



## ***Cedrela odorata* L.: oportunidades para su conservación y mejoramiento genético**

## ***Cedrela odorata* L.: opportunities for its conservation and genetic improvement**

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### **Resumen**

*Cedrela odorata*, conocida comúnmente como cedro rojo, es una especie forestal tropical de alto valor comercial en el mercado internacional de la madera. La fragmentación del paisaje en su área de distribución y la tala clandestina con selección disgénica causan erosión genética en sus poblaciones naturales, lo que disminuye su potencial adaptativo y productivo. Debido a esto, es más susceptible a daños por factores abióticos y bióticos como *Hypsipyla grandella*, su principal plaga y causa de bajo rendimiento en plantaciones comerciales. Es así, que se incluye en las listas de organizaciones internacionales como IUCN y CITES, y en México es protegida por la NOM-059 SEMARNAT-2010; sin embargo, la falta de suficientes evidencias sobre su riesgo real pone en duda su permanencia en esta última. Por ello, aunque se han realizado algunas investigaciones para determinar su diversidad genética en poblaciones de América Central, cariotipo, caracterización de su plastoma y transcriptoma foliar, aún falta información esencial para su manejo eficiente y sostenible. El objetivo de la presente revisión es proporcionar un panorama del conocimiento existente sobre los recursos genéticos de cedro rojo, con el fin de identificar alternativas basadas en herramientas biotecnológicas que permitan la comprensión de la especie y fundamenten el diseño e implementación de programas de mejoramiento genético y conservación a largo plazo. **Palabras clave:** *Cedrela odorata* L., conservación, diversidad genética, genoma, marcadores moleculares, mejoramiento genético.

### **Abstract**

*Cedrela odorata*, commonly known as Spanish cedar, is a tropical forest species of high commercial value on the international timber market. Habitat fragmentation and illegal logging with dysgenic selection cause the genetic erosion of its natural populations, reducing its adaptive and productive potential. Therefore, it is increasingly susceptible to damage by abiotic and biotic factors such as *Hypsipyla grandella*, its main insect pest and the leading cause of low yield in commercial plantations. Spanish cedar is included in the lists of international organizations such as IUCN and CITES, and protected by NOM-059 in Mexico. However, because of the lack of convincing supporting evidence, its permanence in the latter is not guaranteed. Although some research has been done in the past – evaluation of its genetic diversity in Central American populations, karyotyping, characterization of its plastome and leaf transcriptome – essential information is still lacking to establish efficient and sustainable management strategies. The aim of this review is to present an overview of the current knowledge of genetic resources of *C. odorata* in order to identify biotechnological alternatives that would allow a better understanding of this species and substantiate the planning and implementation of tree breeding and long-term conservation programs.

**Key words:** *Cedrela odorata* L., conservation, genetic diversity, genome, molecular markers, tree breeding.

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## Introduction

*Cedrela odorata* L. (Meliaceae), known as Spanish cedar, is one of the most valuable species of Mesoamerican forests (Cortés, 2001). In Mexico, it is naturally distributed on the slopes of the Gulf of Mexico and the Pacific coast (Pennington and Sarukhán, 2005) as well as in Central, South America and the Caribbean islands (Patiño, 1997). It provides environmental services (Romo-Lozano *et al.*, 2017), and also has medicinal properties (Patiño, 1997). This taxa stands out for the great qualities of its wood, such as high durability, color, marbled look and aroma (Mader *et al.*, 2018); hence it is used for fine furniture, musical instruments, crafts (Cintrón, 1990; Romo-Lozano *et al.*, 2017) and tobacco boxes (Rodríguez, 2011). Based upon its economic relevance, it has been introduced to Africa, Southeast Asia and Northeast Australia (GBIF, 2018), as it is the second most commercialized tropical tree species in the world after mahogany (*Swietenia macrophylla* King [Meliaceae]) (Patiño, 1997) with an export price in North America of \$ 958 to \$ 977 USD/ m<sup>3</sup> for sawn timber (ITTO, 2019).

Due to its commercial significance and lack of sustainable management plans, Spanish cedar has been overexploited, causing a decrease and fragmentation of its natural populations, and thus, a gene flow restriction between populations (De la Torre, 2013), and genetic diversity loss (Leshner-Gordillo *et al.*, 2018) which includes highly productive genotypes and individuals potentially resistant to biotic and abiotic stress (Cavers *et al.*, 2003a). In addition to the anthropogenic damage, *C. odorata* natural regeneration is not effective (Rodríguez, 2011) because of fast seed viability loss (García and Abdelnour, 2013); slow growth, since it takes about 40 years to reach a suitable size for timber use (Galván-Hernández *et al.*, 2018), and the attack of *Hypsipyla grandella* Zeller. (Mahogany shoot borer).

