frontiers in Genetics

ORIGINAL RESEARCH
published: 03 January 2022
doi: 10.3389/fgene.2021.791628

# Insights Into Comparative Analyses and Phylogenomic Implications of *Acer* (Sapindaceae) Inferred From Complete Chloroplast Genomes

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*Acer* L. (Sapindaceae) is one of the most diverse and widespread plant genera in the Northern Hemisphere. It comprises 124–156 recognized species, with approximately half being native to Asia. Owing to its numerous morphological features and hybridization, this genus is taxonomically and phylogenetically ranked as one of the most challenging plant taxa. Here, we report the complete chloroplast genome sequences of five *Acer* species and compare them with those of 43 published *Acer* species. The chloroplast genomes were 149,103–158,458 bp in length. We conducted a sliding window analysis to find three relatively highly variable regions (*psbN-rps14*, *rpl32-trnL*, and *ycf1*) with a high potential for developing practical genetic markers. A total of 76–103 SSR loci were identified in 48 *Acer* species. The positive selection analysis of *Acer* species chloroplast genes showed that two genes (*psaI* and *psbK*) were positively selected, implying that light level is a selection pressure for *Acer* species. Using Bayes empirical Bayes methods, we also identified that 20 cp gene sites have undergone positive selection, which might result from adaptation to specific ecological niches. In phylogenetic analysis, we have reconfirmed that *Acer pictum* subsp. *mono* and *A. truncatum* as sister species. Our results strongly support the sister relationships between sections *Platanoidea* and *Macrantha* and between sections *Trifoliata* and *Pentaphylla*. Moreover, series *Glabra* and *Arguta* are proposed to promote to the section level. The chloroplast genomic resources provided in this study assist taxonomic and phylogenomic resolution within *Acer* and the Sapindaceae family.

**Keywords: *Acer*, chloroplast genome, sequence divergence, structural variation, phylogenetics**

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***Edited by:***
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***Specialty section:***
*This article was submitted to Plant Genomics, a section of the journal Frontiers in Genetics*

***Received:*** *08 October 2021*
***Accepted:*** *02 December 2021*
***Published:*** *03 January 2022*

***Citation:***
*Yu T, Gao J, Liao P-C, Li J-Q and Ma W-B (2022) Insights Into Comparative Analyses and Phylogenomic Implications of Acer (Sapindaceae) Inferred From Complete Chloroplast Genomes. Front. Genet. 12:791628. doi: 10.3389/fgene.2021.791628*

## 1 INTRODUCTION

With the rapid development of next-generation sequencing (NGS), the increasing chloroplast (cp) genome sequences of land plants offer comprehensive comparison in genome structure, horticultural improvement in plant breeding (Sonah et al., 2011; Xiong et al., 2015), and phylogenetic reconstruction (Cai et al., 2015; Ruhsam et al., 2015). The cp genome is maternally inherited with high copy numbers per cell, despite being much smaller than other genomes (Yi et al., 2013). The cp genome is commonly used in evolution and phylogenomic analysis, providing supplementary

information hidden in nuclear genomes regarding, for instance, ancient taxa histories and population-area relationships (Timme et al., 2007; Zeb et al., 2019). The cp genome's relatively conserved features make it being broadly applied to plant systematics, biodiversity, biogeography, adaptation, etc. (Wambugu et al., 2015; Brozynska et al., 2016).

*Acer* L. (Maple), composed of more than 124 species, is a diverse genus within the Sapindaceae L. family (Xu et al., 2008), which are primarily deciduous and distributed in temperate Asia, Europe, and North America (van Gelderen et al., 1994; Renner et al., 2008; Xu et al., 2008). Many *Acer* species provide important economic products, such as timber, furniture, and herbal medicines, especially gamma-linolenic acid, and the genus also includes many famous horticultural plants (Bi et al., 2016). Moreover, some *Acer* species are dominant in several forests, responsible for fundamental ecosystem processes (Bishop et al., 2015). High variable leaf characters and complex reproductive characteristics hinder *Acer*'s systematic classification (Cronquist, 1979; Rosado et al., 2018). An accurate phylogeny can facilitate the sustainable utilization of wild genetic resources (Xu et al., 2008). Previously, the phylogenetic trees of *Acer* have been reconstructed by cambial peroxidase isozymes (Santamour, 1982), restriction fragment length polymorphism (RFLP) markers (Pfosser et al., 2002), cp DNA and nuclear DNA (Cho et al., 1996; Ackerly and Donoghue, 1998; Li et al., 2006; Renner et al., 2008; Li et al., 2019; Gao et al., 2020), and cp genome (Areces-Berazain et al., 2020; Wang et al., 2020; Yu et al., 2020; Areces-Berazain et al., 2021). However, limited informative sites, taxa, and evolution models used for the phylogenetic analyses led to the phylogenetic relationship being poorly resolved. Therefore, large-scale plastome data is necessary to acquire a maximum phylogenetic signal in *Acer*.

In this study, we compiled a dataset with the cp genomes of 48 *Acer* species, five of which were newly generated in this study (*A. palmatum*, *A. wilsonii*, *A. flabellatum*, *A. sino-oblongum*, and *A. laevigatum*). Because of the importance of plastomes in systematics, it is necessary to confirm these plastomes' gene order and sequence homology. Therefore, by comparing plastome studies, we aimed: 1) to determine the gene order and gene content of *Acer* cp genomes, 2) to identify divergence hotspots and the positive selective genes in the cp genomes, and 3) to reconstruct the phylogenomic relationships of *Acer* species.

# 2 MATERIALS AND METHODS

## 2.1 Sampling and DNA Extraction

Young leaves of five *Acer* species (*A. palmatum*, *A. wilsonii*, *A. flabellatum*, *A. sino-oblongum*, and *A. laevigatum*) were collected and dried immediately with silica gel for DNA extraction with the modified CTAB method (Doyle, 1987). The sampling information is shown in **Supplementary Table S1**. Species identification was followed by *Maples of the World* (van Gelderen et al., 1994) and *Flora of China* (Xu et al., 2008). Voucher specimens were deposited at the College of Forestry, Beijing Forestry University, China.

