Electronic Journal of Biotechnology 60 (2022) 19–25

Contents lists available at ScienceDirect

Electronic Journal of Biotechnology

journal homepage: www.elsevier.com/locate/ejbt

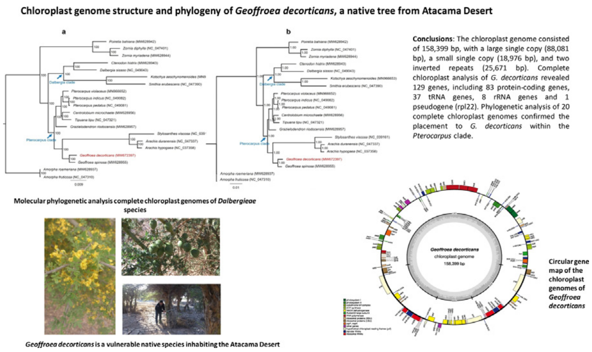
Short Communication

# Chloroplast genome structure and phylogeny of *Geoffroea decorticans*, a native tree from Atacama Desert

Roberto Contreras-Díaz [a,*], Felipe S. Carevic [b], Wilson Huanca-Mamani [c], Rómulo Oses [a], Mariana Arias-Aburto [a], María Navarrete-Fuentes [a]

[a] *Centro Regional de Investigación y Desarrollo Sustentable de Atacama (CRIDESAT), Universidad de Atacama, Copayapu 485, 1530000 Copiapó, Chile*
[b] *Laboratorio de Ecología Vegetal, Facultad de Recursos Naturales Renovables. Universidad Arturo Prat, Campus Huayquique, 1100000 Iquique, Chile*
[c] *Laboratorio de Biología Molecular de Plantas, Facultad de Ciencias Agronómicas, Universidad de Tarapacá, 1000000 Arica, Chile*

## GRAPHICAL ABSTRACT



**Conclusions**: The chloroplast genome consisted of 158,399 bp, with a large single copy (88,081 bp), a small single copy (18,976 bp), and two inverted repeats (25,671 bp). Complete chloroplast analysis of *G. decorticans* revealed 129 genes, including 83 protein-coding genes, 37 tRNA genes, 8 rRNA genes and 1 pseudogene (rpl22). Phylogenetic analysis of 20 complete chloroplast genomes confirmed the placement to *G. decorticans* within the *Pterocarpus* clade.

## ARTICLE INFO

*Article history:*
Received 27 June 2022
Accepted 21 September 2022
Available online 27 September 2022

*Keywords:*
Atacama Desert
Chloroplast genome
Dalbergieae
*Geoffroea decorticans*
Legume
Native tree
Phylogeny
*Pterocarpus* clade
Quadripartite structures

## ABSTRACT

*Background:* *Geoffroea decorticans* is a vulnerable native species inhabiting the Atacama Desert. Here, we describe the structure, gene composition and phylogeny of the complete chloroplast genome of this legume species.

*Results:* The chloroplast genome consisted of 158,399 bp, with typical quadripartite structures: a large single copy (88,081 bp), a small single copy (18,976 bp), and two inverted repeats (25,671 bp). *Geoffroea decorticans* chloroplast genome was similar in size and gene number to that of *G. spinosa*, but it was slightly different in structure. Complete chloroplast analysis of *G. decorticans* revealed 129 genes, including 83 protein-coding genes, 37 tRNA genes, 8 rRNA genes and 1 pseudogene (*rpl22*). In *G. decorticans*, the *rps16* gene showed a deletion, which led to a premature stop codon, probably causing loss of functionality. Phylogenetic analysis of 20 complete chloroplast genomes confirmed the placement to *G. decorticans* within the *Pterocarpus* clade.

*Conclusions:* In this study, we report the complete chloroplast genome of *Geoffroea decorticans* for the first time, which can be used for phylogenetic studies and reconstruction of the biogeography history of the genus *Geoffroea* in South America.

---

Peer review under responsibility of Pontificia Universidad Católica de Valparaíso.

* Corresponding author
*E-mail address:* roberto.contreras@uda.cl (R. Contreras-Díaz).

https://doi.org/10.1016/j.ejbt.2022.09.005
0717-3458/

**How to cite:** Contreras-Díaz R, Carevic FS, Huanca-Mamani W, et al. Chloroplast genome structure and phylogeny of *Geoffroea decorticans*, a native tree from Atacama Desert. Electron J Biotechnol 2022;60. https://doi.org/10.1016/j.ejbt.2022.09.005.

## 1. Introduction

*Geoffroea decorticans* Burkart is a tree or a shrub characteristic of arid and semi-arid areas and distributed in Argentina, Chile, Uruguay, Bolivia and Peru [1]. This species is considered one of the most important wild trees for the indigenous populations established in the Atacama Desert 4000-1700 years ago [2]. *G. decorticans* (also called chañar) has been recognized as a multi-purpose resource providing food and furniture material and expectorant, anticoagulant, and hypoglycemic medicinal products [3,4,5,6,7,8]. In Chile, chañar has been classified as a vulnerable species owing to its restricted geographical distribution and anthropic uses [9]. Therefore, the development of forest management plans and conservation strategies to reduce the risk of their extinction is necessary.

The chloroplast genome provides valuable information to support the conservation of threatened species [10]. Phylogenomic approaches are now widely used to resolve species relationships and the evolution of genomes and gene families [11]. A comprehensive approach to diversity, whether for a clade or a tree, has been one of the most important motifs of systematic research for centuries [12]. A previous study has established that *G. decorticans* belongs to the *Dalbergieae* clade [13]. Molecular phylogenetic studies have revealed three main *Dalbergieae* lineages: the *Adesmia*, *Dalbergia*, and *Pterocarpus* clades [14]. Based on DNA sequence data, some authors have reported that the genus *Geoffroea* Jacq. belongs to the *Pterocarpus* clade [14,15,16]. Moreover, among the genus *Geoffroea* Jacq., the chloroplast genome sequence of *G. spinosa* Jacq. was the first to be reported [17]. However, the genome-wide data of *G. decorticans* have not been studied and its phylogenetic relationship has not been extensively revised. This study aimed to analyze the complete chloroplast genome of *G. decorticans*, in terms of structure, gene composition, and phylogeny.

