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Evaluación de la Diversidad Genética en Dos Tipos de Poblaciones de *Tabebuia rosea* (Bertol) D. C. en el Estado de Campeche

TESIS

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DEDICATORIA Y AGRADECIMIENTOS

“Cuando voy a dormir

Cierro los ojos y sueño

Con el olor de un país

Florecido para mí…”

Canción del Jardinero, María Elena Walsh

A Armando Alayón, sin él no hubiera entrado a la maestría

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PORTADA

INTRODUCCIÓN

México es considerado un país mega diverso y se lo debe, en gran parte, a los ecosistemas presentes en los estados del Sur (Campeche, Yucatán, Quintana Roo, Tabasco y Chiapas). A pesar de la abundancia de recursos naturales y su riqueza biocultural, los porcentajes más altos de cobertura forestal y de hablantes de lengua indígena, presenta los índices de desarrollo humano más bajos del país (Villalobos-Zapata et al. 2010, p.50,51). Esta paradoja genera que los recursos naturales sean foco de una gran presión por parte de factores socioeconómicos, los estados del sur de México posee las tasas de deforestación más altas (Villalobos-Zapata et al. 2010, p.57), afectando a la biodiversidad en todos sus niveles, desde el molecular al ecosistémico. Esta situación se ejemplifica muy bien con la explotación forestal de maderas preciosas, también paradójica, ya que se trata de un recurso natural de altísimo valor pero que por su mal manejo ha generado graves problemas ambientales en la región (Blaser et al. 2011; ITTO 2005).

Las reconocidas especies arbóreas de madera preciosa, *Cedrela odorata* L. y *Swietenia macrophylla* King. crecen en las selvas del trópico mexicano y también otras especies de madera preciosa incipientes en el mercado nacional e internacional como C*ordia dodecandra* A. DC.*, Guaiacum sanctum* L.*, Platymiscium yucatanum* Standl.*, Swartzia cubensis (Britton & P. Wilson) Standl.* y *Tabebuia rosea* (Bertol.) Bertero ex A.DC (P.Macario, comunicación personal), que se han convertido en objetivos muy atractivos para su aprovechamiento tanto legal, como ilegal. La tala ilegal según la SEMARNAT (2012) es la segunda causa de pérdida de cobertura forestal en México; mientras que la tala selectiva de maderas preciosas es el principal disparador del cambio de uso de suelo: el terreno sin estas especies en pie, pierde valor económico, se deforesta y se emprenden otras actividades productivas más redituables (Schulze et al. 2008; SEMARNAT 2012). Considero que uno de los factores clave para el éxito del verdadero desarrollo sustentable es que las comunidades que manejan recursos forestales se beneficien de un uso medido pero redituable de estos. Existen varias alternativas de uso y manejo para las especies forestales y en la matriz heterogénea del Sureste mexicano se combinan acahuales, milpas, sistemas agroforestales, pasturas para ganadería y plantaciones forestales comerciales.

Las plantaciones comerciales de árboles nativos se presentan como una alternativa más limpia de producción maderable y prometen aliviar la presión sobre los bosques. A diferencia de los cultivos anuales las plantaciones proveen servicios ecosistémicos (Scherer-Lorenzen et al. 2007; Redondo-Brenes & Montagnini 2006) a una mayor escala espacial y temporal; y con un manejo apropiado puede contribuir a la conservación (Hartley 2002; Kanowski et al. 2005; Barlow et al. 2007; Brockerhoff et al. 2008), restauración (Lamb 1998), ser fuente de semillas para programas de reforestación (Ferreira et al. 2012) o establecimiento de otras plantaciones en sistemas agroforestales, por ejemplo. En la actualidad, al no existir programas científico-técnicos que busquen realzar las características productivas de las especies forestales nativas, las plantaciones forestales comerciales de árboles nativos en México tropical se encuentran lejos de ofrecer altas tasas de productividad y calidad (reuniones sectoriales CONAFOR, comunicaciones personales), por ende suelen ser sustituidas por especies foráneas como *Gmelina arbórea* Roxb. y *Tectona grandis* L.f que ya han pasado por dicho proceso. Un producto forestal nativo si estuviera domesticado podría lograr altos rendimientos y calidad además de efectos benéficos sobre el ecosistema y generaría un verdadero cambio. Por ejemplo, en Campeche, uno de los estados de mayor importancia forestal de México, por la superficie plantada que presenta y su potencial forestal (CONAFOR 2015a; CONAFOR & COLPOS 2011). *T. rosea* parece tener el perfil deseado para proyectos forestales y agroforestales ya que es nativo, se desarrolla excepcionalmente bien en las provincias fisiográficas de Campeche (Pennington & Sarukhán 1998), es multipropósito (maderable, ornamental, melífero, medicinal, ver más adelante) (CONABIO 2000) y ha presentado uno de los incrementos en área plantada más grandes (de 8 ha a 5000 ha en tan solo 10 años (CONAFOR 2013; CONAFOR 2015b)).

La domesticación de árboles tropicales se encuentra dando sus primeros pasos por la limitante tecnológica y metodológica que presentaba la domesticación convencional (Nichols & Vanclay 2012): los resultados de la autopolinización, las retro cruzas y de la selección de élites son visibles después de muchos años por la longevidad y tardada maduración de los árboles en general. Las herramientas moleculares pueden simplificar la identificación y acelerar los procesos de selección en las distintas etapas del mejoramiento (Harfouche et al. 2012). He aquí la importancia de conocer la diversidad del germoplasma forestal de *T. rosea* que nos dará información valiosa sobre la riqueza del recurso genético forestal en términos biotecnológicos y ecológicos. Responder a preguntas del tipo: ¿Qué niveles de diversidad genética se pueden encontrar en poblaciones con distintas historias de manejo? ¿Existe estructura poblacional entre ellas? ¿Cómo se distribuye esa diversidad en el espacio? ¿Han ocurrido cuellos de botella genéticos en las poblaciones? Este tipo de preguntas nos permitirán diagnosticar el estado del germoplasma forestal que puede verse alterado por: el grado de fragmentación del paisaje (Young et al. 1996; Bacles & Jump 2011), la dispersión de polen y semillas (Hanson et al. 2008), la selección antrópica o natural (Ledig 1992; Henery 2011) y los sistemas de polinización (Ward et al. 2005) entre otras.

Pero, ¿Qué es la diversidad genética y por qué es importante en las especies maderables? La diversidad genética es el componente básico de la biodiversidad, se trata de la variabilidad que existe dentro de una especie a distintas escalas (alelo, genotipo, genoma, acervo genético) y sus respectivas escalas espaciales y temporales. Esta variabilidad es resultante de la acción de las fuerzas microevolutivas, factores ecológicos y antrópicos (Manel et al. 2003). El germoplasma forestal guarda la información de caracteres de interés ecológico y comercial (una industria billonaria), y es la base de la adaptación a cambios ecológicos y climáticos (Jump et al. 2009). La importancia de la diversidad genética ha tomado gran relevancia en el contexto de cambio global ya que es determinante de la estabilidad a largo plazo de los ecosistemas forestales y afecta sus caracteres funcionales e interacciones complejas (Gailing et al. 2009); asegura la continuidad de biomasa y los servicios ecosistémicos (Luck et al. 2003); la resistencia a plagas y enfermedades (Hajjar et al. 2008, p.265) y su capacidad de resiliencia (Reusch et al. 2005; Schaberg et al. 2008). Cuando la diversidad es baja y aumenta la endogamia pueden ocurrir efectos negativos en la supervivencia de las plántulas, la producción de frutos y de semillas (Holtsford &

Ellstrand 1990). En este mismo contexto, el paisaje se ha vuelto una compleja matriz heterogénea en donde las plantaciones forestales comerciales son un componente cada vez más importante: hasta el 7% de la superficie mundial (FAO 2014). En el caso de *T. rosea* en México, las interacciones genéticas entre distintos tipos de poblaciones; urbanas, agroforestales, plantaciones comerciales y nativas son posibles y dependiendo del manejo éstas podrán traer consecuencias negativas (asimilación genética y migración asimétrica [Papa 2005]) o positivas (conservación *ex situ* [Ferreira et al. 2012]) para el estado del germoplasma de la especie.

