OM965624.1_*Solanum violaceum_ subsp._violaceum* since their last divergence from a most recent common ancestor (MRCA).

Furthermore, it is evident from the phylogenetic results that Consensus: *Solanum macrocarpon* rbcL sequence is in polyphyletic relationship with two other clades with bootstrap support values of 21.5% and 28.4% respectively with both clades having members of genus solanum including *KF365997.1_Solanum virginianum, OP711530.1_Solanum aligerum, MZ089981.1_Solanum incanum and KT178123.1_Solanum rostratum, GU135238.1_Solanum tampicense, KJ841576.1_Solanum americanum, KT178124.1_Solanum triflorum* respectively. Regarding the evolutionary divergence of the major clades from their MRCA, the clade containing the consensus has a relatively higher branch length of 0.69% signifying a higher evolutionary divergence while other clades with bootstrap support values 24.2%, 60.8% and 52.5% had branch lengths of 0.08%, 0.09% and 0.26% respectively.

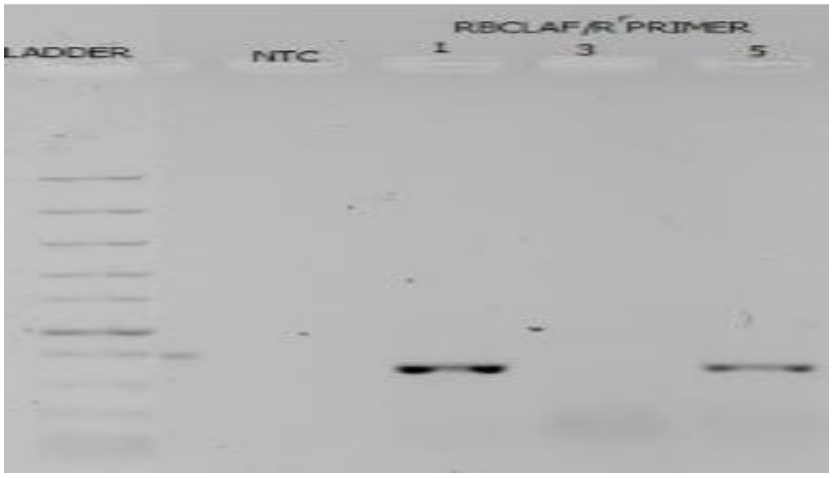

Figure 2. Gel image of amplicons of *S. macrocarpon* using RbcL primer.

Discussion

Evolutionary relationship was inferred using the Maximum Likelihood (ML) method between the consensus: *Solanum macrocarpon* rbcL, other isolates of *Solanum macrocarpon* and other related species. The choice of adopting the ML method was inferred by the strong positive correlation of cophenetic matrix and significance of mantel test (Mantel statistic r = 0.78, p = 0.001), suggesting that these methods provided the most consistent representation of the genetic distances among Solanum sequences used. Also, the likelihood of a phylogenetic tree is proportional to the probability of observing the comparative data (such as aligned DNA sequences) conditional on the tree and the tree that maximizes the likelihood can be chosen as the best estimate of phylogeny; this is the method of maximum likelihood (Huelsenbeck, 2019). Maximum Likelihood estimation conducted for this study revealed that the Consensus: *Solanum macrocarpon* rbcL sequence clustered with *MH722376.1_Solanum macrocarpon*; an identical

species thus inferring the accuracy of rbcL primers in identifying *Solanum macrocarpon* to the species level. This finding is consistent with the work of Ralte and Singh (2021), where 15 Solanaceae species were successfully identified using rbcL DNA regions. However, the branch length values of the former and later inferred evolutionary divergence between the two where Consensus: *Solanum macrocarpon* rbcL sequence had a relatively longer branch length with a difference of 0.17% signifying a slightly higher genetic diversity than *MH722376.1_Solanum macrocarpon.* Branch lengths have been considered an indicator of feature diversity on the assumption that a longer branch represents more opportunity for evolutionary change and the development of unique characteristics (Faith, 2018 as cited in Ritchie *et al*., 2020). This difference might be due to environmental factors or the distal isolation of the 2 species as *MH722376.1_Solanum macrocarpon* with 708bp was isolated in Thailand according to (Prommanee *et al*., 2018 as cited in NCBI, 2024) while the consensus with 569bp was isolated in Nigeria with a bootstrap support value of 48.2 at their node. According to Liu *et al*. (2023), the isolation-by-distance (IBD) reveals that genetic differentiation among populations increases with geographic distance, while the isolation-by-environment (IBE) assumes a linear relationship between genetic variation and environmental differences among populations.

