Revista Mexicana de Biodiversidad 85: 808-822, 2014
DOI: 10.7550/rmb.43422

Perspectives on the systematics and phylogenetics of *Guaiacum* (Zygophyllaceae): complexities in conservation of endangered hardwoods due to fragmentation, introgression, and intermittent gene flow

Perspectiva en la sistemática y filogenia de *Guaiacum* (Zygophyllaceae): dificultad en la conservación de maderas duras económicamente importantes debido a fragmentación, introgresión y flujo intermitente de genes

Joseph R. Dertien[1]✉ and Melvin R. Duvall[2]

[1]*Department of Biological Sciences, 3700 West 103rd Street, Saint Xavier University, Chicago, IL 60655, USA.*
[2]*Department of Biological Sciences, 1425 W. Lincoln Hwy, Northern Illinois University, DeKalb, IL 60115, USA.*
✉ *dertien@sxu.edu*

Abstract. The systematics of the economically important, endangered hardwoods in *Guaiacum* are unclear with regard to taxonomic ranks, and the relationships among taxa. This is partially due to a lack of diagnostic characters and minimal geographic sampling in previous studies. Nevertheless, systematic relationships are important to inform trade regulations and management practices for these species. This is especially true for Mexico, which is both the primary exporter and the center of diversity for *Guaiacum*. Systematic and biogeographic issues in *Guaiacum* were investigated by analyses of nuclear and chloroplast DNA markers from specimens sampled throughout the range. Phylogenetic and statistical parsimony analyses showed well-supported divergences within the group, including a deep divergence between *G. officinale* and other taxa with additional biogeographically correlated subdivisions. There is also an indication that accessions from Chiapas, Mexico are genetically intermediate between *G. sanctum* and *G. coulteri*, while minor segregates of *Guaiacum* (*G. palmeri, G. guatemalense*) were not well distinguished by either morphological or molecular characters. The genetic structuring among the major groups of *Guaiacum* shows evidence of isolation induced by fragmentation of the range, with the structure largely maintained with only occasional long distance gene flow between remote populations.

Key words: dry tropical forest, haplotypes, hardwoods, Larreoideae.

Resumen. La sistemática de las especies maderables, económicamente importantes y en peligro de extinción en *Guaiacum* aún no aclara con respeto a la clasificación taxonómica y las relaciones entre los taxa. Esto se debe parcialmente a la falta de rasgos diagnósticos y a reducidas muestras geográficas en estudios previos. Sin embargo, los aspectos en la sistemática y las relaciones filogenéticas de las especies son importantes a considerar en la regulación comercial y en las prácticas de manejo de las especies. Esto es especialmente importante para México ya que es tanto el exportador más importante, como el centro de diversidad para *Guaiacum*. En este trabajo se investigaron aspectos sistemáticos y biogeográficos en *Guaiacum* analizando marcadores nucleares y de cloroplastos de ADN de especímenes muestreados de su área de distribución. Los análisis filogenéticos y de parsimonia estadística mostraron divergencia bien sustentada dentro del grupo, incluyendo una divergencia profunda entre *G. officinale* y los otros taxa con subdivisiones adicionales asociadas a la biogeográfia. También hay evidencia de accesiones de Chiapas, México, como genéticamente intermedias entre *G. sanctum* y *G. coulteri*, mientras que otras especies de *Guaiacum* (*G. palmeri*, *G. guatemalense*) no se distinguen bien sea por rasgos morfológicos o moleculares. La organización genética entre los mayores grupos de *Guaiacum* muestra evidencia de un aislamiento provocado por fragmentación en su distribución, con la estructura en gran parte mantenida por un flujo ocasional de genes a larga distancia entre poblaciones lejanas.

Palabras clave: bosques tropicales secos, haplotipos, árboles maderables, Larreoideae.

Recibido: 20 noviembre 2013; aceptado: 24 abril 2014

Introduction

Guaiacum L. (Zygophyllaceae R. Br.) is a New World genus comprised of a group of 4 to 8 commonly recognized taxa of tropical and subtropical hardwoods. These trees and shrubs are distributed primarily within the arid and semi-arid regions of the Caribbean basin and Mexico, and represent economically important species characterized by extremely dense and resinous wood.