## 2.2 Chloroplast Genome Sequencing, Assembling, and Annotation

Purified genomic DNA was sequenced using an Illumina MiSeq sequencer (Shanghai OE Biotech Co., Ltd.). A paired-end library was constructed with an insert size of 300 bp, yielding at least 8 GB of 150 bp paired-end reads for each species. Clean reads were obtained with NGSQC Toolkit v2.3.3 (cut-off read length for HQ = 70%, cut-off quality score = 20, trim reads from 5′ = 3, trim reads from 3′ = 7) (Dai et al., 2010). MITObim v. 1.8 (Hahn et al., 2013) was used to assemble the following reference cp genomes: *A. buergerianum* subsp. *ningpoense* (KF753631) (Yang et al., 2015), *A. miaotaiense* (KX098452) (Zhang et al., 2016), *A. davidii* (KU977442) (Jia et al., 2016), and *A. morrisonense* (KT970611) (Li et al., 2017). Annotation was performed using DOGMA (Wyman et al., 2004). Protein-encoding genes (PCG), tRNAs, rRNAs were annotated by BLAST searches (https://blast.ncbi.nlm.nih.gov/Blast.cgi) with manual adjustment error. The boundaries between the representative *Acer* cp genome regions were determined with the online tool IRscope (Amiryousefi et al., 2018), and ten representative species form main groups of *Acer* were highlighted.

## 2.3 Identifying Cp SSRs

MISA (MIcroSAtellite, http://pgrc.ipk-gatersleben.de/misa/) was used to detect simple sequence repeats (SSRs) with criteria of minimal repeat numbers ten in mono-nucleotide SSR, four in di- and tri-nucleotide, and three in tetra-, penta-, and hexa-nucleotide SSRs motifs.

## 2.4 Divergence Hotspot Identification

Cp sequences were aligned by MAFFT (Katoh et al., 2005), and sliding window analysis was then used to estimate nucleotide variation (π) with 600-bp window length and 200-bp step size using DnaSP 5.0 (Librado and Rozas, 2009).

## 2.5 Positive Selected Analysis

The CodeML program in PAML 4.7.1 (Yang, 2007) was used to test the positive selection of *Acer* cp genes under the site-specific models. The dN, dS, and ω (= dN/dS) values were calculated with seqtype = 1, model = 0, Nssites = 0, 1, 2, 7, 8 based on 77 protein-coding genes shared by 48 *Acer* species. A maximum-likelihood phylogenetic tree was reconstructed using whole cp genomes by PhyML v3.0 (Guindon et al., 2005). Likelihood ratio tests (LRT) were used to compare models between M1 (neutral) and M2 (positive selection) and between M7 (beta) and M8 (beta and ω). *p*-value was calculated using the internal CHI2 program in PAML 4.7.1 (Yang, 2007).

## 2.6 Phylogenomic Reconstruction

To reconstruct the phylogeny, 58 cp genome sequences comprising five new plastome sequences, 43 plastomes of *Acer* species from GenBank, and ten outgroup species were used (**Supplementary Table S2**). BioEdit version 7.1.11 (Hall, 1999) was used to align sequences with manual refinement and finally generated a total of 184,290 bp alignment length. The 5′ and 3′ ends of the sequences were trimmed to equal lengths for