The phylogenetic analysis placed members in the genus Solanum; OM965625.1_*Solanum violaceum_subsp._multiflorum*, OM965624.1_*Solanum violaceum* subsp. *violaceum, and MK122638.1_Solanum pubescens* in the same clade with the consensus indicating that they all share the same most recent common ancestor (MRCA) at the node with bootstrap support value of 56.7%. However, in terms of evolutionary divergence as regards this clade, *MK122638.1_Solanum pubescens* was revealed to be the most diverse amongst members of the clade with the highest branch length of 1.02% and this placed it in a paraphyletic relationship with the consensus. It is noteworthy that in this clade, 2 subspecies of *Solanum violaceum* namely *Solanum violaceum* subsp. multiflorum and *Solanum violaceum* subps violaceum with accession numbers OM965625.1 and OM965624.1 respectively are the least divergent and closest to the MRCA and could be inferred as an ancestor or close relative of an ancestor of other members of the clade as they were observed to have no branch length from the most recent common ancestor.

With respect to the origin node, with 21.5% bootstrap support value, the consensus *Solanum macrocarpon* formed a polyphyletic relationship with three other clades in the tree with members viz; *KF365997.1_Solanum virginianum, OP711530.1_Solanum aligerum, KT178123.1_Solanum rostratum, GU135238.1_Solanum tampicense, KJ841576.1_Solanum americanum,* and *KT178124.1_Solanum triflorum.* It should be noted that *MZ089981.1_Solanum incanum* was the closest to the node with no branch length and not clustering to any clade signified a close relationship with the ancestor present at the node and it could be possible that *Solanum incanum* is an ancestor or close relative to an ancestor in which some other members evolved from.

Conclusion

This study utilized DNA barcoding of the *rbcL* region to conduct a phylogenetic analysis of *S. macrocarpon*, unveiling crucial evidence about its evolutionary relationships and species diversification. The consensus sequence derived in this study was found to be more evolutionarily advanced than the only *S. macrocarpon* rbcL sequence available in the NCBI database. This research provides a more evolutionarily advanced isolate of *S. macrocarpon*, which could be valuable for crop improvement.

Supplementary Materials

The supplementary material for this article can be found online at: https://www.jpmb-gabit.ir/article_712459.html.

Supplementary Figure 1. The sequence of rbcL gene from Solanum macrocarpon.

Supplementary Table 1. Forward and reverse sequences of primer used.

Supplementary Table 2. Preparation of PCR mixture.

Supplementary Table 3. Thermo-cycler PCR condition for barcode amplification.

Supplementary Table 4. Thermo-cycler PCR condition for cycle sequencing reaction.

Author Contributions

Conceptualization, A.K.A. and A.N.; methodology, B.A. and S.K.O; software, A.N.; validation, K.I.D., M.M., and B.U.O.; formal analysis, B.A. and S.K.O.; investigation, A.N.; resources, A.K.A. and A.N.; data curation, A.K.A.; writing—original draft preparation, A.N.; writing—review and editing, B.A.; visualization, S.K.O.; supervision, A.K.A.; project administration, A.K.A.; All authors have read and agreed to the published version of the manuscript.

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Conflict of Interest Statement

The authors declare no conflict of interest.

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مقاله پژوهشی

تجزیه و تحلیل فیلوژنتیکی گیاه *Solanum macrocarpon*: روابط تکاملی و تنوع گونه‌ها

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چکیده: بادمجان آفریقایی با نام علمی *Solanum macrocarpon* L. در سراسر جهان به منظور کاربردهای دارویی و آشپزی مصرف می‌شود. علیرغم ارزش بسیار زیاد آن، تحقیقات اندکی در مورد تنوع گونه‌های بادمجان و روابط تکاملی وجود دارد. این مطالعه به دنبال بررسی روابط تکاملی و تنوع گونه‌ها با استفاده از داده‌های فیلوژنتیک مولکولی، توالی‌های DNA به‌دست‌آمده از ژن *rbcL* گونه‌های گیاهی مورد بررسی و مقایسه قرار گرفت. برای ترسم درخت فیلوژنی در نرم‌افزار MEGA11 و با استفاده از الگوریتم‌های Maximum Likelihood و Neighbour-Joining صورت گرفت. مقایسه توالی ژن *rbcL* شناسایی شده در این تحقیق با توالی ژنی NCBI نشان داد توالی بدست آمده از تفاوت اندکی با توالی ثبت شده با کد دسترسی *MH722376.1* برخوردار بود. نتایج همولوژی بر مبنای این ژن نشان داد که گونه‌های *Solanum violaceum* subsp.*multiflorum*، *Solanum violaceum* subsp.violaceum و *Solanum pubescens* از رابطه تکاملی نسبتا نزدیکتری با *S. Macrocarpon* برخوردار بودند. نتایج این تحقیق اطلاعات ارزشمندی در مورد روابط تکاملی و تنوع گونه‌های *S. macrocarpon* فراهم می‌نماید که می‌تواند در برنامه‌های اصلاحی گیاهان، افزایش عملکرد و بیوسیستماتیک استفاده شود.

کلمات کلیدی: آنالیز فیلوژنتیک، DNA بارکدینگ، بادمجان، *RBCL*.

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