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Spatial structure of genetic and chemical variation in native populations of the mile-a-minute weed *Mikania micrantha*

Ángel Eliezer Bravo-Monzón [a, b, 1], Antonio González-Rodríguez [b], Francisco Javier Espinosa-García [b, *]

[a] Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México, Mexico
[b] Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Antigua Carretera a Pátzcuaro No. 8701, Col. Ex-hacienda de San José de la Huerta, C.P. 58190, Morelia, Michoacán, Mexico

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ABSTRACT

We examined the spatial distribution and potential relationship of genetic and volatile terpenoid diversity in 13 Mexican populations of *Mikania micrantha* (Asteraceae) from the Atlantic and Pacific watersheds using six specific microsatellites. A low genetic diversity was observed in all populations ($H_E = 0.00–0.37$), which may be attributed to clonal reproduction and/or their marginal location relative to the whole species distribution in the Americas. We found a significant genetic differentiation between regions, and more genetic structure in Atlantic populations where a Mantel test also showed a pattern of isolation by distance ($r^2 = 0.478$, $P = 0.002$). In addition, we detected three genetic barriers that match geographic barriers and may be responsible for population isolation. The geographic patterns of genetic diversity were compared to those from chemical diversity but we found no correlation between the genetic and chemical distances of the populations. Our results suggest that neutral molecular markers and adaptive traits like defensive metabolites provide complementary information that may prove useful during the selection of biocontrol agents for invasive plant species.

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1. Introduction

The genetic diversity of invasive plant species is recognized as one of the major drivers of their colonization success (Sakai et al., 2001). It is currently assumed that the amount, type, and organization of genetic diversity will define the populations' capacity to adapt to unfavorable conditions in the new environment (Barrett, 1992; Jones and Gomulkiewicz, 2012). In this context, genetic variation studies may help identify the evolutionary processes that cause a species to become invasive (Allendorf and Lundquist, 2003).

Furthermore, the spatial distribution of genetic diversity within and among populations can be affected by ecological factors and physical barriers that limit plant reproduction and dispersal (Loveless and Hamrick, 1984; Ward, 2006). Selection, gene flow, genetic drift and breeding system are the factors considered responsible for the distribution of genetic variation in plant populations (Ward et al., 2008). Genetic structure studies of invasive plants at large spatial scales can help identify source populations, as well as the possible introduction routes (Rijal et al., 2015; Ward, 2006).

Genetic variation can be measured using neutral or adaptive markers, and although most studies frequently employ a variety of neutral markers (AFLP, ISSR, and RAPD), the geographic structure of plant populations has also been described with chemical markers such as fatty acids (Martínez-Díaz et al., 2017; Ovando-Medina et al., 2011), terpenoids (Vieira et al., 2001) and various secondary metabolites (Martínez-Díaz et al., 2015). If the same limiting factors of dispersal and gene flow affect the spatial structure of genetic and chemical variation, a spatial correlation of these two features may occur. Such relationship has been detected in studies of commercially important species comparing neutral genetic markers and volatile terpenoids in individual plant species (Keskitalo et al., 2001; Skoula et al., 1999), plant populations (Fracaro et al., 2005; Nan et al., 2003), and cultivars (Böszörményi et al., 2009).

* Corresponding author.
E-mail addresses: abravomonzon@gmail.com (Á.E. Bravo-Monzón), agrodrig@cieco.unam.mx (A. González-Rodríguez), espinosa@cieco.unam.mx (F.J. Espinosa-García).
[1] Present address: Colegio de Postgraduados, Campus Montecillo, Carretera México-Texcoco Km. 36.5, Montecillo, C.P. 56230, Texcoco Estado de México, Mexico.

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However, in those studies, the assessment of the geographic structure of the chemical and genetic variation is limited or nonexistent (although see Külheim et al., 2011; for an exception). Understanding the spatial structure of genetic diversity in the native range of an invasive plant can help us identify distinct geographic regions to search for effective biological control agents adapted to particular genotypes (Gaskin et al., 2011).

In the present study, we were interested in examining the potential relationship between the neutral genetic diversity and chemical diversity in Mexican populations of *Mikania micrantha* (Asteraceae), a tropical American weed that has become a serious invasive in Southeast Asia. This species propagates by vegetative reproduction or seeds that are dispersed by wind, water, and animals (Tripathi et al., 2012); flowers are self-incompatible and insect-pollinated (Hong et al., 2007). Its native distribution includes all wet Neotropical areas from central Mexico throughout northern Argentina (Holmes, 1990). In Mexico, *M. micrantha* can be found in the tropical watersheds near the Atlantic and Pacific coasts, where it forms patchy populations of few individuals (Bravo-Monzón, pers. obs.). Volatile terpenes (Bravo-Monzón et al., 2014) and sesquiterpene lactones (Ríos et al., 2014) are the major foliar secondary metabolites of this plant. Furthermore, distinctive terpenoid phenotypes determine differential feeding in *Stolas punicea*, a *M. micrantha* specialist insect (Bravo-Monzón et al., 2016). Various microsatellite markers have been developed for this species (Hong et al., 2008; Yan et al., 2011), which have been used for describing the population genetics in the invaded range (Geng et al., 2016), but not in its native range.