Para el género *Tabebuia* estudios previos demostraron que la diversidad genética se mantenía en niveles similares al comparar poblaciones: urbanas y de vegetación secundaria (*T. roseo-alba* (Ridl.) Sandwith, Feres et al. 2009), en paisajes continuos y fragmentados *(T. ochracea* A.H. Gentry Moreira et al. 2009) y, entre huertos semilleros y pruebas de progenie (*T. rosea*, López et al. 2015). Los coeficientes de endogamia fueron altos para todas las poblaciones, además se documentó diferenciación poblacional y estructura genética espacial para *T. aurea* (Silva Manso) Benth. & Hook.f. ex S.Moore (Braga & Collevatti 2011) pero no para *T. ochracea* (Moreira et al. 2009) o *T. roseo-alba* (Collevatti et al. 2014). Todos estos trabajos fueron realizados en Brasil (a excepción de López et al. 2015, que se realizó en Colombia) donde las poblaciones de "Ipês", nombre por el cual se conoce a las Tabebuias en dicho país, han sido reducidas y algunas poblaciones amazónicas están en riesgo (Schulze et al. 2008) debido a la gran demanda del mercado. El gran interés económico ha sido acompañado por el interés científico-técnico con diversas publicaciones en relación al manejo y ecología de la especie (Cuadro 1)

Cuadro 1. Trabajos científicos sobre *Tabebuia rosea*.

Temática general	Foco del trabajo	Referencia
Multipropósito	Sombra ganado y cacao	(Haggar et al. 2011; Somarriba & Beer 2010)
	Sumidero de carbono	(Kirby & Potvin 2007)(Ziska et al. 1991)

	Tolerancia petróleo	(Pérez-Hernández et al. 2013)
	Manejo de semilla	(Andreuccetti Maeda & Ferraz Matthes 1984)
Plantaciones	Desempeño	(Quevedo et al. 2010; Molina Castillo 2012; Sánchez Rueda et al. 2011; Van Breugel et al. 2011; Wishnie et al. 2007; Paul et al. 2011)
	Manejo agroecológico	(Plath et al. 2011; Esquivel et al. 2007)
	Restauración y Reforestación	(Jerez et al. 2014; Riedel et al. 2012; Butterfield 1995; Yanes et al. 1996; Schweizer et al. 2013; Celis & Jose 2011; Wishnie et al. 2007)
Plantación en monocultivo vs plantaciones mixtas	Uso de agua y nutrientes	(Schwendenmann et al. 2015; Oelmann et al. 2009)
	Herbivoría	(Riedel et al. 2012; Riedel et al. 2013; Plath, Dorn, Riedel, et al. 2012)
	Afectación a otras especies	(Plath, Dorn, Barrios, et al. 2012)
Mejoramiento	Propagación *in vitro*	(Suárez et al. 2006; Schuler G. et al. 2005)

El objetivo general de este trabajo fue evaluar los niveles de variabilidad genética presentes en una población artificial, sembrada deliberadamente, es decir una plantación comercial de *T. rosea*, y en una población natural cercana que ha sido “dejada en pie” (*sensu* Casas et al. 2007) en un pastizal natural por los rancheros que se benefician así de la sombra de estos árboles para su ganado. Específicamente se utilizaron diez marcadores moleculares microsatélites (desarrollados por Braga et al. 2007 para el género *Tabebuia* y por López et al. 2015 para la especie *T. rosea*) en conjunto con cuatro marcadores moleculares de inter secuencia simple repetida (ISSR, del inglés “Inter Simple Sequence Repeat”) para generar datos que nos permitan describir niveles de diversidad genética para cada población, estructuración poblacional entre estas, si presentan o no estructura genética espacial y si han presentado cuellos de botella genéticos en el pasado. Esperamos que los resultados de este estudio puedan tener un impacto en temas tan variados como la conservación genética, el manejo forestal, la restauración génica y el mejoramiento de *T. rosea*.

ARTICULO

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Genetic variability of a *Tabebuia rosea* (Bertol. D. C.) commercial plantation is representative of the native genetic diversity found in Campeche, Mexico: A case study

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Abstract

When new national policies were published in 2014 with a focus on genetic diversity levels, seed production units and forest germplasm management, the genetic variability of *Tabebuia rosea* in Mexico was unknown. In this study, genetic variability was assessed by different metrics, including genetic diversity estimates, spatial genetic structure, genetic bottleneck occurrence and cluster analysis, in 34 plants from a commercial plantation and 31 plants from a native population in Campeche State using SSR and ISSR molecular markers. In general, the commercial plantation and the native population shared genetic diversity levels (Expected heterozygosis $P = 0.55$; Number of alleles $P = 0.38$) and showed spatial genetic structure. The SSR data showed low but significant (0.087 ± 0.032) population differentiation; the inbreeding coefficient was significantly high (0.34 ± 0.11 for native population and 0.41 ± 0.068 for commercial plantation). The population differentiation from the ISSR data was not significant (0.088 ± 0.21). Spatial genetic structure was significant for the first distance class in both populations (31 meters in commercial plantation and 96 meters in native population) using SSR data, while with ISSR data it was significant only in the native population up to the second distance class (172 meters). Cluster analysis showed no differentiation between individuals from either population using both molecular markers, as all individuals were intermingled in dendrograms. No genetic bottlenecks were detected in the populations studied. We recommend further work to characterize the genetics of native and planted populations to inform *T. rosea* improvement and conservation programs.

Keywords

Spatial genetic structure; genetic diversity index; forest genetic resources; tropical timber species; molecular ecology

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Introduction

Tabebuia rosea plantations for timber production have increased rapidly in size in tropical Mexico; during the last decade, a six-hundred-fold increase in planted area was recorded (CONAFOR 2013; CONAFOR 2015a). More than half the plantations of this Neotropical multipurpose tree established in the southern Mexican states of Chiapas and Campeche, and ca. 25 % in the latter state (CONAFOR 2015a). Within the physiographic province of the "Peninsula de Yucatan" (Cervantes-Zamora et al. 1990), the Campeche State has the highest potential for timber production; specifically, the "Carso y Lomeríos de Campeche" physiographyc region (CONAFOR 2015b).

In Mexico, a recent federal regulation on seed production (NMX-AA-169-SCFI-2014, SE 2014) urges producers to guarantee that 1) genetic diversity levels are similar to those found in native populations and 2) the provenance of the planted material belongs to the same physiographic region. Currently, commercial plantations in tropical Mexico do not account for either of these factors primarily because of the genetic information gap at this geographic scale. Additionally, wild populations of *T. rosea* are disappearing from natural landscapes because of deforestation rates that are among the highest in tropical Mexico (CONAFOR 2015b). The species can currently be found primarily in secondary vegetation patches, known locally as "acahuales" or "Hupche" in maya, as tolerated individuals in pasture lands or in some local yards. This type of management for native perennial species, defined by Casas et al. (2007) as let standing management, is common for multipurpose trees where there is no logging or special selection made.

