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Molecular phylogeny and evidence for natural hybridization and historical introgression between *Ceriops* species (Rhizophoraceae)

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ABSTRACT

Ceriops (Rhizophoraceae) is a genus comprised of five species of mangroves distributed in tropical and subtropical coastal regions. In this study, sequences from nuclear ribosomal ITS and the plastid *trn*L intron are used to construct molecular phylogenies of this genus revealing two species complexes, the *C. tagal* complex (*C. tagal* and *C. australis*), and the *C. decandra* complex (*C. decandra*, *C. pseudodecandra* and *C. zippeliana*), each forming a distinct clade. All five species, including the newly designated species *C. pseudodecandra*, are well supported. However, natural hybridization and historical introgression between *Ceriops* species are also demonstrated. The ITS sequences of *Ceriops* species, in contrast to their plastid *trn*L intron sequences, show a great amount of homoplasy during evolution. Historical introgression originating from natural hybridization was demonstrated based on the additivity of ITS sequences from putative parents. Of the five *Ceriops* species, *C. pseudodecandra* is a relatively isolated species. *C. decandra* and *C. zippeliana* show mutual introgression in most populations. According to both the nuclear ITS sequences and the plastid *trn*L intron, an intermediate form from Darwin is likely a natural hybrid, with *C. tagal* and *C. australis* respectively the maternal and paternal parents.

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1. Introduction

'Mangroves' are the intertidal vascular plants, mostly trees and shrubs, distributed in regions of estuaries, deltas and riverbanks or along the coastlines of tropical and subtropical areas (Tomlinson, 1986; Saenger, 2002). *Ceriops* Arn. is one of four mangrove genera in the Rhizophoraceae (Tomlinson, 1986). *Ceriops* has a widespread geographical range from eastern

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Africa, throughout tropical Asia, northern Australia to Melanesia, Micronesia and southern China (Hou, 1958; Tomlinson, 1986; Duke, 2006). *Ceriops* species are typically constituents of the inner mangroves, often forming pure stands on better drained sites, and stunted stands in exposed and highly saline sites within the reach of occasional tides (Hou, 1958).

In revising the genus *Ceriops*, Hou (1958) recognized just two species, *C. decandra* and *C. tagal*. White (1926) and Tomlinson (1986) recognized an additional variety *C. tagal* (Perr.) C. B. Rob. var. *australis* C. T. White, originally reported from Australia and Papua New Guinea. Based on polyacrylamide gel electrophoresis analysis of isozymes from the populations of *Ceriops* in northern Australia, Ballment et al. (1988) raised this variety to specific rank as *C. australis*, which was later supported by both morphological and molecular evidence (Sheue et al., 2009b).

Of these three species of the genus *Ceriops*, *C. tagal* is the most widely distributed (Tomlinson, 1986). The species *C. decandra* was also reported as widely distributed across India, Indochina, the Malay Peninsula, Indonesia and northern Australia (Duke, 1992; Tomlinson, 1986). However, the highly genetically divergent populations reported as *C. decandra* (Tan et al., 2005) were divided into three species, including *C. decandra*, *C. zippeliana* Blume, and a new species *C. pseudodecandra* Sheue, Liu, Tasi & Yang by Sheue et al. (2009a, 2010), based on morphological, palynological and DNA evidence. Thus, the genus *Ceriops* is now regarded as having five extant species, *C. australis*, *C. decandra*, *C. pseudodecandra*, *C. tagal* and *C. zippeliana*.

Despite clear differentiation between *C. tagal* and *C. australis* at five sympatric locations in north Queensland, Australia, as determined by isozyme markers (Ballment et al., 1988) and DNA evidence (Sheue et al., 2009b), there are anecdotal accounts of intermediate forms (see Ballment et al. (1988)). Moreover, an intermediate form between *C. tagal* and *C. australis* can be found in Darwin (Sheue et al., 2009b), and elsewhere in the Northern Territory, Australia (Sheue, personal observation), suggesting that some hybridization may have occurred in nature.