## 2. Materials and methods

Leaves were collected from a chañar tree in Copiapó, Chile (27° 18’ 42.26“ S 70° 30’ 7.56” W; Voucher EIF13815). DNA was extracted using a method described by Contreras et al. [18]. The DNA was then quantified using Qubit$^{TM}$ 3.0 fluorometer. The sequencing library was prepared with the TruSeq Nano DNA LT Kit. Sequencing was performed on an Illumina sequencing platform. Paired-end sequences of 150 bp were generated for each read (R1 and R2). The filtered reads were assembled using SPAdes 4 software, version 3.13.0 [19]. The chloroplast was annotated with CPGAVAS2 [20] and PGA [21] softwares, and then manually corrected. The graphical map of the chloroplast was generated by Organellar Genome DRAW (OGDRAW) [22], and the complete nucleotide sequence was deposited in the GenBank database (MW672397.1). The chloroplast structures (LSC/IR, IR/SSC) of *G. decorticans* and 8 closely related species of the *Dalbergioid* s.l. clade [23] such as *G. spinosa* Jacq., *Stylosanthes viscosa* (L.) Sw., *Tipuana tipu* (Benth.) Kuntze 1898, *Arachis duranensis* Krapov. & W.C. Greg, *Dalbergia sissoo* Roxb. ex DC., *Smithia erubescens* (E. Mey.) Baker f., *Zornia myriadena* Benth. and *Amorpha fruticosa* L. were visualized and compared using IRScope [24]. The complete chloroplast genome sequence of *G. decorticans* and 17 species of the *Dalbergioid* clade [23], including two *Amorpheae* species as outgroups (*Amorpha roemeriana* Scheele and *A. fruticosa*), were aligned using MAFFT v7 [25], and gaps were trimmed using TrimAL v1.4 [26]. The genome sequence data were analyzed using the maximum likelihood (ML) and the Bayesian inference (BI) methods. The best-fitting nucleotide substitution model of sequence evolution, model TPM1+I+G4, was determined using the Corrected Akaike Information Criterion (AICc) with JModelTest2 on XSEDE [27]. The ML analyses were performed using RAxML-HPC BlackBox v.8.1.12 [28] with 1,000 bootstrap replicates; and the BI analysis was conducted using MrBayes on XSEDE v.3.2.7 [29] with the CIPRES Science Gateway v3.3 [30]. The Markov chain Monte Carlo (MCMC) algorithm was calculated for 5,000,000 generations, and the sampling tree for every 1,000 generations. The first 25% of generations were discarded as burn-in. In the analysis, bootstrap (BS) values were estimated in the ML, and the reliability of clades in the Bayesian analysis was evaluated by means of posterior probability (PP).

## 3. Results

The chloroplast genome of *G. decorticans* comprises 158,399 bp, the two inverted repeat (IR) regions were of 25,671 bp each, one of the smallest in the *Dalbergioid* clade, and separated by a large single-copy region (LSC) of 88,081 bp and a small single-copy region (SSC) of 18,976 bp (Fig. 1). A total of 129 genes were identified, including 83 coding genes, 8 rRNA genes, 37 tRNA genes, and 1 pseudogene (*rpl22*) (Table 1). The DNA sequence for *rps16* gene of *G. decorticans* contained a deletion, which resulted in a stop codon in the functional domain of the protein; therefore, this truncated gene was not considered for chloroplast genome annotation (Table 1). Length of the IR region of other species of the *Dalbergioid* clade varied between 25,239 bp and 25,828 bp (Fig. 2). Length of the LSC region of *G. decorticans* (88,081 bp) was smallest to that of *G. spinosa* (88,615 bp), and in the other species, length of the LSC region varied between 84,625 bp and 88,615 bp. In all species of the *Dalbergioid* clade, length of the SSC region varied between 18,602 bp and 19,018 bp (Fig. 2). The GC content of *G. decorticans* chloroplast genome was equal to that of *G. spinosa* (36.2%) and similar to that of the rest of species of the *Dalbergioid* clade.

The IR-SSC and IR-LSC limits of *G. decorticans* were compared with that of other species of the *Dalbergioid* clade. In the intergenic spacers between *rpl2-rps19* genes, specifically in the junction between the LSC-IRb region (JLB), the *rpl2* of *G. decorticans* was found to be partially extended in the LSC region (41 bp) compared with that of other *Dalbergioid* species (Fig. 2). Similarly, in all *Dalbergioid* species, the *ycf1* gene was found extend over the JSA junction (Fig. 2). In *G. decorticans*, *ycf1* and *ndhF* genes were found to extend at JSB junction, whereas, these genes not found to extend at JSB junction in *G. spinosa*; in fact, the *ndhF* gene of *G. spinosa* was present 21 bp away from the JSB junction (Fig. 2). In *S. viscosa* and *A. duranensis*, which are very closely related to *G. decorticans*, the *ycf1* and *ndhF* genes were also found to extend at JSB junction (Fig. 2).

The trees generated using complete chloroplast genome sequences of 20 species of the *Dalbergioid* clade based on ML and BI showed similar topologies (Fig. 3). The ML tree revealed four main clades, all of which were highly supported with BP=100. Clade I comprised *Poiretia bahiana*, *Zornia diphylla* and *Zornia myr-*