**TABLE 1 |** General features of the *Acer* chloroplast genomes compared in this study.

| Species | Total (bp) | GC (%) | LSC (bp) | SSC (bp) | IR (bp) | Accession no |
|---|---|---|---|---|---|---|
| *Acer acuminatum* | 155,548 | 37.9 | 85,358 | 18,046 | 26,072 | MN864496 |
| *Acer amplum* | 156,225 | 37.9 | 86,121 | 18,066 | 26,019 | NC034932 |
| *Acer buergerianum* subsp. *ningpoense* | 156,911 | 37.9 | 85,315 | 18,094 | 26,751 | NC034744 |
| *Acer caesium* subsp. *giraldii* | 154,176 | 38.1 | 82,759 | 17,895 | 26,761 | MK479225 |
| *Acer cappadocicum* | 157,353 | 37.9 | 85,723 | 18,040 | 26,798 | NC051956 |
| *Acer carpinifolium* | 155,212 | 38.0 | 85,448 | 17,724 | 26,020 | MN864497 |
| *Acer catalpifolium* | 157,349 | 37.9 | 85,745 | 18,066 | 26,769 | MF179637 |
| *Acer caudatifolium* | 158,458 | 37.8 | 86,911 | 18,059 | 26,744 | MK479226 |
| *Acer cinnamomifolium* | 156,227 | 37.9 | 85,928 | 18,121 | 26,079 | NC056164 |
| *Acer cissifolium* | 155,997 | 37.9 | 85,790 | 18,051 | 26,078 | MW067037 |
| *Acer davidii* | 157,044 | 37.9 | 85,410 | 18,112 | 26,761 | KU977442 |
| *Acer fenzelianum* | 156,535 | 37.9 | 85,166 | 18,077 | 26,646 | NC045527 |
| *Acer flabellatum* | 156,472 | 37.9 | 84,876 | 18,088 | 26,754 | MF787384[a] |
| *Acer tataricum* subsp. *ginnala* | 156,184 | 38.1 | 85,485 | 18,032 | 26,047 | MN864511 |
| *Acer glabrum* | 156,373 | 37.9 | 86,034 | 18,211 | 26,064 | MN864498 |
| *Acer griseum* | 156,857 | 37.9 | 85,227 | 18,134 | 26,748 | KY511609 |
| *Acer henryi* | 156,325 | 37.9 | 86,034 | 18,097 | 26,097 | MW067048 |
| *Acer laevigatum* | 156,905 | 37.9 | 85,323 | 18,084 | 26,749 | MF521832[a] |
| *Acer longipes* | 157,137 | 37.9 | 85,531 | 18,068 | 26,769 | MG751775 |
| *Acer lucidum* | 157,612 | 38.1 | 86,838 | 18,094 | 26,340 | MK479214 |
| *Acer mandshuricum* | 156,234 | 37.9 | 86,043 | 18,059 | 26,066 | MW067055 |
| *Acer miaotaiense* | 156,595 | 37.9 | 86,327 | 18,068 | 26,100 | KX098452 |
| *Acer micranthum* | 156,399 | 37.9 | 86,147 | 18,128 | 26,062 | MN864500 |
| *Acer morrisonense* | 157,197 | 37.8 | 85,655 | 18,086 | 26,728 | KT970611 |
| *Acer negundo* | 155,938 | 37.9 | 85,678 | 18,092 | 26,084 | MN841452 |
| *Acer nikoense* | 156,082 | 37.9 | 85,866 | 18,148 | 26,034 | MN864499 |
| *Acer nipponicum* | 156,225 | 37.8 | 85,823 | 18,232 | 26,085 | MN864502 |
| *Acer oblongum* | 155,686 | 38.0 | 85,665 | 17,821 | 26,100 | NC056208 |
| *Acer palmatum* | 157,023 | 37.9 | 85,342 | 18,167 | 26,757 | KY457568[a] |
| *Acer paxii* | 149,103 | 37.5 | 78,768 | 17,474 | 26,366 | MK479215 |
| *Acer pentaphyllum* | 156,220 | 37.9 | 85,938 | 18,148 | 26,067 | MN864505 |
| *Acer pictum* subsp. *mono* | 156,985 | 37.9 | 85,378 | 18,069 | 26,769 | MG751776 |
| *Acer pilosum* | 155,586 | 38.0 | 85,313 | 18,139 | 26,076 | MN864506 |
| *Acer platanoides* | 156,385 | 37.9 | 86,098 | 18,107 | 26,090 | NC051959 |
| *Acer pseudosieboldianum* | 157,053 | 37.9 | 85,392 | 18,169 | 26,746 | MW067066 |
| *Acer robustum* | 156,790 | 37.9 | 85,127 | 18,115 | 26,774 | MK479212 |
| *Acer rubrum* | 155,683 | 37.9 | 85,383 | 18,086 | 26,107 | MN864509 |
| *Acer saccharum* | 155,684 | 37.9 | 85,393 | 18,033 | 26,129 | NC051960 |
| *Acer sino-oblongum* | 157,121 | 37.9 | 85,558 | 18,119 | 26,722 | KY987160[a] |
| *Acer sterculiaceum* subsp. *sterculiaceum* | 156,258 | 38.0 | 86,014 | 18,048 | 26,098 | MN864510 |
| *Acer sutchuenense* subsp. *tienchuanense* | 156,063 | 37.9 | 85,127 | 18,115 | 26,774 | NC049166 |
| *Acer takesimense* | 157,023 | 37.9 | 85,371 | 18,160 | 26,746 | NC046488 |
| *Acer tegmentosum* | 156,435 | 37.8 | 86,139 | 18,103 | 26,097 | NC056233 |
| *Acer tetramerum* | 154,078 | 38.1 | 83,199 | 17,895 | 26,492 | MK479228 |
| *Acer truncatum* | 156,262 | 37.9 | 86,019 | 18,073 | 26,085 | MH716034 |
| *Acer wilsonii* | 157,067 | 37.9 | 85,419 | 18,128 | 26,760 | MG012225[a] |
| *Acer yangbiense* | 155,706 | 38.0 | 86,593 | 18,097 | 25,508 | MN315285 |
| *Acer yangjuechi* | 157,088 | 37.9 | 85,483 | 18,069 | 26,768 | MG770234 |

[a]*Sequences obtained in this study.*

subsequent phylogenetic analyses. Phylogenetic relationships were reconstructed using Bayesian inference (BI), maximum likelihood (ML), and maximum parsimony (MP) by MrBayes 3.2 (Ronquist et al., 2012), PhyML v3.0 (Guindon et al., 2005), and PAUP*4.0b10 (Swofford, 2003), respectively. The best-fitting substitution model (GTR + I + G) was determined using Modeltest 3.7 (Posada and Buckley, 2004). In the Bayesian analyses, two independent Markov Chain Monte Carlo (MCMC) permutations were initiated. Each consisted of one cold and three heated MCMC chains for $10^8$ generations and sampled every $10^4$ generations. The first 2,000 trees were discarded as burn-in to ensure that the chains had become stationary. The ML analysis was initiated from a BIONJ tree, with support values for the nodes estimated by 1,000 bootstrap replicates. In the MP analysis, all character states were treated as unordered and equally weighted, and a heuristic search was performed with 1,000 replicates of random addition of sequences, tree-bisection-reconnection branch-swapping, and MULTREES. Bootstrap analysis was conducted in 1,000 replicates with the same heuristic search settings described above.

**TABLE 2 |** Genes present in the *Acer* chloroplast genome.

| Group of gene | Genes name |
|---|---|
| Photostsyem I | *psaA*, *psaB*, *psaC*, *psaI*, *psaJ* |
| Photostsyem II | *psbA*, *psbB*, *psbC*, *psbD*, *psbE*, *psbF*, *psbh*, *psbI*, *psbJ*, *psbK*, *psbL*, *psbM*, *psbN*, *psbT*, *psbZ* |
| Cytochrome b/f complex | *petA*, *petB**, *petD**, *petG*, *petL*, *petN* |
| ATP synthase | *atpA*, *atpB*, *atpE*, *atpF**, *atpH*, *atpI* |
| NADH dehydrogenase | *ndhA**, *ndhB**, *ndhC*, *ndhD*, *ndhE*, *ndhF*, *ndhG*, *ndhH*, *ndhI*, *ndhJ*, *ndhK* |
| RubisCO large subunit | *rbcL* |
| RNA polymerase | *ropA*, *ropB*, *ropC1**, *ropC2* |
| Ribosomal proteins (SSU) | *rps2*, *rps3*, *rps4*, *rps7*, *rps8*, *rps11*, *rps12***, *rps14*, *rps15*, *rps16**, *rps18*, *rps19* |
| Ribosomal proteins (LSU) | *rpl2**, *rpl14*, *rpl16**, *rpl20*, *rpl22*, *rpl23*, *rpl32*, *rpl33*, *rpl36* |
| Other gene | *clpP***, *matK*, *accD*, *ccsA*, *infA*, *cemA* |
| Proteins of unknown function | *ycf1*, *ycf2*, *ycf3***, *ycf4*, *ycf15* |
| ORFs | *Orf42* |
| Transfer RNAs | 31 tRNAs (six contain a single intron) |
| Ribosomal RNAs | *rrn4.5*, *rrn5*, *rrn16*, *rrn23* |