The genetic diversity of forest resources plays a defining role in both adaptation and population resilience of commercial plantations and native populations (Booy et al. 2000; Schaberg et al. 2008; Jump et al. 2009). Additionally, when plant species are cultivated in their natural distribution range alongside native populations, the gene pool is maintained by both reservoirs and their interactions (Vanden Broeck et al. 2005; Chwedorzewska et al. 2008). For that reason, most sustainable timber production policies to date are focused on the use and distribution of genetic material (FAO 2014); as such, information regarding these matters must be readily available for decision makers.

Genetic variability occurs at different spatial and temporal scales; as a result of the interactions among micro-evolutionary forces and both ecological and anthropic factors, affecting the distribution patterns of gene and allele frequencies (Manel et al. 2003). In the case of commercial plantations, the provenance and number of mother plants selected (Kitzmiller 1990; Chwedorzewska et al. 2008), seed collect method (random or systematic) (Kitzmiller 1990) and nursery practices (Campbell and Sorensen 1984; İçgen et al. 2006) define the genetic diversity of the planted stands. A reduction in genetic diversity compared to native populations is expected if seed collection from relatively few sources causes a bottleneck (Campbell and Sorensen 1984; Savolainen and Kärkkäinen 1992; Vander Mijnsbrugge et al. 2010) or when collection is driven by productivity traits resulting in directional selection (Henery 2011). For native populations, bottlenecks caused by extensive logging, thinning or natural disasters may reduce genetic diversity (Lemes et al. 2008; Siong Ng et al. 2009; Carneiro et al. 2011). In contrast to gene flow and high outcrossing rates, the typical characteristics of tropical trees allow the maintenance of high levels of genetic diversity and prevention of spatial genetic structure (Hamrick et al. 1992; Hamrick and Godt 1996). Population differentiation is expected when isolation of populations is enough to reduce gene flow via pollen or seed dispersal (Wright 1978). At a local scale, if gene dispersal is limited and a nonrandom distribution of genotypes occurs in a restricted area, genetic neighborhoods develop (Vekemans and Hardy 2004). Within these neighborhoods, individuals have a higher genetic similarity, causing genetic autocorrelations with geographic distance (Vekemans and Hardy 2004).

For the *Tabebuia* genus, previous studies have demonstrated that the genetic diversity is similar for several populations: between *T. roseo-alba* urban plantations and secondary vegetation in Brazil´s Cerrado (Feres et al. 2009), between continuous and fragmented landscapes in Brazil´s Cerrado for *T. ochraceae* (Moreira et al. 2009) and between seed orchards and progeny trials from different provenances in Colombia for *T. rosea* (López et al. 2015). Population differentiation and spatial genetic structure has been documented for *T. aurea* (Braga and Collevatti 2011) but not for *T. ochracea* (Moreira et al. 2009) nor for *T. roseo-alba* (Collevatti et al. 2014).

The goals of this study were to compare the genetic diversity and spatial genetic structure and to test for population differentiation and genetic bottlenecks for a commercial plantation and a native population using SSR (Braga et al. 2007; López et al. 2015) and ISSR molecular markers. The *Tabebuia rosea* populations in this study were a) a commercial plantation containing an artificial population deliberately sown for timber production with untraced seedlings obtained from local nurseries, which is a common practice for the vast majority of commercial plantations in the region, and b) one of the closest native populations, located in a pasture land found 125 Km from the plantation (Figure 1).

Materials and methods

Study site

This study was conducted in the state of Campeche, including Carso and Lomeríos physiographic region, in Southeast Mexico. As shown in Figure 1, the region occupies most of the south part of the Yucatán Peninsula and includes three states. This region is characterized by an Aw_2 climate, with an average of 1000 to 1400 mm annual rain, 26.2° C mean temperature and two months of water deficit followed by a summer rainy season (Villalobos-Zapata et al. 2010). Both populations studied are located inside the Calakmul - Bala´an K´aax biodiversity corridor, which is part of the Mesoamerican Biological Corridor (CONABIO-CGCRB 2014).

Place Figure 1 here

Two types of *Tabebuia rosea* populations were compared: 1) A nine-year-old commercial plantation (18° 57’ 33’’ N; 90° 46’ 35’’ W) containing *T. rosea, Cedrela odorata* and *Swietenia macrophylla* and 2; a “let standing” *T. rosea* population (18° 08’ 42’’ N; 91° 36’ 17’’ W) in pasture land *sensu* Casas et al. (2007). At the commercial plantation the three species mentioned above are intermingled in random manner, and individuals are sown 3 meters apart. The pasture land population has *T. rosea* individuals reaching up to 70 cm diameter at breast height (DBH) and a large number of juveniles. The species is dominant and colonizing the area effectively with little interspecific competition, as it is one of the few trees that can tolerate flooded vertisols.

Sampling strategy

Due to differences in population density between the commercial plantation (770 individuals per hectare) and the pasture land (0.9 individuals per hectare), collection was random from the commercial plantation and systematic from the pasture land population. Foliar tissue was collected for each selected individual. In the pasture land population, all individuals (31) with more than 5 cm DBH were collected within a ca. 55 ha area. A similar number of individuals (34) from commercial plantation were randomly selected from a pool of ca. 1800 using row and column Cartesian coordinates (Figure 2). Two young leaves were collected from each individual, kept in a paper envelope inside a Ziploc bag containing 100 g of silica gel (to dry samples and avoid fungi infection), and transported to the Ecophysiology and Biodiversity Laboratory at the Autonomous University of Yucatán.

Place Figure 2 here

SSR and ISSR analysis

To isolate genomic DNA, 1.5 g of leaf tissue was ice-dried in liquid nitrogen. DNA extraction was performed with the QIAGEN® (Hilden, Germany) Plant DNeasy mini Kit according to the manufacturer´s protocol. The quality of genomic DNA was confirmed visually via electrophoresis in 0.8% agarose gels run at 150 V in sodium-borate buffer (Brody and Kern 2004).

At first, 18 microsatellite (SSR) primer combinations were evaluated using the protocols of López et al. 2015 and Braga et al. 2007. Eleven inter-simple sequence repeat (ISSR) primers were also tested from the University of British Columbia Database primer set 9 (Table 1) using a standardized protocol established locally.

Place Table 1 here

PCR products from SSR were obtained using a 15-µL reaction volume containing: 6 µL of 2X GoTaq® Mix (Promega, Madison, USA); 0.25 µM each forward and reverse SSR primers; 20 ng of template DNA, and; ddH_2O and 1 % BSA, and were amplified on a Select BioProducts Thermocycler (Select Cycler II, #SBT9610. Edison, USA) with the following conditions: initial denaturing step at 95 °C for 10 min, followed by 30 cycles of 94 °C for 1 min, 56 °C for 1 min, and 72 °C for 1 min, and then a final extension step of 72 °C for 5 min. To record band presence, 7 µL of PCR products was run on a 4 % agarose gel, as previously described. Twenty selected samples of PCR products of SSR were run in 6 % polyacrylamide gels in 0.5% Tris-borate-EDTA electrophoresis buffer (Sambrook and Russell 2001) to verify the resolution of agarose gels. Patterns of banding in both polyacrylamide and agarose gels were in agreement, and final lectures were conducted with agarose gels. A 100 pb DNA ladder (New England BioLabs. Ipswich, USA) was used to estimate the size of the DNA fragments in both agarose and polyacrylamide electrophoresis.