The latter has become the main limiting factor for establishment and productivity of Spanish cedar commercial plantations (López-Ochoa *et al.*, 2015; Santos *et al.*, 2015). In this regard, Marquetti (1990) has indicated the presence of a natural hybrid originated from the cross between *C. odorata* and *Cedrela cubensis* Bisse, for which the author describes greater heterosis, as well as better growth and resistance to the borer in

comparison to their parents. However, *C. cubensis* is considered a synonym for *C. odorata* (The plant list, 2013) and there is still lacking evidence to support such statement. We must highlight that plantations performance is subjected to the quality of the site, since biotic, abiotic factors and their interaction with management, affect the productive capacity of the plantation, therefore, depending on these conditions trees could reach high volume yields in a short or long time (Murillo-Brito *et al.*, 2017).

From the aforementioned circumstances, *C. odorata* is considered a vulnerable species by the International Union for the Conservation of Nature (IUCN) (IUCN, 2017), and is also protected by the Convention on International Trade in Endangered Species of Fauna and Wild Flora (CITES, 2017). In Mexico, it is included in the Official Mexican Standard 059-SEMARNAT 2010 (Semarnat, 2010); however, it has been suggested that its permanence in such category is not justified (Ruiz-Jiménez *et al.*, 2018). Therefore, the objective of this paper was to present the main advances related to the genetics of the Spanish cedar, in order to identify useful opportunities for its improvement and conservation.

### **The genome of *Cedrela odorata***

Spanish cedar is part of the Meliaceae family, characterized by a high and variable number of chromosomes; for example, species of the *Soyimida*, *Toona* and *Cipadessa* genera have a diploid chromosomic number ( $2n$ ) equal to 56, which suggests a common and paleopolyploid origin (Styles and Vosa, 1971; Khosla and Styles, 1975). Compared to other forest taxa such as the *Picea* and *Pinus* genera ( $2n = 24$ ) (Fuchs *et al.*, 1995; Nkongolo, 1996; Pavy *et al.*, 2008), some members of the Meliaceae family have a diploid number more than two times greater.

Styles and Vosa (1971) identified two cytotypes for *C. odorata*:  $2n = 50$  and  $56$ , and suggest that the populations with the lowest chromosome number are located in Central America and the Caribbean Islands, while those with the largest numbers are in Mexico and South America. However, Khosla and Styles (1975) discarded the relationship of cytotypes with their geographical origin and estimated a chromosomal

length of 2.0 to 5.0  $\mu\text{m}$  and 60  $\mu\text{m}$  for the total chromatin size, which became the first reference on the size of the genome.

The sequence of the nuclear genome of Spanish cedar is unknown. The only characterized Meliaceae is *Azadirachta indica* A. Juss. (Nim), whose size is 364 Mpb with just over 20 000 genes (Krishnan *et al.*, 2012). With this reference and information on taxa with close phylogeny such as Rutaceae (*Citrus sinensis* (L.) Osbeck, GenBank NC\_023046-54), Malvaceae (*Theobroma cacao* L.; GenBank GCF\_000208745), Brassicaceae (*Arabidopsis thaliana* (L.) Heynh ., GenBank NC\_003070-76) or Vitaceae (*Vitis vinifera* L., GenBank NC\_012007-25), the genome size of *C. odorata* would be expected to be around 500 Mpb (Jaillon *et al.*, 2007; Argout *et al.*, 2011; Xu *et al.*, 2013). However, it should be considered that *A. indica* has a chromosomal number  $2n = 28$ , that is, half of that of Spanish cedar and, assuming that its genome is the product of a polyploidy (Khosla and Styles, 1975), it could be twice as large as that of Nim.

On the other hand, with the Illumina sequencing platform, the plastome (chloroplast genome) of *C. odorata* has been elucidated: 158 558 bp (GenBank MG724915), where the Long Single Copy (LSC) and Short Single Copy (SSC) is 86 390 bp and 18 380 bp, respectively, while the Inverted Region (IR) is 26 894 bp. The list of annotated genes, that is, those with identified putative functions, shows a total of 112 different genes of which 78 encode for proteins, 30 for tRNA (transfer RNA) and 4 for rRNA (ribosomal RNA) (Mader *et al.*, 2018). The intergenic region *rrn16-rrn23* of the chloroplast has also been characterized, with which the vector pCBL5 was constructed, allowing its direct transformation by homologous recombination. This type of transformation reduces the risk of contamination by pollen from transgenes to wild individuals because plastids are inherited by the mother. This has the potential to generate transgenic varieties resistant to pests such as the Mahogany shoot borer (López-Ochoa *et al.*, 2015).