*A single asterisk (*) preceding gene names indicate intron-containing genes, and double asterisks (**) preceding gene names indicate two introns in the gene.*

# 3 RESULTS AND DISCUSSION

## 3.1 Choroplast Genome Organization of *Acer*

The nucleotide sequences of the 48 *Acer* cp genomes ranged from 149,103 bp (*A. paxii*) to 158,458 bp (*A. caudatifolium*) (**Table 1**). These cp genomes revealed a typical quadripartite structure similar to most angiosperms, with LSC, SSC, and IRs (IRa and IRb) regions. The LSC, SSC, and IR regions were 78,768–86,911 bp, 17,474–18,232 bp, and 25,508–26,798 bp long, respectively (**Table 1**). The guanine (G) and cytosine (C) proportion (GC%) varied from 37.5 to 38.1%, in which 34 species have a stable GC content of 37.9%. The GC content was higher in the IR region than the LSC and SSC regions.

A total of 117 genes included four unique rRNAs, 31 tRNAs, and 82 PCGs (**Table 2**). Most cp genes were single copy, whereas 23 genes exhibited double copies, including four rRNA (*4.5S*, *5S*, *16S*, and *23S* rRNA), nine tRNA genes (*trnA-UGC*, *trnI-CAU*, *trnI-GAU*, *trnL-CAA*, *trnM-CAU*, *trnN-GUU*, *trnR-ACG*, *trnT-GGU*, and *trnV-GAC*), and 10 PCG (*ndhB*, *rpl2*, *rps12*, *rpl23*, *rps19*, *rps7*, *ycf1*, *orf42*, *ycf2*, and *ycf15*). A total of 18 genes had introns, and three genes (*ycf3*, *clpP,* and *rps12*) contained two introns. Despite typically highly conserved, gene relocation and structural variation in IR and single-copy regions are very common (de Santana Lopes et al., 2018; Shearman et al., 2020; Guo et al., 2021). The cp genome structures of 10 representative *Acer* species are shown in **Supplementary Figure S1**. Two main types of *Acer* species were recognized: the first group was represented by *A. catalpifolium*, *A. buergerianum*, *A. negundo*, whose LSC-IRB junction region comprised the *rpl22* gene; the second group was composed of *A. micranthum*, *A. lucidum*, *A. yangbiense*, *A. tataricum* subsp. *ginnala*, *A. carpinifolium*, *A. glabrum*, and *A. caesium*, whose LSC-IRB junction comprised the *rps19* or *rpl2* gene regions, or the spacer region between *rps19* and *rpl2*. The structure of the three species in the first group was relatively stable and had the same distance between *rpl22* and the LSC-IRB junction. However, in the second group, the distance of *rps19* and *rpl2* from the LSC-IRB junction significantly varied. These structural pattern variations are similar to those of Saxifragaceae species (Li et al., 2019). Compared with the LSC-IRB junction, the SSC-IRB junction showed clear conservativeness, except for the deletion of pseudogene *ycf1* (φ *ycf1*) in *A. trigonatum*. SSC-IRB junctions of *Acer* species were all located in the *ycf1* gene, and the length of the *ycf1* fragment in the IRB region was 1,244–1,284 bp. The length of the *ndhF* gene starting site from the SSC-IRB junction was 32–48 bp.

## 3.2 SSRs Analysis of the *Acer* Cp Genomes

A total of 5,136 SSR loci were detected in the 48 *Acer* species, with the highest number in *A. tegmentosum* (137) and the lowest number in *A. palmatum* (59) (**Figure 1A**), in which six SSR types in *A. negundo*, five types in 21 species, four types in other 24 species, and three types in the remaining two species (*A. palmatum* and *A. buergerianum*). Most SSRs were mono- and di-nucleotide motifs; the former was the most abundant SSR type, being detected at 3,251 loci (60.95% of the total number), while 1,714 di-nucleotide repeats (32.13%) were detected. The least frequent type was penta-nucleotide, which was detected in only 12 loci in all *Acer* species (**Figure 1B**). The mono-nucleotide SSRs mostly comprised short polyA and polyT repeats, which have also been reported in other species, including *Salvia miltiorrhiza* (Lamiaceae) (Qian et al., 2013) and three *Veroniceae* species (Plantaginaceae) (Choi et al., 2016). Most SSRs were detected in intergenic regions. Within the coding regions, the SSRs were concentrated in *ycf1* and *ycf2*, which is consistent with other species such as *Cynara cardunculus* (Curci et al., 2015) and *Vigna radiata* (Tangphatsornruang et al., 2009). Thus, the highly variable *ycf1* coding region may potentially be applied as an alternative marker for plastid candidate barcodes to solve the phylogenetic controversy (Dong et al., 2015). SSR information may be crucial for understanding the genetic diversity status of *Acer* species worldwide.

## 3.3 Divergence Hotspot of *Acer* Species

The sliding window analysis showed that nucleotide variability was higher in *psbZ-rps14*, *rpl32-trnL*, and *ycf1* than in other regions (**Figure 2**). Maximum nucleotide polymorphism was 0.023, showing that those cp genomes were relatively conserved.