Guaiacum sanctum L. is the most abundant and economically important species, and has therefore been the species of greatest conservation focus. Studies of population structure, density, and regeneration in the chief exporting country of Mexico have been conducted (López-Toledo et al., 2010, 2011b), and population level genetic studies have been conducted for Caribbean, Mexican, Floridian (Dertien and Duvall, 2009), and Costa Rican populations (Fuchs and Hamrick, 2010a, b). Furthermore, *Guaiacum sanctum* could act as an umbrella species in terms of conservation, as protection of populations could also benefit other endangered flora and fauna (López-Toledo et al., 2011a). *Guaiacum coulteri* A. Gray has been studied less extensively, primarily because it has lower economic importance and does not occur in protected areas (López-Toledo et al., 2010). The population genetics of *G. unijugum* Brandegee have also been studied for conservation purposes as it is a relatively rare endemic of the Cape region of Baja California, Mexico (McCauley et al., 2010).

Despite various conservation and genetic studies, the number of species within the genus remains unresolved, with as few as 4 and as many as 8 species commonly recognized. (Grow and Schwartzman, 2001a, b; Axelrod, 2002). The absence of clear species delimitation within the genus is particularly problematic for trade regulation by the Convention on International Trade in Endangered Species or Wild Fauna and Flora (UNEP-WCMC, 2007), developing management practices of *Guaiacum* species by exporting countries, and assessing extinction risk for species or local populations (IUCN, 2007). In practice, taxonomic distinctions are frequently based on geographic origin rather than morphological, reproductive, or genetic criteria. Currently, the entire genus is listed on CITES Appendix II because of the inability to distinguish timber of the different species and a taxonomy that is complicated by numerous synonyms, unsettled taxonomic ranks, and invalidly published names. The listing effectively renders all species of *Guaiacum* endangered from a regulation standpoint (López-Toledo et al., 2010) regardless of what is known about the status of individual populations.

Previous phylogenetic studies of *Guaiacum* have only included a single species as an exemplar, and were therefore not informative at the species level (Sheahan and Chase, 2000; Lia et al., 2001). Other studies attempting to delimit species using morphological characters were not inclusive of all species, and failed to identify characters suitable for consistent unambiguous identification (Grow and Schwartzman, 2001b). Specifically, suites of morphological character combinations yield conflicting results in taxonomic identifications for specimens found in southern Mexico and Central America (Grow and Schwartzman, 2001b), an area coincidentally of great importance to the harvesting and trade of *Guaiacum*. A more robust analysis of evolutionary relationships within *Guaiacum* could provide useful insight for a future taxonomic revision, and a clearer understanding of these phylogenetic relationships could be directly applicable to conservation practices.

This study is an attempt to resolve evolutionary relationships, identify consistent genetic patterns, and discover novel genetic patterns among *Guaiacum* species by using a combination of analyses appropriate for several taxonomic levels. Maximum parsimony methods can resolve deeper nodes but leave shallower relationships unresolved where variation is lacking among closely related accessions. Statistical parsimony analyses, however, can resolve relationships down to single mutations separating closely related individuals in a manner similar to DNA barcoding (Schindel and Miller, 2005; Collins and Cruickshank, 2013). Any contrasting patterns from nuclear and chloroplast DNA markers can indicate potential hybridization events (Soltis and Kuzoff, 1995), and geographic correlations with genetic patterns may indicate populations of greater taxonomic or conservation interest.

In addition to broadly resolving evolutionary relationships, this study is designed to address the following particular phylogenetic and taxonomic issues associated with the genus:

1) Guaiacum guatemalense Planch. ex Vail and Rydberg while often identified as a distinct species in herbarium collections, is most commonly accepted as a synonym of *G. sanctum* (http://www.theplantlist.org). Individual specimens identified as *G. guatemalense* possess intermediate and shared morphological characteristics of *G. sanctum* and *G. coulteri,* suggesting a hybrid origin (Porter, 1972). This putative species is found in a region near the intersection/overlap of the ranges *G. coulteri* and *G. sanctum*; *2) Guaiacum angustifolium* Engelm. and its synonym *Porlieria angustifolia* (Engelm.) A. Gray*,* may be more accurately described as a subspecies or variety of *G. coulteri*; *3) Guaiacum unijugum* is a species endemic to the Cape region of the Baja peninsula. The species status is questionable, as its unique morphology may be