PCR products from ISSR were obtained using a 15-µL reaction volume containing 6 µL of 2X GoTaq® Mix (PROMEGA), 1 µM ISSR primer, 20 ng of template DNA, ddH$_2$O and 1 % BSA and were amplified with a Select BioProducts Thermocycler. Amplification conditions were as follows: initial denaturing step at 94 °C for 4 min, followed by 40 cycle of 94 °C for 1 min, 56 °C for 1 min, and 72 °C for 2 min, with a final extension step of 72 °C for 10 min. To record band presence, 7 µL of PCR products was run on a 0.8 % agarose gel.

Genetic diversity and spatial genetic structure

To compare genetic diversity between populations and test for population differentiation, the following genetic indices were estimated: Average number of alleles (Na), percentage of polymorphic loci (PPL), expected heterozygosity (He, for SSR; Nei 1978 and Hj, for ISSR; Lynch & Milligan 1994), observed heterozygosity (Ho), F_{IS} (Wright 1978), F_{ST} (Weir & Cockerham 1984) and G_{ST} (Pons & Petit 1996). Lower and upper limits were estimated with SPAGeDi v. 1.3d for He, G_{ST} and F_{IS} (Hardy et al. 2001); AFLP surv v. 1.0 for Hj and F_{ST} (Vekemans 2002); and TFPGA v. 1.3 for observed heterozygosity for SSR (Miller 1997). Hj and F_{ST} from ISSR data were estimated using F_{IS} estimates from SSR as a prior with AFLP-surv v. 1.0 (Vekemans 2002). To check differences among He, Ho and Na, Student t-tests were conducted using InfoStat v2011 (Di Rienzo et al. 2011). Correlation among fragment size and fragment frequency was verified as not significant (Pearson r Sp = 0.0640 P = 0.67); ISSR fragments can be consider homologous (Vekemans et al. 2002).

SPAGeDi v. 1.3 was used to test for spatial genetic structure correlation between the distance classes and kinship coefficient (F_{ij}, Ritland 1996) within those distance classes. A jackknife procedure was implemented to assess significance of pairwise kinship coefficient estimates, where significance of auto correlations was assessed using a 1000 permutations test. Due to sample area differences, the six class intervals for the commercial plantation and pasture land population were set as 0.031, 0.049, 0.066, 0.087, 0.112 and 0.189 Km and 0.096, 0.172, 0.245, 0.378, 0.687, and 1.054 Km, respectively.

An UPGMA dendrogram to heuristically test genetic similarities among individuals from commercial plantation or pasture land populations was constructed using PHYLIP v. 3.2 (Felsenstein 1989) and edited with MEGA v. 6.0 (Tamura et al. 2013).

Bottleneck software v. 1.2.02 (Cornuet and Luikart 1996) was used to test for recent bottlenecks on each population. The program estimates the expected heterozygosity under mutation–drift equilibrium (H_{eq}) from observed allele frequencies under the Step Mutation model. Then, it tests whether H_{eq} estimates are lower than estimates for heterozygosity under Hardy–Weinberg equilibrium (H_E) using sign, standardized differences and Wilcoxon tests.

Results

Allele and genetic diversity were slightly lower in the commercial plantation than in the pasture land population for both molecular markers. The average alleles per locus was 3.3 (min: 1; max: 5) and 11.75 (min: 7; max: 16) from

SSR and ISSR data, respectively. The total number of alleles and expected heterozygosis estimated from both SSR and ISSR were slightly lower in the commercial plantation than in the pasture land population; however, no differences were found using paired t-tests for SSR or ISSR (t = -0.61, P = 0.55, and t = -0.97, P = 0.38 for number of alleles and expected heterozygosis, respectively) (Tables 2 and 3). The observed heterozygosis was not significantly different between the commercial plantation and pasture land population (t = -0.51, P = 0.61). F_{IS} estimates were similarly high in both the commercial plantation and the pasture land population. Estimated F_{ST} and G_{ST} from SSR were significantly different from 0; the estimated F_{ST} from ISSR was not significantly different.

Place Tables 2 and 3 here

Spatial genetic structure was detected in both populations with SSR molecular markers; however, it was not detected in the commercial plantation using ISSR molecular markers. KC and distances were significantly correlated with positive values for distance classes lower than 0.031 Km in the commercial plantation (-b slope linear distance = -0.21 ± 0.19) and 0.096 Km in the pasture land population (-b slope linear distance = -0.02 ± 0.01) using SSR data. With ISSR data**,** positive KC values were found only in the pasture land population up to the second distance class (0.172 km, -b slope linear distance= -0.051±0.02). (Figure 3).

Place Figure 3 here

The dendrograms of SSR and ISSR data showed genetic similarities between populations. In both dendrograms, individuals from the commercial plantation and pasture are intermingled, with the exception of two nodes that grouped three individuals from the pasture land population SSR analysis and one node that grouped four individuals from the pasture land population ISSR analysis (Figure 4).

Place Figure 4 here

The heterozygosity expected under mutation and gene drift equilibrium was similar to heterozygosity expected under Hardy-Weinberg equilibrium according to a two-tailed Wilcoxon test on SSR data for both the commercial plantation (one tail test for excess P = 0.23 and for deficiency P = 0.81) and pasture land population (one tail test for excess P = 0.62 and for deficiency P=0.42)

Discussion

Allelic and genetic diversity were similar in both the commercial plantation and pasture land populations. The genetic differentiation between populations was significant for SSR markers only. Spatial genetic structure was detected among lower distances classes in both the commercial plantation and the pasture land population with SSR markers and for the pasture land population with ISSR markers. Grouping of the individuals based on kinship coefficient was not determined by the origin of the individual (i.e., commercial plantation or pasture land population). There was no evidence for recent genetic bottlenecks or expansions for either population according to the bottleneck test.

Similar levels of allelic and genetic diversity were found in both commercial plantation and pasture land populations of *Tabebuia rosea.* When seeds for plantation establishment are selected from phenotypes with desirable traits, a reduction in polymorphism is expected. Furthermore, when these are gathered without a systematic bias and/or from a sufficiently large number of mother trees, selection and gene drift should not affect allelic or genetic diversity. For instance, in *Araucaria angustifolia* plantations established from plants bought at local nurseries (which usually obtain their seeds from native populations), allelic and genetic diversity in native and commercial stands were similar (Stefenon et al. 2008; Ferreira et al. 2012). Currently, in tropical areas of Mexico, there is no formal breeding program for *T. rosea*, and locals usually use surrounding native populations as seed sources (local producers, personal communication). These two conditions may explain the similarity in allelic and genetic diversity between the two populations examined in this study.

The estimates of allelic and genetic diversity for the pasture land population in this study were among the lowest values published for both the genus (Braga et al. 2007; Feres et al. 2009; Braga and Collevatti 2011; Feres et al. 2012; Collevatti et al. 2014) and the species (López et al. 2015). Estimates from NA, He and Ho were similar to those found in a fragmented and isolated population of *Tabebuia ochracea* in Brazil´s Cerrado (Moreira et al. 2009). The pasture land population analyzed in this study was also located in fragmented matrix isolated by urban settlements and agroforestal systems (“milpas” and “parcelas”) where owners tolerate the presence of *Tabebuia rosea* because it provides shade to cattle. Fragmentation of habitat increases isolation among remnant populations and reduces population size (Young et al. 1996); this may cause a reduction in genetic diversity in fragmented populations compared to continuous populations (Hall et al. 1996; Jump and Peñuelas 2006). Previous logging activity (Degen et al. 2006; André et al. 2008) domestication, or *in situ* management (Casas et al. 2007) of the species can also impact the levels of genetic diversity. *T. ochracea* and *T. rosea* are “let standing” populations in pasture lands where cattle are present. Selection of plants that provide better shelter to the cattle is expected, and cattle browsing on seedlings and juveniles of the species can cause a reduction in genetic diversity (Sánchez Rueda et al. 2011). This hypothesis, as well as new analyses from other populations in the region, should be tested in future works with this species.