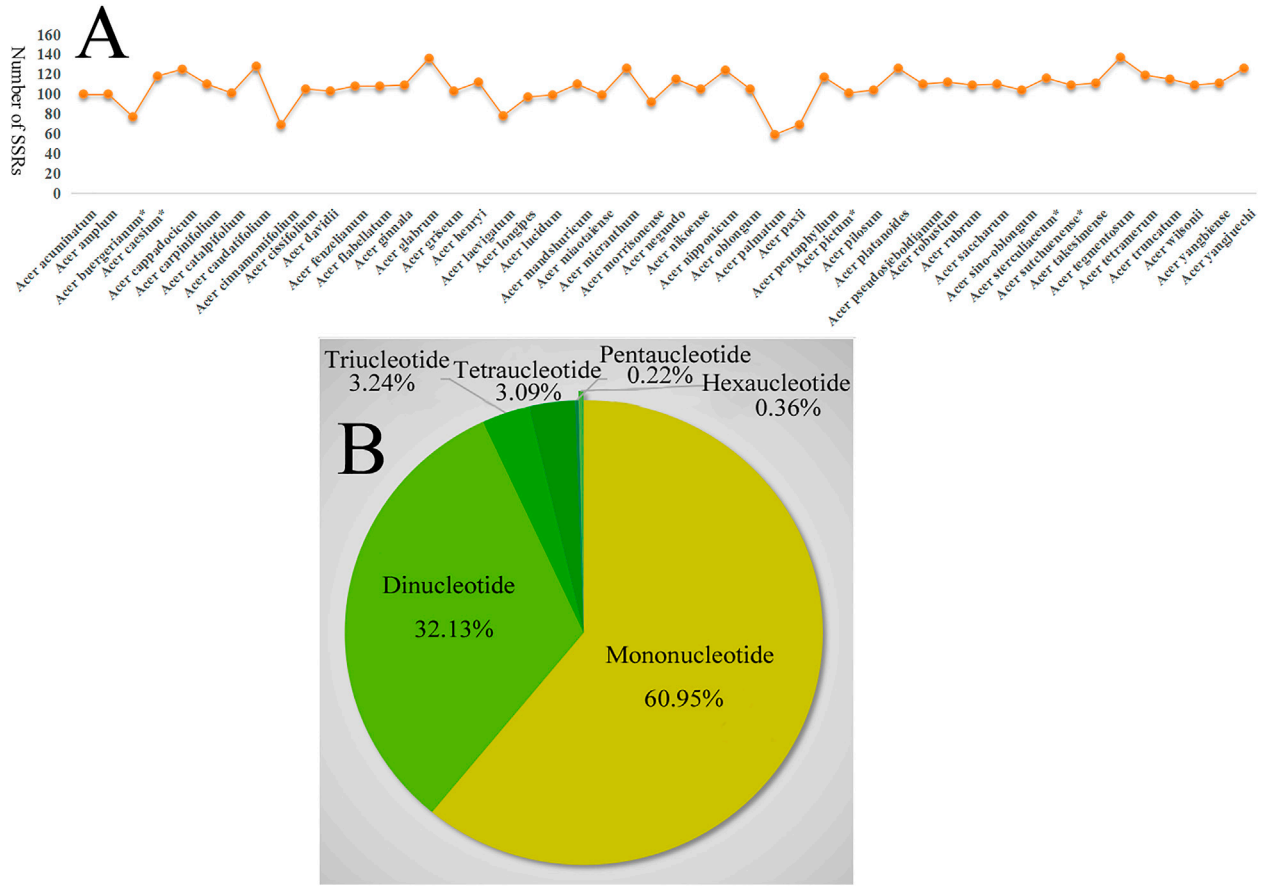


**FIGURE 1 | (A)** Number of SSRs in the *Acer* species chloroplast genome. **(B)** Number of SSRS types of chloroplast genome in 48 *Acer* species.

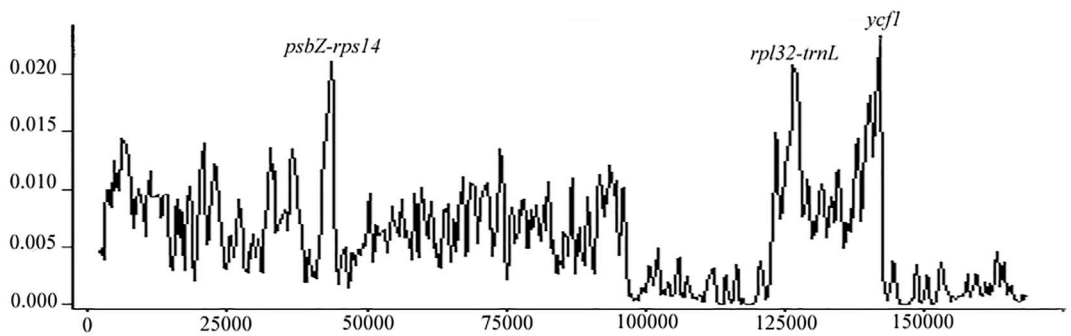


**FIGURE 2 |** Sliding-window analysis on the cp genomes for *Acer* species.

One highly variable region was found in the LSC region, and two were distributed in the SSC region, indicating the most stable region in the IR, followed by the LSC. In the *Acer* section *Platanoidea*, the *trnH-psbA*, *psbN*-trn*D*, *psaA-ycf3*, *petA-psbJ*, and *ndhA* introns were suggested as highly variable (Yu et al., 2020). With a comparison of 16 *Acer*, Areces-Berazain et al. (2020) defined the most variable regions in the SSC, in which *ycf1*, *ndhF-rpl32*, and *rpl32-trnL* had the highest nucleotide polymorphisms (Areces-Berazain et al., 2020). Accordingly, we concluded that the SSC region could apply for molecular barcoding in *Acer*, where *rpl32-trnL* and *ycf1* are the most appropriate candidates. The function of the *ycf1* gene in the cp genome has not been determined and is generally treated as an open reading frame (Dong et al., 2012). The *ycf1* gene, which showed high polymorphism in previous studies, may be designed as the molecular marker for phylogenetic analyses (Dong et al., 2015; He et al., 2017).