Regarding the transcriptome, RNA sequencing of foliar tissue shows 52 181 gene models whose length varies between 200 bp and 37 635 bp (Finch *et al.*, 2019), which supports the hypothesis suggesting that Spanish cedar genome doubles that of *A.*

*indica* (Krishnan *et al.*, 2012). Among these putative genes, between 65% and 70% are homologous with those present in tree genomes such as *Populus trichocarpa* Torr. & A. Gray ex Hook. and *Quercus lobata* Née. This transcriptomic study is the first of th species with alast generation sequencing technology approach (Finch *et al.*, 2019).

## **Contributions of molecular biology to the phylogenetic study of Spanish cedar**

The *Cedrela* genus species are cryptic, i.e. based on morphological traits; they cannot be precisely identified because the evolutionary divergence of their genomes is not expressed in the phenotype (Cavers *et al.*, 2013). Therefore, molecular markers are an alternative to solve this kind of problems, since they allow to describe the population structure, genetic diversity, phylogenetic relationships, migratory routes and hybridization processes, among others (Alía *et al.*, 2003).

Some of the main contributions and advances obtained by means of molecular approaches applied to evolutionary studies in *Cedrela* are discussed below. Variation analysis of the internal transcribed spacer (ITS) 18S-26S and trnS-trnG, and some chloroplast genes (*e.g* psbB, psbT, psbN) have showed that divergence between *Cedrela* and *Toona* genera occurred 46.6 to 50.6 million years. Likewise, during the Miocene, Central America was the origin of diversification of *Cedrela*, which resulted in the emergence of two lineages that migrated to North and South America (Muellner *et al.*, 2010; Cavers *et al.*, 2013; Koecke *et al.*, 2013). Several species of the genus have also been reclassified: 8 to 17 and six more that are not yet accepted (Cavers *et al.*, 2013; Koecke *et al.*, 2013; The plant list, 2013).

In another study based on the use of molecular markers from the chloroplast, five haplotypes were identified in Central America, the interaction zone between the two great lineages of North and South America (Cavers *et al.*, 2003b). Subsequently, the analysis included populations from the Caribbean and South America, through ITS, nuclear and chloroplast microsatellites 22 haplotypes were characterized, justifying

the need to reclassify some ecotypes, as well as new *Cedrela* species (Cavers *et al.*, 2013). With such background, at least three evolutionary divergences are evidenced and they are coincidental with the colonization of Mesoamerica by the South American flora. The first two took place before and after the formation of the Isthmus of Panama, and the third, at the end of the Pleistocene.

### **Genetic diversity**

Genetic diversity of *C. odorata* has been assessed in populations of Central and South America through the use of molecular markers such as RAPD, AFLP, microsatellites and chloroplast sequences, which evidenced a greater inter-population diversity than within populations, which is related to the average annual rainfall and allows differentiating between populations in dry regions (north of the *Yucatán* Peninsula) from those in humid areas (*Costa Rica*) (Gillies *et al.*, 1997; Cavers *et al.*, 2003a, 2003b; Navarro *et al.*, 2005; De la Torre *et al.*, 2008).

Genetic diversity is essential for long-term evolution and conservation, as well as for breeding and management of genetic resources (Jump *et al.*, 2008). Considering climate change effects, it is essential to preserve the gene flow and variability in the hereditary material, since these increase the potential for adaptation to abiotic and biotic stress (Jiménez and Collada, 2000; Jump *et al.*, 2008).

### **Impact of provenance and genotype on susceptibility to *Hypsipyla grandella***

As mentioned before, the main biotic limitation to the productivity of commercial plantations of Spanish cedar is the attack of the mahogany shoot borer. This lepidopteran feeds on the main bud of the plant causing slow growth, bifurcations and proliferation of codominant branches, which considerably reduces the commercial value of wood (Cornelius and Watt, 2003). Indirectly, this results in illegal logging of phenotypically outstanding individuals from natural populations and also decreases their availability for sustainable timber utilization (da Silva *et al.*, 1999).