Genetic differentiation between populations was significant; this was expected due to the distance between populations (125 Km). F_{ST} and G_{ST} values obtained from SSR data indicate differentiation between the commercial plantation and pasture land population; however, F_{ST} from ISSR does not indicate this difference. Estimates from dominant and co-dominant markers usually differ slightly (Gerber et al. 2000; Jia et al. 2011), which is expected because their screening targets in the genome are not the same. Bolibok et al. 2005 specifically studied the ISSR and SSR combination for genetic studies and obtained the highest polymorphic information content (PIC) for ISSR markers; the result was a recommendation to use them with the SSR markers that are locus specific.

Moreira et al. 2009 obtained significant F_{ST} with SSR markers in populations of *Tabebuia* that were only 10 Km apart, and it is common in the literature to find differences even when the allele diversity is similar between native populations of wind dispersed trees and a conspecific commercial plantation (Thomas et al. 1999; Stefenon et al. 2008). A founder effect in the commercial plantation through the sub sampling of the full genetic pool of the species may cause the observed population differentiation. Additionally, we believe that the seed collection method caused the unintentional gathering of many related individuals, and inbreeding is the main cause of population differentiation; this is similar to a report by Ferreira et al. 2012 on *Araucaria angustifolia* commercial plantations in Brazil.

Breeding among close relatives can accelerate this differentiation process, and high inbreeding coefficients appear as a constant in the genus and in a wide range of population types, including a highly impacted population (Feres et al. 2009), a continuous population (Moreira et al. 2009) and offspring (Feres et al. 2012). In these cases, high levels of inbreeding were associated with the species short flower display period; this is also true for *T. rosea,* which blooms for less than two months during the dry season in the study area. This flowering behavior, when combined with the patchy distribution of the species may favor bi-parental inbreeding (Stacy et al. 1996; Feres et al. 2012) where spatial genetic structure is present, as fewer pollinators reach isolated groups of individuals (Stacy et al. 1996; Cascante et al. 2002).

Spatial genetic structure (SGS) was detected among lower distances classes in both the commercial plantation and the pasture land populations with SSR markers. Both populations were constituted in different manners; humans deliberately sowed one, whereas the other was sown by wind seed dispersal. Therefore, distinct agents cause the SGS for each population. In the commercial plantation, SGS was found within the first distance class (31 meters), which means that trees within 10 rows are more strongly related than the average relationship. If the seeds were collected from a reduced number of mother plants, or if they came from closely related lineages, a spatial genetic structure would be produced.

The SGS in pasture land population was detected within 96- (SSR) and 172- (ISSR) meter distance classes. These distances are within the ranges found for other species of the genus (Braga and Collevatti 2011; Collevatti et al. 2014). Because the seed dispersal mechanism plays a fundamental role in the correlation among kinship and geographical distances (Hamrick et al. 1993; Hardy et al. 2006) and in this case is the same, we believe slight environmental differences between sites may have determined the extent to which SGS was observed. Variations in population structure, landscape, availability of recruitment microsites and predominant wind direction among *T. rosea* sites in this study and the Brazilian sites where Collevatti et al. 2014 and Braga and Collevatti 2011 studied other *Tabebuia* species may have affected seed shadows and recruitment of new individuals around the mother plants.

Grouping of the individuals based on kinship coefficient was not determined by the origin of individual (i.e., commercial plantation or pasture land population). Dendrograms show that, at a regional level, the genotypes are similar and that the commercial plantation actually carries diversity present in the physiographic regions wild populations, represented by the pasture land population. As expected, this result indicates that provenance of the plants growing in the commercial plantation is from local populations. Similarities between commercial plantations and native stands of Neotropical trees were also found in continental (Mwase et al. 2010) and sub-continental assessments (Ansari et al. 2012), indicating that the genetic variation distribution has extensive boundaries.

No genetic bottlenecks on heterozygosity were detected in either population. We expected to observe polymorphism loss due to the long logging history in the region resulting in a decrease in the population´s effective number; however, this was not observed in our analysis. Trees usually have large populations sizes, high rates of gene flow, a long life spans, and preferential outcrossing mating systems (Petit and Hampe 2006); as a result, genetic bottlenecks rarely occur even in fragmented landscapes (Kaufman et al. 1998; White et al. 2002) or under intense logging regimes (Fageria and Rajora 2013). Even the most logged species in Brazil´s seasonally dry forests, *Tabebuia impetiginosa*, showed no genetic bottlenecks (Collevatti et al. 2012). The test for genetic bottleneck used in this study assumes that the number of generations required to detect the effects on heterozygosity is proportional to the effective population size ($0.25 \times 2N_e$ = Number of generations after bottleneck). The only available estimate of generation time for the genus is 12 years for *T. impetiginosa* (Collevatti et al. 2012). If we assume a similar value for *T. rosea*, a decrease in the effective population size down to 20 would be necessary to detect the excess in heterozygosis needed for ten generations. This number of generations dates back 120 years, near the beginning of the 20th century, when massive extraction of *Haematoxylum campechianum*, gum exploitation of *Sapota manilkara* and selective extraction of *Cedrela odorata* and *Swietenia macrophylla* had reduced natural vegetation to almost half of its original area (INE 1999). Presumably the drastic reduction in forest cover did not led to a decrease of effective population size down to 20 in the remnant fragments where the pasture land was founded and *T. rosea* populations may have only suffered light logging or lost individuals by collateral damage at the time. In the case of the commercial plantation, under the 12-year generation time estimate, the analyses suggest that seeds were collected from more than two mother trees.

Commercial plantations and “let standing” populations in pasture lands are the main population types found in the Southern Tropical Mexico. In this study, we found that the commercial plantation maintains similar levels of allelic richness and heterozygosis to one of the closest native populations of *Tabebuia rosea,* but the values are lower than those of other species of the genus. SGS was found in both populations, and although individuals from both populations grouped together according to the genetic similarity analysis, there is evidence for population differentiation. Due to new business opportunities for certified seed production and the urgency of conservation of *Tabebuia rosea*, we recommend continuing studies on genetic variability.

Conflict of interest

The authors declare that they have no conflict of interest

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Figure legends and Table headings

Figure 1. Area of Study. The Mexican Campeche state map; the dotted limited area corresponds to the Carso and Lomeríos de Campeche physiographic region. Stars correspond to the commercial plantation (A) and pasture land population (B).

Figure 2. Spatial distribution of individuals. The physical location of analyzed individuals in each population: (a) commercial plantation, and (b) pasture land population. The arrow indicates geographic north.

Figure 3. Spatial genetic structure correlograms. Kinship coefficient versus distance for six ranges of spatial separations of analyzed trees. The upper row (a and b) corresponds to the commercial plantation, while the lower row (c and d) corresponds to the pasture land population. The left column (a and c) corresponds to ISSR data and the right column (b and d) to SSR data. Error bars in dots correspond to standard error calculated by the Jackknife method.