**TABLE 3 |** Detection of positive selection sites of chloroplast genes in *Acer* genus.

| Genes | Model | Parameters | 2ΔL | Sites |
|---|---|---|---|---|
| *accD* | M0 (one ratio) | ω = 0.312 | | |
| | M1 (neutral) | −3,194.888 | 4.319 | |
| | M2 (selection) | −3,192.729 | | 8 |
| | M7 (beta) | −3,194.917 | 4.405 | |
| | M8 (beta&ω) | −3,192.714 | | 13 |
| *atpA* | M0 (one ratio) | ω = 0.414 | | |
| | M1 (neutral) | −3,062.544 | 68.257 | |
| | M2 (selection) | −3,028.416 | | 12 |
| | M7 (beta) | −3,062.550 | 68.092 | |
| | M8 (beta&ω) | −3,028.500 | | 12 |
| *atpB* | M0 (one ratio) | ω = 0.195 | | |
| | M1 (neutral) | −2,767.483 | 19.820 | |
| | M2 (selection) | −2,757.573 | | 3 |
| | M7 (beta) | −2,768.353 | 21.511 | |
| | M8 (beta&ω) | −2,757.597 | | 3 |
| *clpP* | M0 (one ratio) | ω = 0.290 | | |
| | M1 (neutral) | −1,222.189 | 75.140 | |
| | M2 (selection) | −1,184.619 | | 5 |
| | M7 (beta) | −1,222.474 | 70.978 | |
| | M8 (beta&ω) | −1,186.985 | | 6 |
| *ndhA* | M0 (one ratio) | ω = 0.215 | | |
| | M1 (neutral) | −2,101.206 | 16.580 | |
| | M2 (selection) | −2092.916 | | 3 |
| | M7 (beta) | −2,101.626 | 17.610 | |
| | M8 (beta&ω) | −2092.821 | | 3 |
| *ndhD* | M0 (one ratio) | ω = 0.238 | | |
| | M1 (neutral) | −2,926.687 | 24.031 | |
| | M2 (selection) | −2,914.671 | | 5 |
| | M7 (beta) | −2,926.898 | 24.425 | |
| | M8 (beta&ω) | −2,914.686 | | 5 |
| *ndhF* | M0 (one ratio) | ω = 0.398 | | |
| | M1 (neutral) | −5,574.424 | 97.807 | |
| | M2 (selection) | −5,525.520 | | 13 |
| | M7 (beta) | −5,577.921 | 109.337 | |
| | M8 (beta&ω) | −5,523.252 | | 22 |
| *PetD* | M0 (one ratio) | ω = 0.271 | | |
| | M1 (neutral) | −942.151 | 11.366 | |
| | M2 (selection) | −936.469 | | 4 |
| | M7 (beta) | −942.381 | 11.793 | |
| | M8 (beta&ω) | −936.484 | | 4 |
| *psaI* | M0 (one ratio) | ω = 3.320 | | |
| | M1 (neutral) | −190.292 | 23.988 | |
| | M2 (selection) | −178.298 | | 2 |
| | M7 (beta) | −192.000 | 27.404 | |
| | M8 (beta&ω) | −178.298 | | 2 |
| *rbcL* | M0 (one ratio) | ω = 0.323 | | |
| | M1 (neutral) | −2,649.421 | 94.692 | |
| | M2 (selection) | −2,602.075 | | 8 |
| | M7 (beta) | −2,649.889 | 95.034 | |
| | M8 (beta&ω) | −2,602.372 | | 8 |
| *rpoA* | M0 (one ratio) | ω = 0.425 | | |
| | M1 (neutral) | −1960.904 | 18.516 | |
| | M2 (selection) | −1951.646 | | 9 |
| | M7 (beta) | −1961.168 | 19.006 | |
| | M8 (beta&ω) | −1951.665 | | 9 |
| *rpoB* | M0 (one ratio) | ω = 0.170 | | |
| | M1 (neutral) | −6,023.244 | 25.005 | |
| | M2 (selection) | −6,010.741 | | 9 |
| | M7 (beta) | −6,023.711 | 25.873 | |
| | M8 (beta&ω) | −6,010.775,053 | | 9 |
| *rpoc1* | M0 (one ratio) | ω = 0.263 | | |
| | M1 (neutral) | −4,017.309 | 50.238 | |
| | M2 (selection) | −3,992.190 | | 11 |
| | M7 (beta) | −4,018.563 | 51.186 | |

(Continued in next column)

## 3.4 Positive Selection Analysis

Seventy-three protein-coding gene sites were identified to be positively selected under the CodeML codon substitution models. Two genes (*psaI* and *psbK*) were detected to be positively selected with ω > 1 under the one-ratio model (M0), and nine genes (*rps8*, *rpoC2*, *rps16*, *ycf1*, *ndhG*, *matK*, *rpl22*, *petN*, and *ycf2*) with ω between 0.5 and 1.0, indicating relaxation of selective constraint. We also identified cp genes with sites under positive selection in models M2 and M8, which rejected the null models M1 and M7, respectively (**Table 3**). In model M2, 41 genes had 1–10 sites, three genes had 11–20 sites, and three genes had more than 20 sites under positive selection. In model M8, 37 genes had 1–10 sites, five genes had 11–20 sites, and four genes had more than 20 sites under positive selection (**Figure 3**). Among them, 20 genes have significantly positively-selected sites based on Bayes empirical Bayes (BEB) posterior probability, including two subunits of the ATP gene (*atpA* and *atpB*), three NADH dehydrogenase genes (*ndhA*, *ndhD*, and *ndhH*), one of the cytochrome b/f complex genes (*petD*), one of Photostsyem I (*psaI*), one of RubisCO large subunit gene (*rbcL*), four RNA polymerase genes (*ropA*, *ropB*, *ropC1*, and