Variation in susceptibility to *H. grandella* relates to the geographical origin of *C. odorata* genotypes; for example, it has been estimated a frequency of attacks ranging from 0.8 to 2.4 per tree, suggesting the existence of fast-growing and tolerant families to the borer (Newton *et al.*, 1999; Cornelius and Watt, 2003; Navarro *et al.*, 2005). Likewise, in a study with clones produced by grafting in *Tezonapa Veracruz*, Mexico, selection of highly productive genotypes represented a genetic gain of 82 % for volume, a 10.9 % decrease in the incidence of attacks and 6.3 % more recovery after the damage caused by the borer (Sampayo-Maldonado *et al.*, 2019). The study evidences the genotypic variation in the species, and demonstrates that genetic improvement for obtaining pest resistant trees is possible, as well as to increase the productive potential in economically viable plantations. Nevertheless, it is necessary to identify genotypic traits linked to the phenotypes of interest.

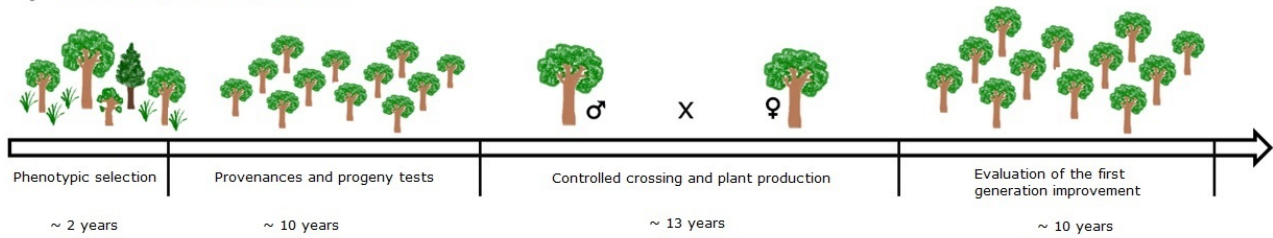
### **Traditional and assisted by molecular biology genetic improvement**

Genetic improvement aims to develop varieties of high economic, ecological or social value and involves repeated processes of activities such as selection, breeding and genetic evaluations (White *et al.*, 2007). One of the main strategies of traditional genetic improvement is the phenotypic selection of the best mature individuals, followed by the establishment of provenance and progeny tests to estimate the genetic and environmental components (Zobel and Talbert, 1988). However, traditional methods are limited by the long reproductive cycles of most forest species, which represents several years and even decades depending on their biology (Figure 1) (Grattapaglia, 2017).

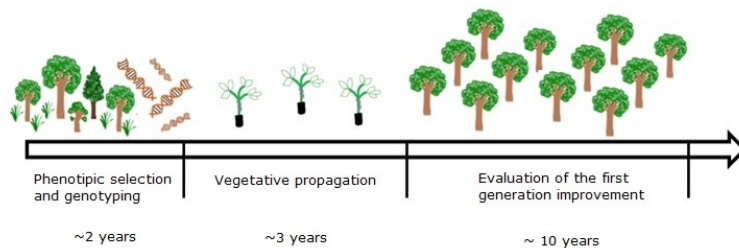




**a) Traditional genetic improvement**



**b) Genetic improvement assisted by biotechnology**



**a)** Traditional genetic improvement. The estimated time for a complete cycle is 35 years because in *C. odorata* sexual maturity occurs at about 12-15 years to which three to seven more must be added to perform the early evaluation of the phenotypic features of interest. **b)** Genetic improvement assisted by biotechnology. The use of tools such as tissue culture and molecular markers, leads to an approximate 50 % reduction in time in comparison to traditional genetic improvement since genotypic traits associated to the phenotype of interest can be evaluated in seedlings (Own elaboration).

**Figure 1.** Schematic representation of the stages of a *Cedrela odorata* L. genetic improvement program.

In addition, this type of genetic improvement in forest species is mainly based on economic traits to obtain better wood yields. Most of these studies and especially in tropical species are not based on specific ideotypes that can serve as a reference for genetic improvement, which are important for the quality and heterogeneity of the established materials and that, additionally, can be considered as forest germplasm



producing units (Dickmann and Gold, 1994; Solís-Guillén *et al.*, 2017). Selection is even more difficult when the characters of interest are complex; for example, wood properties, resistance to pests and diseases, as well as tolerance to abiotic stress (Nehra *et al.*, 2005).