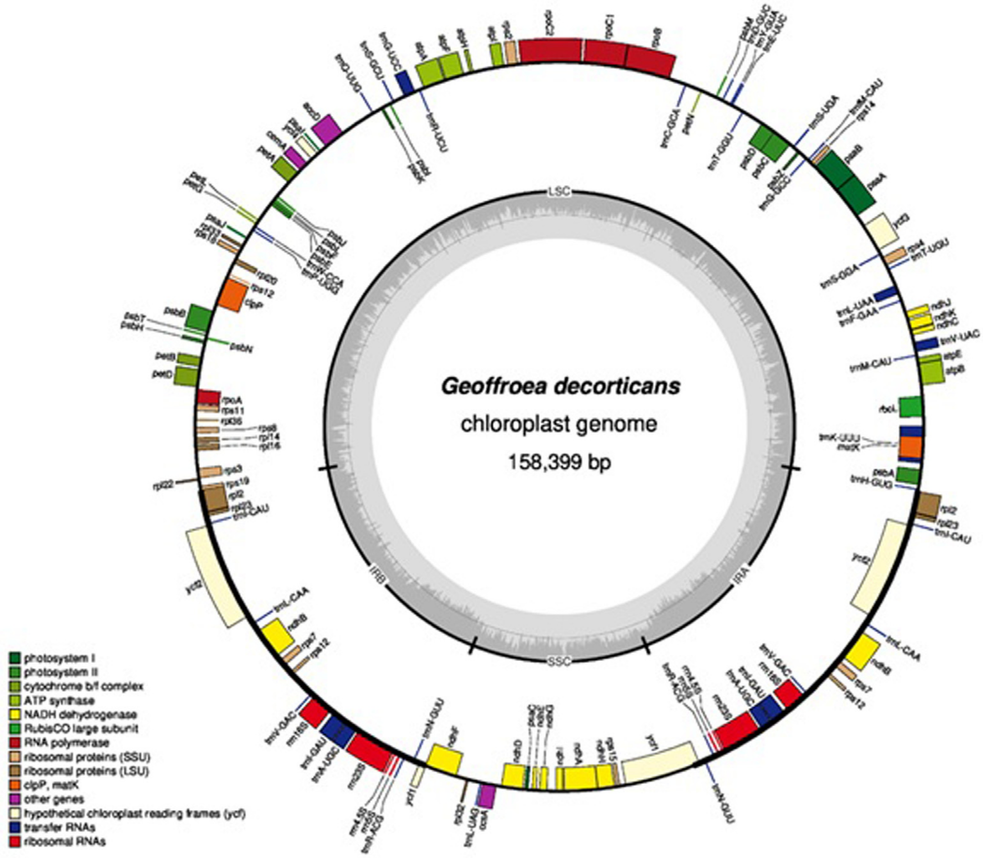


**Figure 1.** Circular gene map of the chloroplast genomes of *Geoffroea decorticans*. Genes were colored according to their functional group. Small single copy (SSC), large single copy (LSC), and inverted repeats (IRA, IRB) were indicated.

**Table 1**
Gene composition in the *Geoffroea decorticans* chloroplast genome.

| Category of genes | Group of genes | Name of genes | N° |
|---|---|---|---|
| Photosynthesis | Photosystem I | *psaA, psaB, psaC, psaI, psaJ* | 5 |
| | Photosystem II | *psbA, psbB, psbC, psbD, psbE, psbF, psbH, psbI, psbJ, psbK, psbL, psbM, psbN, psbT, psbZ* | 15 |
| | ATP synthase | *atpA, atpB, atpE, atpF*[b], *atpH, atpI* | 6 |
| | NADH-dehydrogenase | *ndhA*[b], *ndhB*[a,b], ndhC, ndhD, ndhE, ndhF, ndhG, ndhH, ndhI, ndhJ, ndhK | 12 |
| | cytochrome b/f complex | *petA, petB, petD*[b], *petG, petL, petN* | 6 |
| | Large subunit RUBISCO | *rbcL* | 1 |
| Protein synthesis and DNA replication | Transfer RNAs | *trnA-UGC*[a,b], *trnC-GCA, trnD-GUC, trnE-UUC, trnF-GAA, trnfM-CAU, trnG-UCC*[b], *trnG-GCC, trnH-GUG, trnI-GAU*[a,b], *trnI-CAU*[a], *trnK-UUU*[b], *trnL-UAA*[b], *trnL-CAA*[a], *trnL-UAG, trnM-CAU, trnN-GUU*[a], *trnP-UGG, trnQ-UUG, trnR-ACG*[a], *trnR-UCU, trnS-GGA, trnS-UGA, trnS-GCU, trnT-GGU, trnT-UGU, trnV-UAC*[b], *trnV-GAC*[a], *trnW-CCA, trnY-GUA* | 37 |
| | Ribosomal RNAs | *rrn16S*[a], *rrn23S*[a], *rrn4.5S*[a], *rrn5S*[a] | 8 |
| | Ribosomal Protein large-subunit | *rpl14, rpl16, rpl2*[a,b], *rpl20, rpl22, rpl23*[a], *rpl32, rpl33, rpl36* | 11 |
| | DNA dependent RNA polymerase | *rpoA, rpoB, rpoC1*[b], *rpoC2* | 4 |
| | Ribosomal Protein Small-subunit | *rps11, rps12*[a,b], *rps14, rps15, rps18, rps19, rps2, rps3, rps4, rps7*[a], *rps8* | 13 |
| Other functions | Subunit of Acetyl-CoA-carboxylase | *accD* | 1 |
| | c-type cytochrome synthesis gene | *ccsA* | 1 |
| | Envelop membrane protein | *cemA* | 1 |
| | Protease | *clpP* | 1 |
| | Maturase | *matK* | 1 |
| Unknown function | Conserved open reading frames | *ycf1*[a], *ycf2*[a], *ycf3*[b], *ycf4,* | 6 |

[a] Duplicated genes.
[b] Genes containing introns.