**TABLE 3 |** (*Continued*) Detection of positive selection sites of chloroplast genes in *Acer* genus.

| Genes | Model | Parameters | 2ΔL | Sites |
|---|---|---|---|---|
| | M8 (beta&ω) | −3,992.970 | | 11 |
| *rpoc2* | M0 (one ratio) | ω = 0.528 | | |
| | M1 (neutral) | −10233.557 | 465.104 | |
| | M2 (selection) | −10001.005 | | 45 |
| | M7 (beta) | −10233.873 | 461.100 | |
| | M8 (beta&ω) | −10003.323 | | 48 |
| *rps8* | M0 (one ratio) | ω = 0.524 | | |
| | M1 (neutral) | −856.327 | 14.975 | |
| | M2 (selection) | −848.840 | | 4 |
| | M7 (beta) | −854.884 | 12.935 | |
| | M8 (beta&ω) | −848.417 | | 5 |
| *rps11* | M0 (one ratio) | ω = 0.273 | | |
| | M1 (neutral) | −746.510 | 7.472 | |
| | M2 (selection) | −742.774 | | 1 |
| | M7 (beta) | −746.512 | 7.466 | |
| | M8 (beta&ω) | −742.779 | | 1 |
| *rps19* | M0 (one ratio) | ω = 0.320 | | |
| | M1 (neutral) | −603.312 | 16.924 | |
| | M2 (selection) | −594.850 | | 3 |
| | M7 (beta) | −603.357 | 17.004 | |
| | M8 (betaω) | −594.855 | | 3 |
| *ycf1* | M0 (one ratio) | ω = 0.632 | | |
| | M1 (neutral) | −14774.834 | 157.711 | |
| | M2 (selection) | −14695.978 | | 42 |
| | M7 (beta) | −14774.915 | 156.596 | |
| | M8 (beta&ω) | −14696.617 | | 61 |
| *ycf2* | M0 (one ratio) | ω = 0.840 | | |
| | M1 (neutral) | −10754.288 | 44.430 | |
| | M2 (selection) | −10732.073 | | 81 |
| | M7 (beta) | −10754.623 | 45.095 | |
| | M8 (beta&ω) | −10732.076 | | 81 |
| *ycf3* | M0 (one ratio) | ω = 0.161 | | |
| | M1 (neutral) | −899.336 | 16.519 | |
| | M2 (selection) | −891.077 | | 1 |
| | M7 (beta) | −900.724 | 19.279 | |
| | M8 (beta&ω) | −891.084 | | 1 |

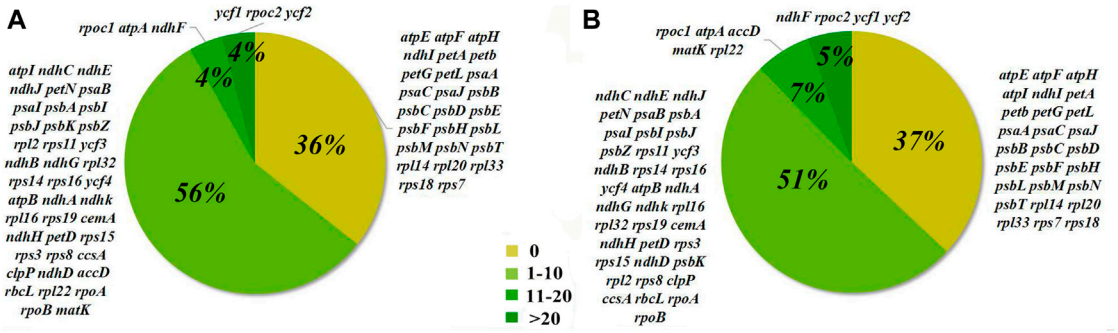


**FIGURE 3 |** Percentages of the number of sites selected from 73 coding genes in 48 *Acer* species. A, analysis results of Model M2. B, analysis results of Model M8.

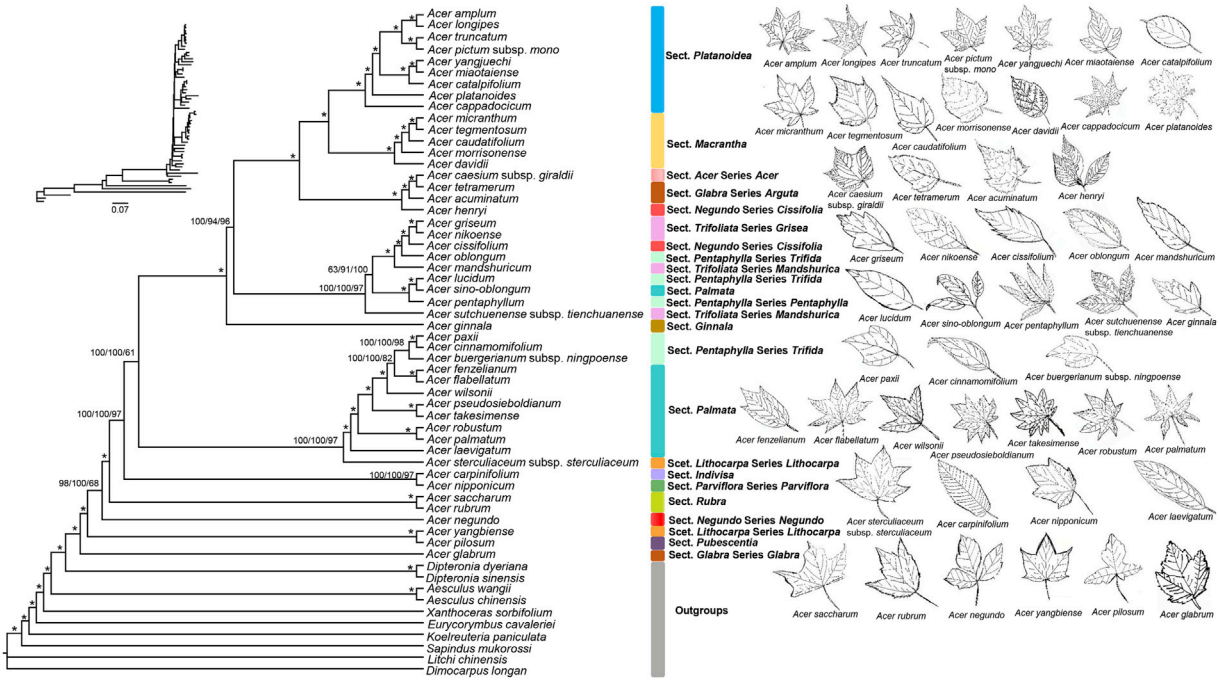


**FIGURE 4 |** Phylogenetic tree of 48 *Acer* species inferred by Bayesian Inference (BI), Maximum Likelihood (ML) and Maximum Parsimony (MP) methods, based on the whole cp genome sequences. The numbers above the branches are the posterior probabilities of BI and bootstrap values of ML and MP. Asterisks represent nodes with maximal support values in all methods. Each Section was marked in the same colour.

*ropC2*), three ribosomal protein genes (*rps8*, *rps11*, and *rps19*), and *accD*, *clpP*, *ycf1*, *ycf2*, and *ycf3*.