To construct phylogenies and obtain evidence on historical introgression and natural hybridization of *Ceriops*, we used both plastid and nuclear ribosomal DNA. Because these two forms of DNA are inherited differently, they provide a good means for detecting reticulate evolution in plants by comparing nuclear and plastid phylogenies. Maternal inheritance has been shown to occur for plastid DNA (cpDNA) in most flowering plants (Derepas and Dulieu, 1992). Nuclear ribosomal DNA (nrDNA) is inherited biparentally. It has repeated sequences organized into families in tandem arrays in the nucleolar organizer regions of chromosomes in all eukaryotes (Rogers and Bendich, 1987). Copy numbers of nrDNA vary in different species from a few hundred to several thousand. Each repeat unit consists of a non-transcribed spacer known as an intergenic spacer (IGS) and a transcription unit coding for the precursor of rRNA. Ribosomal repeat sequences are usually identical due to concerted evolution via unequal crossing over (Schlotterer and Tautz, 1994) and biased gene conversion (Hillis et al., 1991; Linaresa et al., 1994). Incongruence between loci from the plastid and nrDNA often indicates gene flow (Soltis and Kuzoff, 1995), allowing the detection of historical introgression or natural hybridization.

Natural hybridization and subsequent introgression have been characterized based on molecular evidence in several plant taxa (e.g., Mao et al., 1995; Brar and Khush, 1997; Rieseberg et al., 1999; Tsai et al., 2006). Hybrid species were identified by full or partial ITS sequence additivity of the putative parental species based on direct sequencing of PCR products (Sang et al., 1995; Campbell et al., 1997; Hugall et al., 1999; Andreasen and Baldwin, 2003; Chiang et al., 2001; Tsai et al., 2006; Soltis et al., 2008). Partial sequence additivity was suggested to come from partial homogenization of parental ITS repeat sequences via gradients of gene conversion (Sang et al., 1995). In contrast, the complete homogenization of parental repeat sequences in certain hybrid species could not be detected by ITS sequences (Wendel et al., 1995). If a hybrid species shows ITS sequences from one parent via gene conversion, but cpDNA inherited from the other parent, incongruencies between the ITS and cpDNA phylogenies will be shown in the hybrid species (e.g., Soltis and Kuzoff, 1995; Lihova et al., 2006; Kim and Donoghue, 2008).

To construct a molecular phylogeny and understand the natural hybridization and historical introgression between *Ceriops* species, we analyzed the sequences of the nuclear ribosomal ITS and plastid *trn*L introns for the five species of *Ceriops* from a broad geographical range, widely representing these species. Because these two DNA markers represent biparental and maternal inheritance, respectively, in most flowering plants (see Derepas and Dulieu (1992), Sang et al. (1995), Wendel et al. (1995)), the direction of introgression also can be assessed in this study.

2. Materials and methods

2.1. Plant materials

During 2000 to 2007, we collected 38 specimens from the five *Ceriops* species (*C. australis*, *C. tagal*, *C. decandra*, *C. zippeliana* and *C. pseudodecandra*) from India to Australia (Table 1, Fig. 1). *Ceriops* distribution ranges (Fig. 1) were obtained from herbarium records and field surveys over the period 2000–2011. In addition, we collected specimens from five outgroup species representing three other genera of the tribe Rhizophoreae, and one outgroup species from the tribe Gynotrocheae. All voucher specimens of this study were deposited in the Herbarium of the Department of Life Sciences (TCB) of National Chung Hsing University.

2.2. DNA extraction

Using the cetyltrimethylammonium bromide (CTAB) method (Doyle and Doyle, 1987), total DNA was extracted from fresh etiolated leaves. Ethanol-precipitated DNA was dissolved in TE (Tris–EDTA) buffer and stored at −20 °C. Qiagen (Valencia, CA,

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