*iadena*; clade II (*Dalbergia* clade) comprised four species—*Ctenodon histrix*, *Dalbergia sissoo*, *Kotschya aeschynomenoides* and *Smithia erubescens*; clade III (*Pterocarpus* clade) comprised eleven species—*Pterocarpus violaceus*, *Pterocarpus indicus*, *Pterocarpus pedatus*, *Centrolobium microchaete*, *Tipuana tipu*, *Grazielodendron riodocensis*, *Stylosanthes viscosa*, *Arachis duranensis*, *Arachis hypogaea*, *G. decorticans* and *Geoffroea spinosa*; clade IV comprised the outgroup species *Amorpha roemeriana* and *A. fruticosa* (Fig. 3a). The BI tree showed four clades with high support (PP = 1.00), and its topology was similar to that of the ML tree (Fig. 3b). The *Pterocarpus* clade

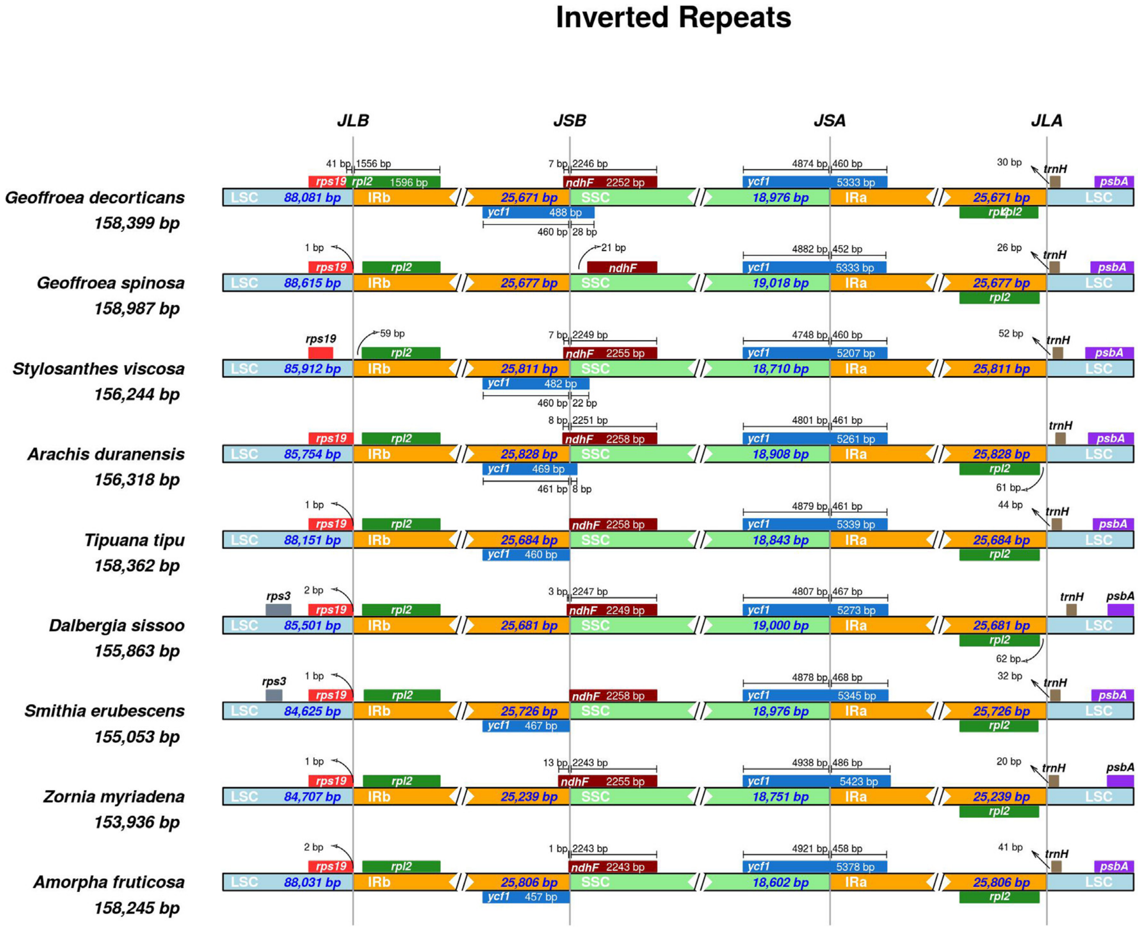


**Figure 2.** Comparison of chloroplast genomes between the Long Single Copy (LSC), Short Single Copy (SSC) and Inverted Repeat (IRa and IRb) junction regions amongst nine *Dalbergioid* species.

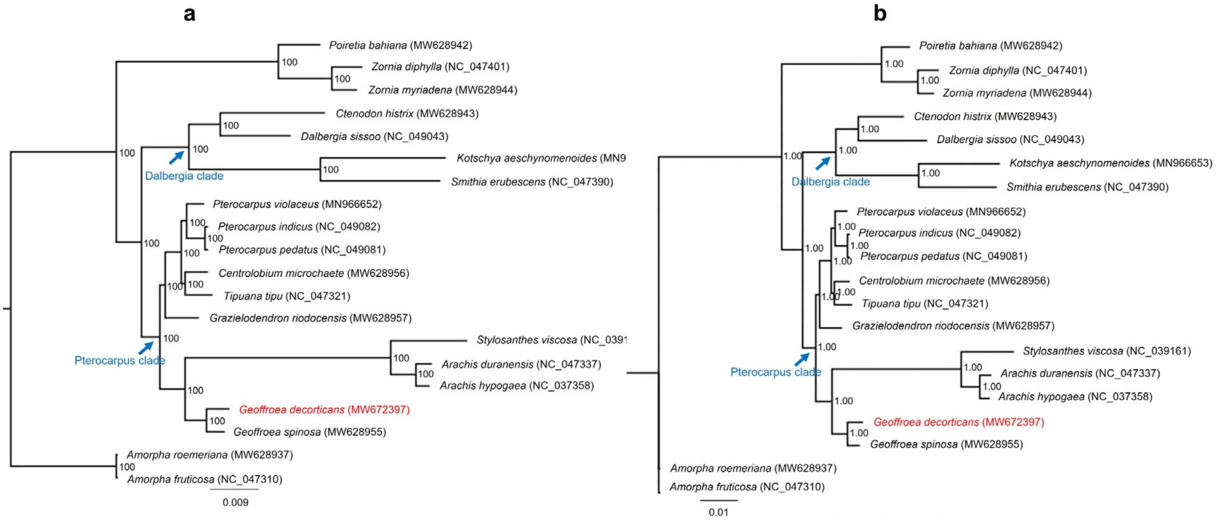


**Figure 3.** Molecular phylogenetic analysis of complete chloroplast genomes of eighteen *Dalbergieae* species and two outgroup species (*A. roemeriana* and *A. fruticosa*) are inferred by ML (A) and BI (B) methods. Maximum likelihood bootstrap values (ML) and Bayesian posterior probabilities (PP) are shown in the branches on A and B trees, respectively.

was divided into two subclades: one containing *P. violaceus, P. indicus, P. pedatus, C. microchaete, T. tipu* and *G. riodocensis* (ML, BP = 100; BI, PP = 1.00), and the other containing *S. viscosa, A. duranensis, A. hypogaea, G. decorticans and G. spinosa* (ML, BP = 100; BI, PP = 1.00) (Fig. 3). Thus, *G. decorticans* was strongly resolved as a sister species of *G. spinosa* (ML, BP =100; BI, PP = 1.00) (Fig. 3).