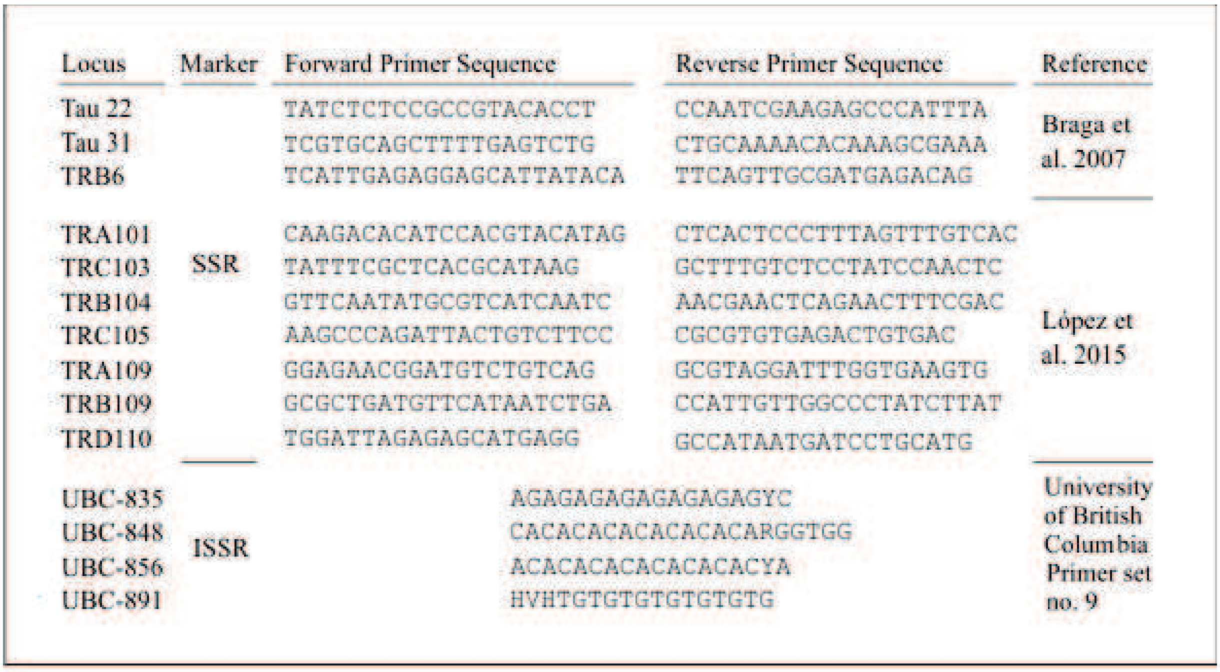
Figure 4. Clustering dendrograms. ISSR (a) and SSR (b) genetic similarity for all individuals sampled in commercial plantation (open dots) and pasture land population (black dots).

Table 1. Primers employed in this study.

Table 2. Genetic diversity data.

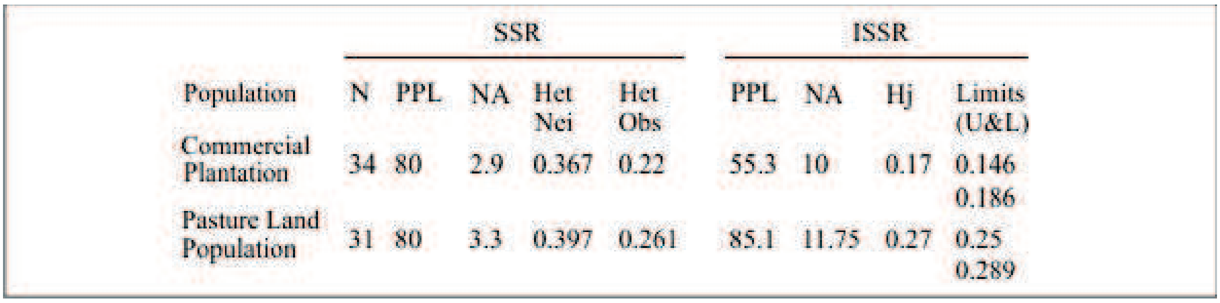
Table 3. Genetic differentiation data on populations.

Table 1



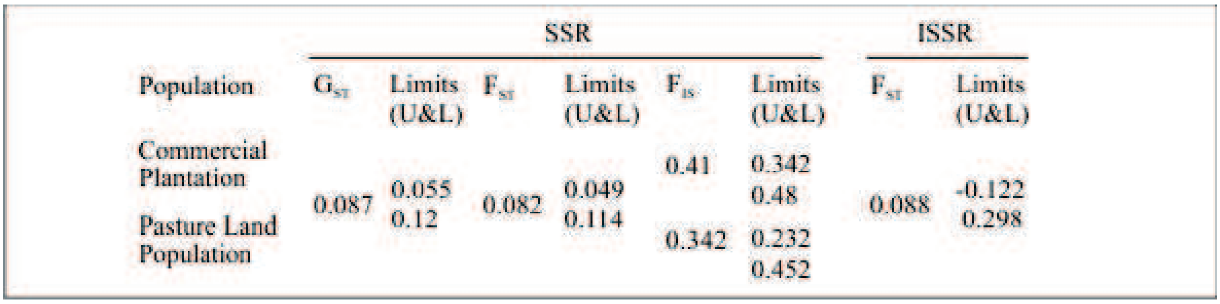
Locus	Marker	Forward Primer Sequence	Reverse Primer Sequence	Reference
Tau 22	SSR	TATCTCTCCGCCGTACACCT	CCAATCGAAGAGCCCATTTA	Braga et al. 2007
Tau 31		TCGTGCAGCTTTTGAGTCTG	CTGCAAAACACAAAGCGAAA	
TRB6		TCATTGAGAGGAGCATTATACA	TTCAGTTGCGATGAGACAG	
TRA101		CAAGACACATCCACGTACATAG	CTCACTCCCTTTAGTTTGTCAC	López et al. 2015
TRC103		TATTTCGCTCACGCATAAG	GCTTTGTCTCCTATCCAACTC	
TRB104		GTTCAATATGCGTCATCAATC	AACGAACTCAGAACTTTCGAC	
TRC105		AAGCCCAGATTACTGTCTTCC	CGCGTGTGAGACTGTGAC	
TRA109		GGAGAACGGATGTCTGTCAG	GCGTAGGATTTGGTGAAGTG	
TRB109		GCGCTGATGTTCATAATCTGA	CCATTGTTGGCCCTATCTTAT	
TRD110		TGGATTAGAGAGCATGAGG	GCCATAATGATCCTGCATG	
UBC-835	ISSR	AGAGAGAGAGAGAGAGYC		University of British Columbia Primer set no. 9
UBC-848		CACACACACACACACARGGTGG		
UBC-856		ACACACACACACACACYA		
UBC-891		HVHTGTGTGTGTGTG		

Table 2



	SSR					ISSR			
Population	N	PPL	NA	Het Nei	Het Obs	PPL	NA	Hj	Limits (U&L)
Commercial Plantation	34	80	2.9	0.367	0.22	55.3	10	0.17	0.146 0.186
Pasture Land Population	31	80	3.3	0.397	0.261	85.1	11.75	0.27	0.25 0.289

Tabla 3



	SSR						ISSR	
Population	G_{ST}	Limits (U&L)	F_{ST}	Limits (U&L)	F_{IS}	Limits (U&L)	F_{ST}	Limits (U&L)
Commercial Plantation	0.087	0.055 0.12	0.082	0.049 0.114	0.41	0.342 0.48	0.088	-0.122 0.298
Pasture Land Population					0.342	0.232 0.452		