The positive selection of cp genes has been widely studied in angiosperms and demonstrated at the protein level (Li et al., 2020). In this study, *psbK* and *psbI*, the subunits of the cp photosynthetic system (Li et al., 2019), were positively selected in *Acer*. To our knowledge, the positive selection of *psbK* and *psbI* was not common in angiosperms. The high ω implies a unique attribute of *Acer* to adapt to different light environments. Most of the 20 genes with codons positively selected detetced under the BEB algorithm had one or two positively selected codons, but the *ycf1*, *ycf2*, and *rpoC2* genes contained more than 40 sites under selection. Although we don't have enough evidence to make definite inferences, past researches, for example, have indicated that *ycf1* is exceptionally divergent across land plants (Dong et al., 2015; Mower et al., 2019) and *rpoC2* had the most positive selective sites among the cp genes in *Siraitia* species (Shi et al., 2019). They indicated that *rpoC2* had a higher evolutionary rate in several species. These genes that undergo positive selection might result from adaptation to specific ecological niches.

## 3.5 Phylogenetic Analysis

Most nodes of the reconstructed phylogenomic tree had 100% bootstrap support values, indicating a suitable evolutionary

placement for *Acer* species (**Figure 4**). The results showed that *Acer* and *Dipteronia* are monophyly, which is consistent with previous studies (Renner et al., 2008; Gao et al., 2020; Wang et al., 2020; Areces-Berazain et al., 2021). *Acer pictum* subsp. *mono* is traditionally considered sister to *A. truncatum* but not to *A. yangjuechi* (van Gelderen et al., 1994; Xu et al., 2008). However, Yu et al. (2020) proposed *A. pictum* subsp. *mono* and *A. yangjuechi* as sister species according to the "local varieties." The leaves of *A. pictum* subsp. *mono* and *A. truncatum* has 5-lobed and glabrous abaxially, while *A. yangjuechi* (synonym for *A. miaotaiense* in *Maples of the World* and *Flora of China*) is 3-lobed, undulate margin and obtuse lobes. In addition, our study showed that each branch within the *Platanoidea* section had high support, which is consistent with morphological classification (van Gelderen et al., 1994; Xu et al., 2008). Our results strongly support that section *Platanoidea* and section *Macrantha* are sister sections (**Figure 4**), similar to previous studies (Renner et al., 2008; Areces-Berazain et al., 2020; Wang et al., 2020). The morphological characteristics of the two sections are similar, such as simple leaves with 3- or 5-lobed or unlobed (Xu et al., 2008). However, this result is still inconsistent with some studies, such as Li et al. (2019) and Areces-Berazain et al. (2021), which may be due to different marker selection and single model in the phylogenetic analysis.

In *Maples of the World*, section *Glabra* comprises species from the *Glabra* and *Arguta* series (van Gelderen et al., 1994). However, many studies, including the present one, have shown a certain genetic distance between these two series (Li et al., 2019; Areces-Berazain et al., 2020; Gao et al., 2020; Areces-Berazain et al., 2021). Series *Glabra* is monotypic, containing only *A. glabrum* and its subspecies. They are mainly shrubs with 5-merous and 8-stamens flowers distributed in North America, unlike Series *Arguta*, with 4-merous and 4-6 stamens distributed in East Asia (van Gelderen et al., 1994). Therefore, dividing the two series into two sections is more appropriate, as de Jong (2004) proposed. Species of sections *Trifoliata* and *Pentaphylla* were mixed (**Figure 4**), suggesting their sister relationship (Li et al., 2019; Gao et al., 2020; Wang et al., 2020; Areces-Berazain et al., 2021). These two sections have compound leaves, distinguishing them from most other sections in *Acer* (Xu et al., 2008). The Section *Palmata* was not monophyletic as it lacked *A. sino-oblongum*, which is consistent with previous studies (Gao et al., 2017; Wang et al., 2020). Although many studies have placed *A. sino-oblongum* in Section *Palmata* (van Gelderen et al., 1994; Xu et al., 2008), the taxonomic status of this species must be revisited. *Acer yangbiense*, a rare and critically endangered species, is herein shown to be genetically distant from the other species in Section *Lithocarpa*, as in previous studies (Li et al., 2019; Areces-Berazain et al., 2021). This species has pale white to pale gray leaf blade abaxially, entire leaf margin, and slender fruiting pedicels, which are pretty different from other species in the Section *Lithocarpa* (van Gelderen et al., 1994; Xu et al., 2008). Determining the systematic position of *A. yangbiense* is of great significance to conserving this rare and endangered species.

## 4 CONCLUSION

This study compared 48 whole cp genome sequences of *Acer*, which exhibited a typical quadripartite structure and genomic content. The comparative study allowed us to identify hotspot loci and several transferable polymorphic SSR applied as DNA barcodes for species identification and phylogenetic inference. Moreover, the complete plastome data allowed us to obtain the highest phylogenetic resolution to date for the 48 *Acer* species, showing that the cp phylogenomic approach could be employed to tackle the intractable phylogenic problems in *Acer*. The comparative genomic information constitutes a valuable resource in advancing our understanding of plastid evolution and molecular breeding application for the agro-horticulture in *Acer* species.

## DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

## AUTHOR CONTRIBUTIONS

TY and JG conceived and designed the work. TY, JG, and W-BM collected samples. TY and JG performed the experiments and analyzed the data. TY and JG wrote the manuscript. P-CL and J-QL critically reviewed the manuscript. All authors gave final approval of the paper.

## FUNDING

This research was financially supported by the program "The biogeographical feature and competitive hybridization of Maple (*Acer* L.) in East Asia" of National Natural Science Foundation of China (41901063) and Research Program of Science and Technology at Universities of Inner Mongolia Autonomous Region (NJZZ19185) to JG, "Reintroduction Technologies and Demonstration of Extremely Rare Wild Plant Population" of National Key Research and Development Program (2016YFC0503106) to J-QL, Ministry of Science and Technology of Taiwan (MOST 109-2621-B-003-003-MY3 and 109-2628-B-003-001) to P-CL.

## ACKNOWLEDGMENTS

We gratefully thank Editage (www.editage.cn) for English language editing.

## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fgene.2021.791628/full#supplementary-material

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