## 4. Discussion

The Atacama Desert is the driest and oldest desert on the Earth. These extreme environmental conditions result in high dryness and exposure to ultraviolet radiation [31]. Many organisms have adapted to these conditions and play an important role in organism-environment interaction in this fragile ecosystem. Genetic studies on organisms that have been thriving successfully in such harsh environment are of great biological value and understanding their phylogenetic placement in the plant tree of Life is crucial. *G. decorticans* has a wide geographic distribution across the Atacama Desert and is one of the few trees species that can survive in these extreme environmental conditions. To date, a large-scale comparative study of *G. decorticans* plastid genome regarding the phylogeny and structure has not been reported.

The complete chloroplast DNA provides a good understanding of the phylogenetic relationships at family, genus, and species levels [32,33], and has been widely used for evolutionary studies [34]. In the present study, our results showed that the chloroplast genomes of *G. decorticans* and *G. spinosa* had equal percentage of GC content (36,2%), and their size and gene number were also similar [17]. *Geoffroea spinosa* is found near the Amazon in Venezuela, Ecuador, Peru, Bolivia, Paraguay, Argentina and Brazil [35,36]; however, it is not found in Chile. Therefore, the populations of *G. decorticans* in the Atacama Desert are distantly located from the populations of *G. spinosa*. In a previous study, chloroplast genomes of three species of the *Dalbergioid* clade (*C. histrix*, *C. microchaete* and *G. riodocensis*) were reported to have a length of 156,400 bp to 158,908 bp [23], which is similar to that of *G. decorticans*. In the present study, sequence analysis of *G. decorticans* revealed 129 genes, including 83 protein-coding genes, 37 tRNA genes, 8 rRNA genes, and 1 pseudogene (*rpl22*). However, without considering the *rpl22* pseudogene, *G. decorticans* would have the same number of genes as *G. spinosa* (128 genes) [17]. Chloroplast genomes of several species of the *Dalbergieae* clade have 128 genes, without considering gene loss and pseudogenes [17]. However, a previous study revealed that chloroplast genomes of *Pterocarpus spp.* have 130 genes, including 86 protein-coding genes (considering *ycf68* (2x) and *orf42*(2x)), 36 tRNA, and 8 rRNA genes [37], whereas, another study on chloroplast genome of *P. macrocarpus* revealed that it has 127 genes, including 84 protein-coding genes, 35 tRNA, and 8 rRNA genes [38]. In *Pterocarpus* species, *psbJ*, *rpl22* and *trnG-GCC* have been reported to be lost [37], and in *P. macrocarpus, rpl22* and *trnI-CAU*(2x) have been reported to be lost [38]. In addition, in *Dalbergia spp.*, *rpl22* was deleted, but *rps16* was conserved [37,39]. Furthermore, structural rearrangements occur in the chloroplast genome during evolution, resulting in the gains or loss of genes [40]. *G. decorticans* lost the genes *rpl22* (pseudogene), *trnH-GUG* (1x), and *rps16*, similar to the situation observed in five *Pterocarpus spp.* [37], but distinct from that observed in *G. spinosa* and *P. macrocarpus*, in which *rps16* was reported to be present [17,38]. The introns of tRNA genes contain pseudogenes with unknown function; for example, the introns *trnI-GAU* and *trnA-UGC* consist of the pseudogenes *ycf68* and *orf42*, respectively [41]. Moreover, studies on 26 genera have revealed that *rpl22* has been deleted from the chloroplast and transferred to the nuclear genome [42]. In some species of *Fabaceae*, the IR region and genes have been completely lost [32] probably due to nucleotide substitutions and dynamic recombination of chloroplast genomes [43]. Our results revealed that *rps16* was lost in the chloroplast of *G. decorticans*, similar to that in chloroplast of several *Lupinus spp.* [44]. The deletion of *rps16* gene in *G. decorticans* resulted in a premature stop codon, probably causing a loss of functionality. Although some chloroplast genes, such as *rps16*, are essential for plant survival [45], the absence of this gene in the chloroplast can be compensated by the nuclear *rps16* gene [44]. In summary, the chloroplast of *G. decorticans* lost *rpl22* and *rps16* genes, similar to those of most legumes.

The chloroplast size in legumes varies considerably because of expansion, contraction or loss of the IR regions, and these rearrangements are of phylogenetic relevance [17,46]. In *G. decorticans*, *rpl2* gene overlaps with the JLB region; length of the overlapping region is 41 bp. However, we did not find *rpl2* gene to overlap with the JLB region in *Stylosanthes*, *Tipuana*, *Dalbergia*, *Smithia*, *Zornia* and *Arachis*. Although *G. spinosa* and *G. decorticans* are phylogenetically closely related [14], their chloroplast sizes vary moderately. Among all the regions, the length of the LSC region showed the greatest difference (534 bp) between *G. decorticans* and *G. spinosa*. In addition, in the *Pterocarpus* clade, although *Geoffroea*, *Pterocaprus* and *Tipuana* species had LSC regions of similar lengths, lengths of the LSC regions of *Arachis* and *Stylosanthes* species were relatively shorter and varied by approximately 2,000 bp. Similarly, the length of LSC region of mimosoid chloroplasts also showed relative variation among species such as *Adenanthera microsperma* (88,577 bp) and *Leucaena trichandra* (93,690 bp) [47]. Expansion of the IR regions in some legume taxa resulted in a reduction in the size LSC region and, combined with an accumulation of tandem repeats in the LSC, yielded the largest plastome [17]. In all species of the *Dalbergioid* clade, the *ycf1* gene crossed the IRa/SSC border (JSA) and expanded into the IRa region; the length of the expansion varied from 452 to 486 bp. However, in *G. decorticans*, the *ycf1* gene was founded to be extended (28 bp) within the SSC region at the IRb/SSC border (JSB), similar to that in *A. duranensis* (8 bp) and *S. viscosa* (22 bp); but unlike in *G. spinosa*, *T. tipu*, *D. sisso*, *S. erubescens*, and *Z. myriadena*. Furthermore, the *ndhF* gene was found at the JSB junction in *G. decorticans* and other species of the *Pterocarpus* clade, exhibiting substantial differences in the expansion or contraction of IRs. IR expansion is more commonly related to IR/SC junction migration, which incorporates or excludes sequences [17].