Figure 1

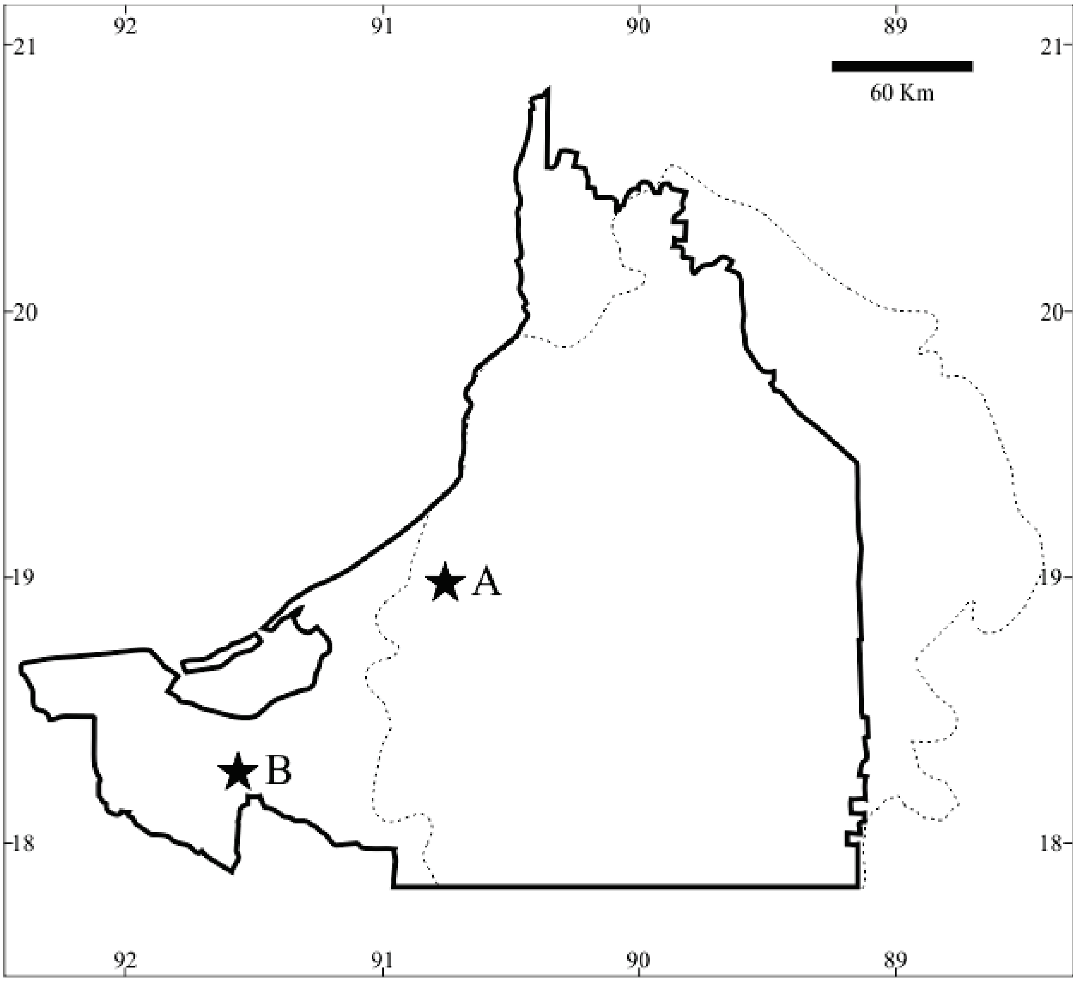


Figure 2

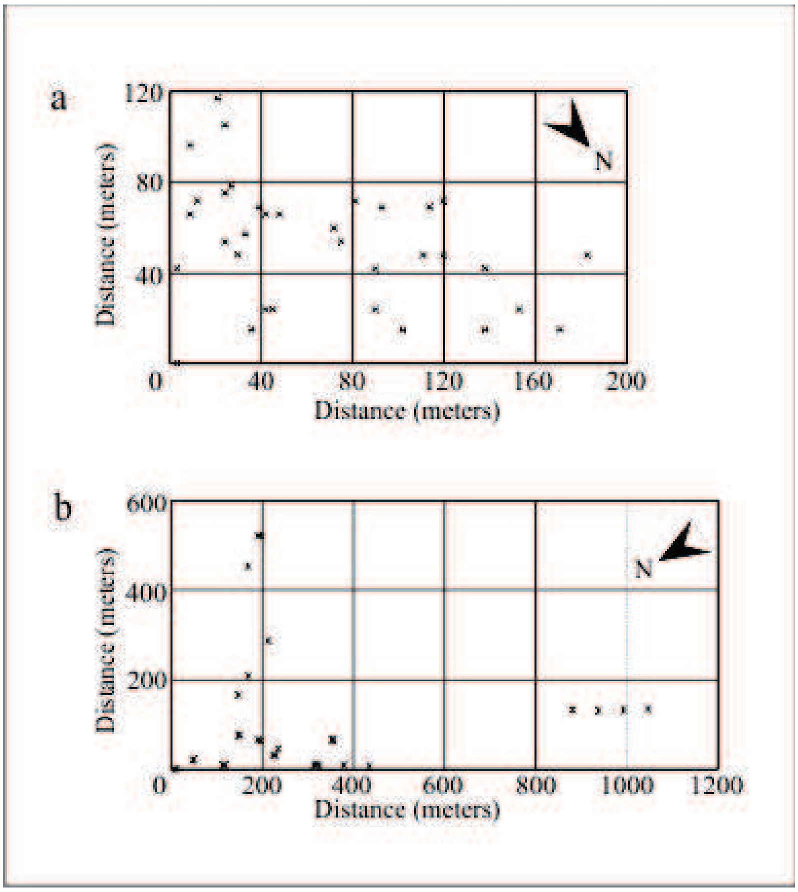

a
120
80
40
0
40
80
120
160
200
Distance (meters)
Distance (meters)
N
b
600
400
200
0
200
400
600
800
1000
1200
Distance (meters)
Distance (meters)
N