The Atlantic and Pacific watersheds of Mexico are separated by numerous geographic barriers of varying magnitude from the Mexican transition zone (Morrone, 2006). We postulate that geographic barriers affecting the chemical structure in populations of *M. micrantha* will also affect their genetic structure, and we, therefore, predict: 1) a high genetic differentiation between Atlantic and Pacific populations, and 2) a positive correlation between chemical and genetic distances among populations.

2. Materials and methods

2.1. Plant material

We collected mature leaves in seven populations of *M. micrantha* along the Atlantic coast of Mexico (Dec. 2007), and six populations along the Pacific coast (Dec. 2009), totalizing 159 individuals (Table 1). An exhaustive sampling was performed to include all available individuals at each population. Leaves were dehydrated with silica gel and kept refrigerated until DNA extraction. Voucher specimens were deposited in two herbaria: 1) IE-Bajío, 196627–196632, and 2) EBUM, 20403, 20404, 22684–22699.

2.2. DNA extraction

Total DNA was extracted from 500 mg of leaf tissue using a previously developed protocol (Su et al., 1998) with minor modifications. Each sample was ground by mortar and pestle in liquid nitrogen. The resulting powder was placed in two Eppendorf tubes (1.5 mL) and extracted twice with 1 mL of acetone at −20 °C and centrifuged at 5000 rpm for 10 min, the supernatant was discarded. Samples were added 1 mL of CTAB buffer and incubated at 60 °C for 2 h. For the extraction, we added 500 μL of chloroform:isoamyl alcohol (24:1) and centrifuged at 13,000 rpm for 10 min. The supernatant was recovered in a new tube and DNA was precipitated with 0.6 volume of cold isopropanol. A DNA pellet was obtained by centrifugation at 3000 rpm for 3 min; the supernatant was discarded and the pellet was let stand in 800 μL of washing buffer (10 mM Tris-HCl at pH 7.5, 80% ethanol) for 20 min. After a final centrifugation at 1000 rpm for 10 min, the supernatant was discarded and the pellet was dried at room temperature for 15 min. The DNA was dissolved in 50 μL of deionized water.

2.3. PCR conditions

We used six microsatellite loci: Mm01, Mm05, Mm07, Mm12, Mm19, and Mm31, developed for *Mikania micrantha* (Hong et al., 2008), in three multiplex reactions with fluorescently labeled primers. Microsatellite amplifications were performed in 5 μL reaction volume containing 10 ng DNA template, 3 μL of Multiplex PCR Master Mix (QIAGEN), 2 μM of each primer and 1 μL of dH_2O using an Eppendorf Mastercycler® thermocycler. The temperatures for PCR amplification consisted of an initial activation step of 95 °C during 15 min, followed by 35 cycles of denaturing at 95 °C for 1 min, annealing at primer-specific temperatures (41.7 °C for Mm01 and Mm07, 45.8 °C for Mm05 and Mm12 and 51.1 °C for Mm19 and Mm31) for 1.5 min, and extension at 72 °C for 1 min. After cycling, there was a final elongation step at 72 °C for 5 min.

Multiplex PCR products (2 μL), 8 μL Hi-Di Formamide, and 0.3 μL GeneScan-500 LIZ (Applied Biosystems) size standard were mixed and placed at 95 °C for 5 min to denature DNA and then analyzed by capillary electrophoresis using an ABI Prism 3100-Avant® (Applied Biosystems, Hitachi, Japan) automated sequencer. We used Peak Scanner™ version 1.0 (Applied Biosystems) to perform fragment analysis and final sizing. Microsatellite data were revised and formatted with the software Excel Microsatellite Tool (Park, 2001). We used Micro-Checker ver. 2.2.3 to identify the presence of null alleles at each locus per population (Van Oosterhout et al., 2004).

Table 1
Location of collection sites of *Mikania micrantha*.

Population		State	Region	Latitude	Longitude	Altitude (m)	Sample size
NPA	Nuevo Padilla	Tamaulipas	Atlantic	24°05′15″N	98°52′17″W	153	6
ABA	Abasolo	Tamaulipas	Atlantic	24°03′07″N	98°22′34″W	60	15
TAM	Tampico	Tamaulipas	Atlantic	22°14′25″N	97°53′26″W	5	15
TUX	Tuxpan	Veracruz	Atlantic	20°56′44″N	97°20′31″W	8	24
ACT	Actopan	Veracruz	Atlantic	19°35′31″N	96°22′55″W	44	6
PAR	Parácuaro	Michoacán	Pacific	19°08′26″N	102°13′56″W	553	14
HUI	Huimanguillo	Tabasco	Atlantic	17°47′58″N	93°23′55″W	39	5
COY	Coyuquilla Norte	Guerrero	Pacific	17°22′48″N	101°03′08″W	209	10
WJA	Welib-Já	Chiapas	Atlantic	17°22′27″N	91°47′58″W	234	13
EPA	El Paraíso	Guerrero	Pacific	17°21′05″N	100°12′43″W	1761	15
SMC	San Miguel Chimalapa	Oaxaca	Pacific	16°42′45″N	94°44′53″W	1276	9
DCA	Dos Caminos	Oaxaca	Pacific	16°22′14″N	97°48′26″W	311	13
SAG	San Agustín	Oaxaca	Pacific	15°42′01″N	96°15′43″W	49	14

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