In previous studies, the molecular phylogeny of some *Geoffroea spp.* was resolved by Bayesian analyses using *matK* sequences [14] and maximum parsimony analyses using *trnK*/*trnL*/*ITS* sequences [15]. However, the genetic relationships of several populations of *G. decorticans* were determined based on inter simple sequence repeat and randomly amplified polymorphic DNA markers [48], and simple sequence repeat (SSR) markers [49]. Furthermore, co-dominant SSR markers specific to *G. decorticans* have recently been developed for studying the phylogeny and diversity of population in the future [9]. In addition, the complete chloroplast genome of *Prosopis tamarugo* Phill, a legume tree endemic to the Atacama desert, was recently phylogenetically analyzed [50]. However, the phylogenetic relationships of *G. decorticans* have not yet been assessed using chloroplast genome data. In our study, the ML and BI analyses of plastome data strongly supported *G. decorticans* and *G. spinosa* as monophyletic groups, which were placed within the *Pterocarpus* clade. The results showed two subgroups in the *Pterocarpus* clade—one group comprised *Pterocarpus*, *Centrolobium*, *Grazielodendron* and *Tipuana* species, and the other group comprised *Stylosanthes*, *Arachis* and *Geoffroea* species, which is consistent with previous phylogenetic studies based on *matK* [14] and *trnK*/*trnL*/*ITS* [15] sequences. The genus *Geoffroea* Jacq. comprised four species (accepted): *G. horsfieldii* (Lesch.) Oken, *G. spinosa* Jacq., *G. violacea* (Aubl.) Pers., and *G. decorticans* (Hook. & Arn.) Burkart; however, the taxonomic status of eight species remains unresolved [9]. Thus, by comparing the complete chloroplast sequence of *G. spinosa* [17] and the plastome of *G. decorticans*, regions with highly variable markers can be identified, which could be used as DNA barcodes for the genus *Geoffroea*. Therefore, accepted *Geoffroea* species that are not yet resolved can be successfully analyzed using chloroplast or *Geoffroea* genus-specific DNA barcode markers. Here, we report the complete chloroplast genome of *G. decorticans*, which can be used for phylogenetic studies and as a tool to reconstruct the biogeography history of the genus *Geoffroea* in South America.

## Author contributions

- Study conception and design: R Contreras-Díaz, FS Carevic, W Huanca-Mamani
- Data collection: R Contreras-Díaz, R Oses, M Arias-Aburto,M Navarrete-Fuentes
- Analysis and interpretation of results: R Contreras-Díaz, FS Carevic, W Huanca-Mamani, M Arias-Aburto, M Navarrete-Fuentes
- Draft manuscript preparation: R Contreras-Díaz, FS Carevic, W Huanca-Mamani, R Oses, M Arias-Aburto
- Revision of the results and approved the final version of the manuscript: R Contreras-Díaz, FS Carevic, W Huanca-Mamani, R Oses, M Arias-Aburto, M Navarrete-Fuentes

## Financial support

This research was financed by the Regional Innovation Fund for Regional Competitiveness (FIC Regional, 2015) of the Regional Government of Atacama, Code BIP 30432984-0 and the project DIUDA 19/18, 22380. In addition, we thank the National Forestry Corporation (CONAF) of the Region of Atacama for sampling authorization.

## Conflict of interest

None.

## References

[1] Cendoya MA, Micca M, Bogino SM. Growth dynamics of Geoffroea decorticans and Parkinsonia praecox and their response to climate in arid and semiarid environments in Argentina. Bosque 2021;42(1):141–50. https://doi.org/10.4067/S0717-92002021000100141.

[2] Ugalde PC, McRostie V, Gayo EM, et al. 13,000 years of sociocultural plant use in the Atacama Desert of northern Chile. Veg Hist Archaeobot 2021;30:213–30. https://doi.org/10.1007/s00334-020-00783-1.

[3] Giménez AM. Anatomía comparada de leño y corteza de *Geoffroea striata* y *Geoffroea decorticans*. Madera y Bosques 2004;10(1):55–68. https://doi.org/10.21829/myb.2004.1011279.

[4] Nuñez L, Mcrostie V, Cartajena I. Consideraciones sobre la recolección vegetal y la horticultura durante el formativo temprano en el sureste de la cuenca de Atacama. Darwiniana 2009;47(1):56–75.

[5] Costamagna MS, Ordoñez RM, Zampini IC, et al. Nutritional and antioxidant properties of *Geoffroea decorticans*, an Argentinean fruit, and derived products (flour, arrope, decoction and hydroalcoholic beverage). Food Res Int 2013;54(1):160–8. https://doi.org/10.1016/j.foodres.2013.05.038.

[6] Castro L. El bosque de la Pampa del Tamarugal y la industria salitrera: el problema de la deforestación, los proyectos para su manejo sustentable y el debate político (Tarapacá, Perú-Chile 1829-1941). Scr 2020;24:641. https://doi.org/10.1344/sn2020.24.26507.