Figure 3

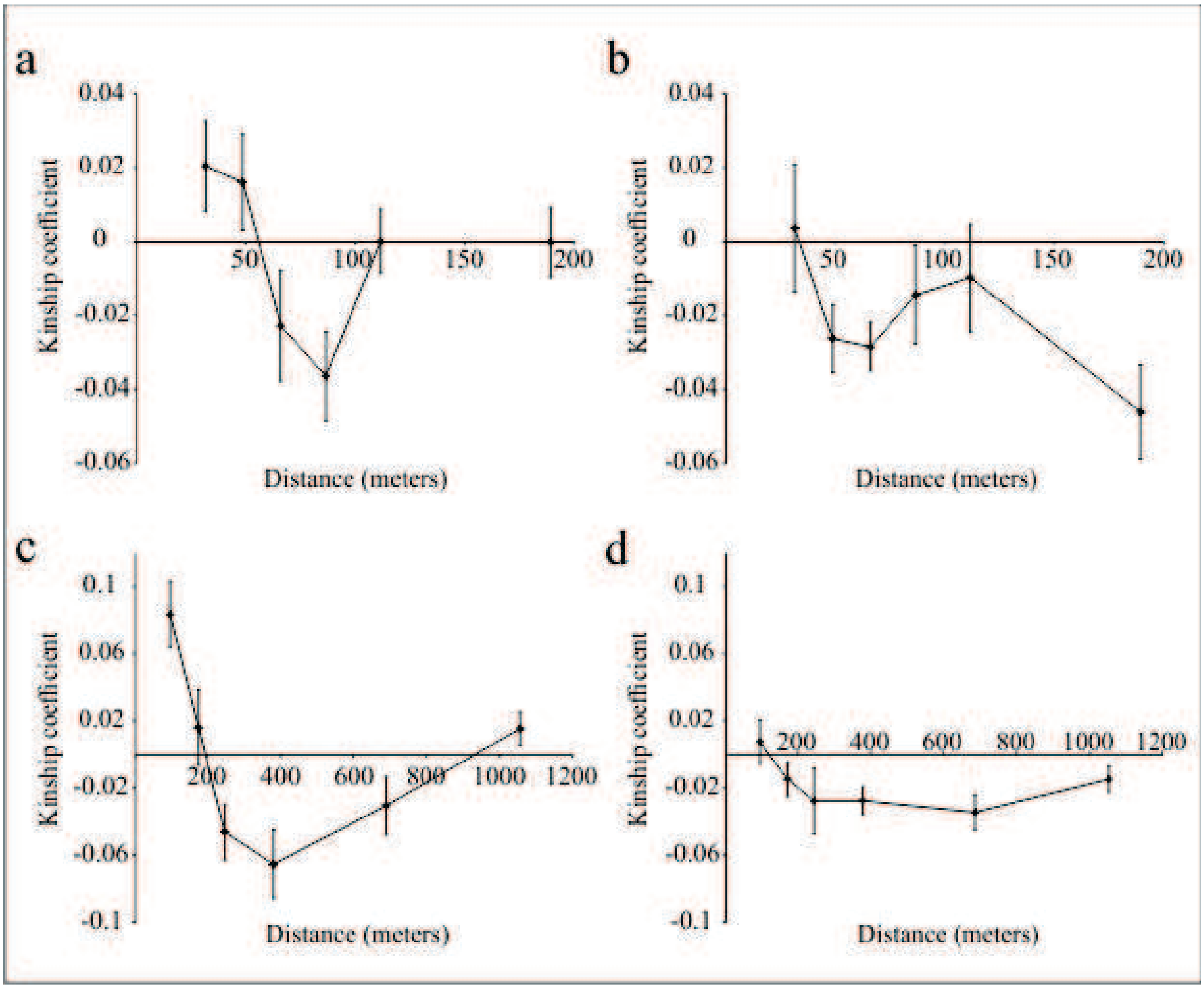
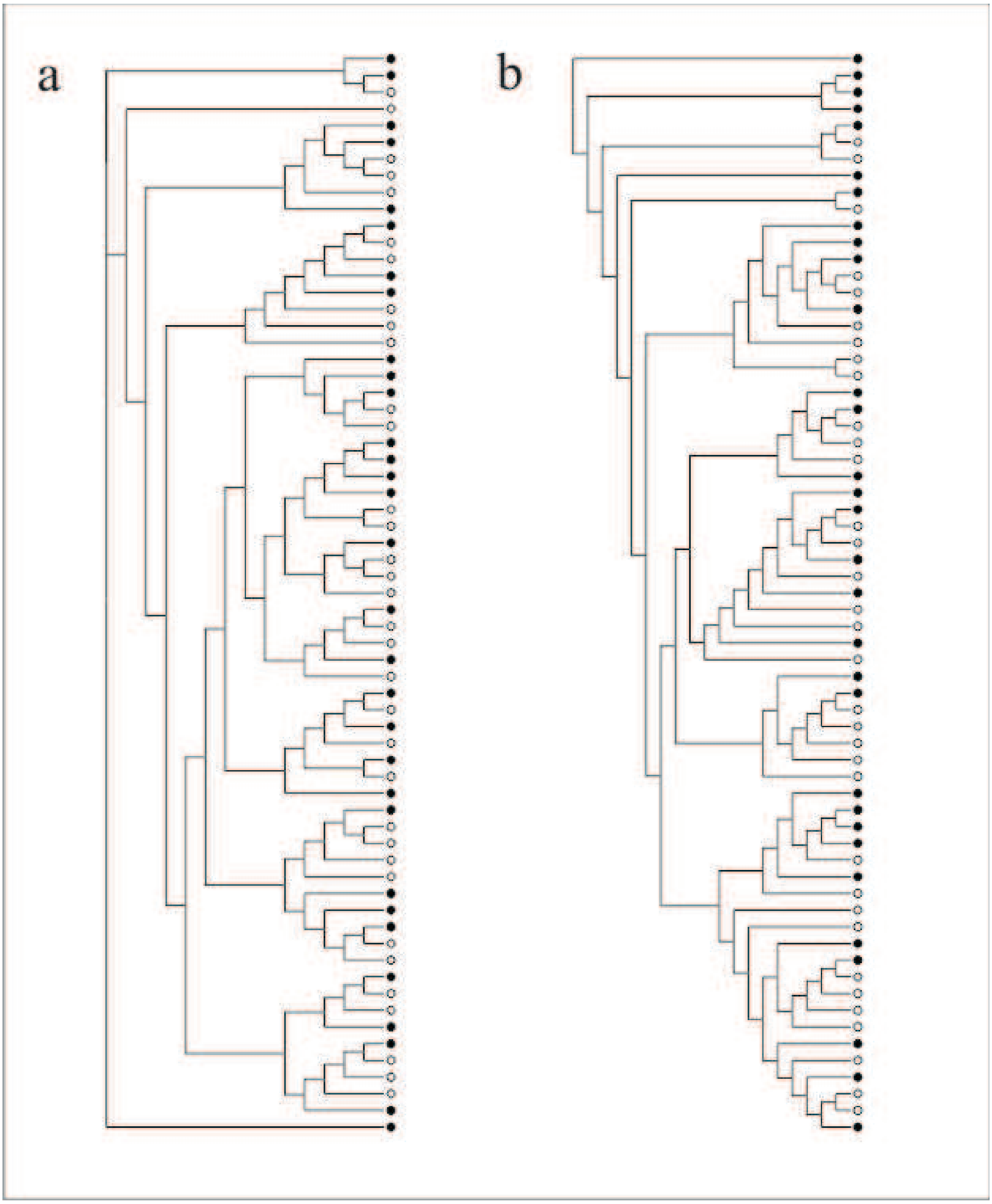

a
Kinship coefficient
0.04
0.02
0
-0.02
-0.04
-0.06
50
100
150
200
Distance (meters)
b
Kinship coefficient
0.04
0.02
0
-0.02
-0.04
-0.06
50
100
150
200
Distance (meters)
c
Kinship coefficient
0.1
0.06
0.02
-0.02
-0.06
-0.1
200
400
600
800
1000
1200
Distance (meters)
d
Kinship coefficient
0.1
0.06
0.02
-0.02
-0.06
-0.1
200
400
600
800
1000
1200
Distance (meters)

Figure 4



CONCLUSIONES

Nuestros resultados apuntan a que la diversidad genética de *T. rosea* es similar en la plantación comercial y en la población nativa del pastizal, pero se trata de valores bajos para el género a pesar de no haber mostrado cuellos de botella genéticos recientes. Las poblaciones mostraron una pequeña diferenciación estadísticamente significativa y ambas presentaron estructura genética espacial con altos índices de endogamia. Desde el punto de vista ecológico no hay riesgos de introgresión genética entre poblaciones, y ambas forman parte del reservorio del acervo génico en la región, aunque se empieza a detectar una leve diferenciación producto, probablemente del submuestreo realizado al recolectar semillas para la siembra de las plántulas de la plantación y/o de la distancia que las separa. Los niveles de polimorfismo son bajos y se necesitaran más trabajos que aborden específicamente este tema para discernir si se trata de una situación de riesgo de conservación. Desde el punto de vista económico, se demuestra que no se está realizando ningún tipo de trabajo o selección para ofrecer a los productores una semilla mejorada con fines productivos. Los datos de distancia de la estructura genética espacial obtenidos (entre 97 y 178 metros para la población natural y 48 y 77 metros para la plantación forestal comercial) pueden ser utilizados para al menos, ayudar a realizar futuras colectas de semilla o polen de una manera más informada y consciente, según el propósito y objetivos de quien lo realice.

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