Biotechnology, particularly molecular biology, offers opportunities for genotyping superior individuals, performing Marker Assisted Selection (MAS), as well as studying genome organization and gene functioning associated with characters of economic importance, among others. One of the main advantages of the new technologies is to reduce the duration of improvement cycles; for example, MAS would allow early selection of characters that are expressed at maturity (Grattapaglia, 2017), or, predictions based on quantitative genomic traits would save time during the evaluation stage (Figure 1) (Park *et al.*, 2016), as estimated for the conifer *Picea abies* (L.) Karst, where traditional improvement cycle requires more than 28 years and can be reduced to less than 10 by means of these tools (Lenz *et al.*, 2019).

In Latin America, there are several studies regarding traditional genetic improvement of *C. odorata*; for example, in *Costa Rica*, early performance and resistance to *H. grandella* of 115 families from 21 backgrounds from Mexico, *Guatemala*, *Honduras*, *Costa Rica* and Panama were assessed under conditions of association with coffee cultivation (Navarro *et al.*, 2004). Height, log diameter, resistance and number of shoots were the variables evaluated and all were highly significant at the provenance level. Heritability coefficients ( $h^2$ ) for all families within the provenances obtained were 0.12 and 0.20 for diameter and height, respectively. In addition, Spanish cedar trees associated with coffee cultivation showed better growth in diameter and height, as well as greater resistance to the Mahogany shoot borer and higher shoot production (Navarro *et al.*, 2004).

In Mexico, the *Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias* (INIFAP) (the National Institute of Forest, Agricultural and Livestock Research (INIFAP) is one of the few institutions dedicated to the domestication of Spanish cedar. Advances include the establishment of two progeny trials that in total

evaluated 210 families from 26 sources in the Gulf of Mexico and southeast of the country (Sánchez *et al.*, 2003; Hernández-Máximo *et al.*, 2016). In both experiments, the individual heritability of the main quantitative variables of economic importance was estimated: height, chest height diameter (DAP) and volume (Table 1); likewise, the estimated genetic correlation for the studied characters was high ( $> 0.90$ ). Therefore, it was concluded that growth variables have moderate to high genetic control.

**Table 1.** Heritability values for the main *Cedrela odorata* L. variables in provenance assays established in “El Palmar” experimental station in Tezonapa, Veracruz, México.

Assessed Variable	Heritability ( $h^2_i$ ) in uneven aged trees (years) at the time of the assessment				Reference
	3	5	7	11	
Height		0.65			Sánchez <i>et al.</i> , 2003
DBH		0.38			
Volume		0.54			
Taper index		0.38			
Height	0.16	0.22	0.25	0.22	Hernández-Máximo <i>et al.</i> , 2016
DBH	0.16	0.21	0.27	0.27	
Volume	0.12	0.18	0.27	0.29	

$h^2_i$  = Individual heritability; DBH = Diameter at breast height.

The process from phenotypes selection to establishment of progeny tests until obtaining genetic parameters required more than 20 years. The 40 best individuals were selected and placed in a clonal trial that resulted in which a genetic gain of 82 % for volume, based on a selection intensity of 10 % (Sampayo-Maldonado *et al.*, 2019).



## Conclusions

Unlike forest species such as *Populus*, *Pinus* or *Eucalyptus* genera, genetic studies on Spanish cedar are emerging. In them, some biotechnological tools have allowed to determine part of their genetic characteristics. Research has mainly focused on populations in the region between *Veracruz, Mexico* and northern South America, which have evidenced the population structure and the relationship between climatic conditions and its natural distribution, suggesting that its genetic pool still has an important potential for adaptation.

However, fragmentation of their populations prevents gene flow and clandestine logging threatens such resources despite its relevance in the Neotropical region. In Mexico, it has not been possible to contribute to the economic development of the rural communities neighboring its area of use. Therefore, it is essential to carry out intensive and extensive studies to characterize the genetic heritage of this species throughout its distribution area in the country, as well as research focused on the physiology of the response to biotic and abiotic stress and generation of technologies for genetic improvement and sustainable use.

With the heyday of the postgenomic era and its relationship with biochemistry, biotechnology, molecular biology, bioinformatics, biostatistics, among others, the study approaches for the genotype-environment interaction has been revolutionized and new alternatives for improvement and conservation of forest species are now available, which does not imply the replacement of traditional techniques, but the complementation of them to make these processes efficient in order to protect the genetic diversity.

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## Conflict of interest

The authors declare no conflict of interests.

## Contribution by author

Lorena Gálvez López: literature review and writing of the manuscript; Miguel Ángel Vallejo Reyna: structuring and writing of the manuscript; Claudia Méndez Espinoza: writing and editing of the manuscript and design of the figure; Javier López Upton: general review of the manuscript.

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