[7] Echeverría J, Paniagua-Zambrana NY, Bussmann RW. *Geoffroea decorticans* (Gillies ex Hook. & Arn.) Burkart FABACEAE. In: Paniagua-Zambrana N, Bussmann R, editors. Ethnobotany of the Andes. Ethnobotany of Mountain Regions. Cham: Springer; 2020. p. 893–6. https://doi.org/10.1007/978-3-030-28933-1_128.

[8] Cotabarren J, Broitman DJ, Quiroga E, et al. GdTI, the first thermostable trypsin inhibitor from *Geoffroea decorticans* seeds. A novel natural drug with potential application in biomedicine. Int J Biol Macromol 2020:148869–79. https://doi.org/10.1016/j.ijbiomac.2020.01.214. PMid: 31981666.

[9] Contreras R, Carevic F, Aburto MA, et al. Desarrollo de nuevos loci de microsatélites para *Geoffroea decorticans* (Gillies ex Hook & Arn.) Burkart. Bol La Soc Argentina Bot 2021;56(4):533–45. https://doi.org/10.31055/1851.2372.v56.n4.32721.

[10] Saldaña CL, Rodriguez-Grados P, Chávez-Galarza JC, et al. Unlocking the complete chloroplast genome of a native tree species from the Amazon Basin, capirona *(Calycophyllum spruceanu*m, Rubiaceae), and its comparative analysis with other Ixoroideae species. Genes (Basel) 2022;13(1):113. https://doi.org/10.3390/genes13010113. PMid: 35052453.

[11] Leebens-Mack JH, Barker MS, Carpenter EJ, et al. One thousand plant transcriptomes and the phylogenomics of green plants. Nature 2019;574:679–85. https://doi.org/10.1038/s41586-019-1693-2. PMid: 31645766.

[12] Smith SA, Brown JW. Constructing a broadly inclusive seed plant phylogeny. Am J Bot 2018;105(3):302–14. https://doi.org/10.1002/ajb2.1019. PMid: 29746720.

[13] Polhill RM, Raven PH. Advances in Legume Systematics. Parts 1 and 2. Royal Botanic Gardens, Kew 1981; 1,050 pp. ISBN: 9780855212247.

[14] Cardoso D, Pennington RT, de Queiroz LP, et al. Reconstructing the deep-branching relationships of the papilionoid legumes. South African J Bot 2013;89:58–75. https://doi.org/10.1016/j.sajb.2013.05.001.

[15] Lavin M, Pennington RT, Klitgaard BB, et al. The dalbergioid legumes (Fabaceae): Delimitation of a pantropical monophyletic clade. Am J Bot 2001;88(3):503–33. https://doi.org/10.2307/2657116. PMid: 11250829.

[16] Klitgård BB, Forest F, Booth TJ, et al. A detailed investigation of the Pterocarpus clade (Leguminosae: Dalbergieae): *Etaballia* with radially symmetrical flowers is nested within the papilionoid-flowered *Pterocarpus*. South African J Bot 2013;89:128–42. https://doi.org/10.1016/j.sajb.2013.07.006.

[17] Lee C, Choi IS, Cardoso D, et al. The chicken or the egg? Plastome evolution and an independent loss of the inverted repeat in papilionoid legumes. Plant J 2021;107(3):861–75. https://doi.org/10.1111/tpj.15351. PMid: 34021942.

[18] Contreras R, van den Brink L, Burgos B, et al. Genetic characterization of an endangered Chilean endemic species, *Prosopis burkartii* Muñoz, reveals its hybrids parentage. Plants 2020;9(6):1–19. https://doi.org/10.3390/plants9060744. PMid: 32545703.

[19] Bankevich A, Nurk S, Antipov D, et al. SPAdes: A new genome assembly algorithm and its applications to single-cell sequencing. J Comput Biol 2012;19(5):455–77. https://doi.org/10.1089/cmb.2012.0021. PMid: 22506599.

[20] Shi L, Chen H, Jiang M, et al. CPGAVAS2, an integrated plastome sequence annotator and analyzer. Nucleic Acids Res 2019;47(W1):W65–73. https://doi.org/10.1093/nar/gkz345. PMid: 31066451.

[21] Qu XJ, Moore MJ, Li DZ, et al. PGA: A software package for rapid, accurate, and flexible batch annotation of plastomes. Plant Methods 2019;15:50. https://doi.org/10.1186/s13007-019-0435-7. PMid: 31139240.

[22] Greiner S, Lehwark P, Bock R. OrganellarGenomeDRAW (OGDRAW) version 1.3.1: Expanded toolkit for the graphical visualization of organellar genomes. Nucleic Acids Res 2019;47(W1):W59–64. https://doi.org/10.1093/nar/gkz238. PMid: 30949694.

[23] Choi IS, Cardoso D, de Queiroz LP, et al. Highly resolved papilionoid legume phylogeny based on plastid phylogenomics. Front Plant Sci 2022;13:823190. https://doi.org/10.3389/fpls.2022.823190. PMid: 35283880.

[24] Amiryousefi A, Hyvönen J, Poczai P. IRscope: an online program to visualize the junction sites of chloroplast genomes. Bioinformatics 2018;34(17):3030–1. https://doi.org/10.1093/bioinformatics/bty220. PMid: 29659705.

[25] Katoh K, Standley DM. MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. Mol Biol Evol 2013;30(4):772–80. https://doi.org/10.1093/molbev/mst010. PMid: 23329690.

[26] Capella-Gutiérrez S, Silla-Martínez JM, Gabaldón T. trimAl: A tool for automated alignment trimming in large-scale phylogenetic analyses. Bioinformatics 2009;25(15):1972–3. https://doi.org/10.1093/bioinformatics/btp348. PMid: 19505945.

[27] Darriba D, Taboada GL, Doallo R, et al. JModelTest 2: More models, new heuristics and parallel computing. Nat Methods 2012;9:772. https://doi.org/10.1038/nmeth.2109. PMid: 22847109.

[28] Stamatakis A. RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 2014;30(9):1312–3. https://doi.org/10.1093/bioinformatics/btu033. PMid: 24451623.

[29] Ronquist F, Teslenko M, Van Der Mark P, et al. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Syst Biol 2012;61(3):539–42. https://doi.org/10.1093/sysbio/sys029. PMid: 22357727.

[30] Miller MA, Pfeiffer W, Schwartz T. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: 2010 Gatew Comput Environ Work GCE 2010. p. 1–8. https://doi.org/10.1109/GCE.2010.5676129.

[31] Azua-Bustos A, González-Silva C, Fairén AG. The Atacama Desert in Northern Chile as an Analog Model of Mars. Front Astron Sp Sci 2022;8:810426. https://doi.org/10.3389/fspas.2021.810426.

[32] Palmer J, Osorio B, Aldrich J, et al. Chloroplast DNA evolution among legumes: Loss of a large inverted repeat occurred prior to other sequence rearrangements. Curr Genet 1987;11:275–86. https://doi.org/10.1007/BF00355401.

[33] Sun J, Wang Y, Liu Y, et al. Evolutionary and phylogenetic aspects of the chloroplast genome of *Chaenomeles* species. Sci Rep 2020;10:11466. https://doi.org/10.1038/s41598-020-67943-1. PMid: 32651417.

[34] Daniell H, Lin CS, Yu M, et al. Chloroplast genomes: Diversity, evolution, and applications in genetic engineering. Genome Biol 2016;17:134. https://doi.org/10.1186/s13059-016-1004-2. PMid: 27339192.

[35] Prado DE, Gibbs PE. Patterns of species distributions in the dry seasonal forests of South America. Ann Missouri Bot Gard 1993;80(4):902. https://doi.org/10.2307/2399937.

[36] Naciri-Graven Y, Caetano S, Prado D, et al. Development and characterization of 11 microsatellite markers in a widespread Neotropical seasonally dry forest tree species, *Geoffroea spinosa* Jacq. (Leguminosae). Mol Ecol Notes 2005;5(3):542–5. https://doi.org/10.1111/j.1471-8286.2005.00982.x.

[37] Hong Z, Wu Z, Zhao K, et al. Comparative analyses of five complete chloroplast genomes from the genus *Pterocarpus* (Fabacaeae). Int J Mol Sci 2020;21(11):3758. https://doi.org/10.3390/ijms21113758. PMid: 32466556.

[38] Zhang J, Li Y, Yuan X, et al. The complete chloroplast genome sequence of *Pterocarpus macrocarpus*. Mitochondrial DNA Part B 2020;5(1):718–9. https://doi.org/10.1080/23802359.2020.1714509. PMid: 33366718.

[39] Song Y, Zhang Y, Xu J, et al. Characterization of the complete chloroplast genome sequence of *Dalbergia* species and its phylogenetic implications. Sci Rep 2019;9:20401. https://doi.org/10.1038/s41598-019-56727-x. PMid: 31892714.

[40] Wicke S, Schneeweiss GM, dePamphilis CW, et al. The evolution of the plastid chromosome in land plants: Gene content, gene order, gene function. Plant Mol Biol 2011;76:273–97. https://doi.org/10.1007/s11103-011-9762-4. PMid: 21424877.

[41] Silva SR, Diaz YCA, Penha HA, et al. The chloroplast genome of *Utricularia reniformis* sheds light on the evolution of the *ndh* gene complex of terrestrial carnivorous plants from the Lentibulariaceae family. PLoS One 2016;11(19): e0165176. https://doi.org/10.1371/journal.pone.0165176. PMid: 27764252.

[42] Gantt JS, Baldauf SL, Calie PJ, et al. Transfer of rpl22 to the nucleus greatly preceded its loss from the chloroplast and involved the gain of an intron. EMBO J 1991;10:3073–8. https://doi.org/10.1002/j.1460-2075.1991.tb07859.x. PMid: 1915281.

[43] Mohanta TK, Mishra AK, Khan A, et al. Gene loss and evolution of the plastome. Genes (Basel) 2020;11(10):1133. https://doi.org/10.3390/genes11101133. PMid: 32992972.

[44] Keller J, Rousseau-Gueutin M, Martin GE, et al. The evolutionary fate of the chloroplast and nuclear *rps16* genes as revealed through the sequencing and comparative analyses of four novel legume chloroplast genomes from *Lupinus*. DNA Res 2017;24(4):343–58. https://doi.org/10.1093/dnares/dsx006. PMid: 28338826.

[45] Fleischmann TT, Scharff LB, Alkatib S, et al. Nonessential plastid-encoded ribosomal proteins in tobacco: A developmental role for plastid translation and implications for reductive genome evolution. Plant Cell 2011;23 (9):3137–55. https://doi.org/10.1105/tpc.111.088906. PMid: 21934145.

[46] Wang YH, Wicke S, Wang H, et al. Plastid genome evolution in the early-diverging legume subfamily Cercidoideae (Fabaceae). Front Plant Sci 2018;9:138. https://doi.org/10.3389/fpls.2018.00138. PMid: 29479365.

[47] Wang YH, Qu XJ, Chen SY, et al. Plastomes of Mimosoideae: structural and size variation, sequence divergence, and phylogenetic implication. Tree Genet Genomes 2017;13:41. https://doi.org/10.1007/s11295-017-1124-1.

[48] Contreras-Díaz R, Porcile Saavedra V, Aguayo CF. Genetic diversity of *Geoffroea decorticans*, a native woody leguminous species from Atacama Desert in Chile. Bosque 2018;39(2):321–32. https://doi.org/10.4067/S0717-92002018000200321.

[49] Contreras R, Porcile V, Aguayo F. Microsatellites reveal a high genetic differentiation among native *Geoffroea decorticans* populations in Chilean Atacama Desert. Bol La Soc Argentina Bot 2019;54(2):225–40. https://doi.org/10.31055/1851.2372.v54.n2.24367.

[50] Contreras-Díaz R, van den Brink L, Navarrete-Fuentes MJ, et al. Characterization of the complete chloroplast genome of *Prosopis tamarugo* (*Prosopis*, Leguminosae), an endangered endemic tree species from the Atacama Desert. Bosque 2021;42(3):365–70. https://doi.org/10.4067/S0717-92002021000300365.