



Original Articles

Patterns of herbivory and leaf morphology in two Mexican hybrid oak complexes: Importance of fluctuating asymmetry as indicator of environmental stress in hybrid plants

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ABSTRACT

Interspecific hybridization is a prevalent process in plant species that may have different ecological and evolutionary consequences. Interactions with herbivorous insects may be altered because of hybridization among host plants. These changes result from the morphological, physiological and chemical traits expressed in hybrid individuals. Therefore, it is of interest to document the changes in traits such as leaf morphology and their consequences on patterns of herbivory by insects in hybrid complexes of plants. Another useful indicator that may serve to evaluate developmental instability resulting from genetic or environmental stress in hybrid plants is fluctuating asymmetry. In this study, we used two previously genetically characterized complexes of hybridizing Mexican oaks as models to compare and understand the relationships between leaf morphology, fluctuating asymmetry and herbivory levels in parental and hybrid individuals. Results indicated that in the *Quercus affinis* × *Q. laurina* complex, hybrid individuals show a distinct morphology in relation to the parental species, while in the *Q. magnoliifolia* × *Q. resinosa* complex, hybrids were similar to *Q. resinosa*. In both hybrid complexes, our results show that hybrid individuals have higher levels of fluctuating asymmetry and herbivory levels, which may reflect higher levels of genetic or environmental stress in comparison to the parental species. These results might help explain why oak species usually remain distinct despite the high frequency of hybridization characteristic of the genus.

1. Introduction

Fluctuating asymmetry (FA) describes random morphological differences between the two sides of a bilateral character in organisms, and it is considered a good indicator of developmental instability caused by genetic and environmental stress (e. g., Palmer and Strobeck, 1986; Møller and Shykoff, 1999; Cornelissen and Stiling, 2005; Cuevas-Reyes et al., 2011b). These morphological changes in plants (Palmer and Strobeck, 2003; Cornelissen and Stiling, 2010; Cuevas-Reyes et al., 2011a) can be caused by abiotic factors such as pollution (Zvereva et al., 1997; Cornelissen et al., 2003), nutrient or water stress (Freeman et al., 2004), and biotic factors as hybridization (Albarrán-Lara et al.,

2010) and the incidence of pathogens and herbivores (Zvereva et al., 1997).

Because the degree of FA reflects the inability of individuals to maintain homeostasis during development under stressful conditions (Møller and Swaddle, 1997), high levels of FA are usually correlated with low performance (i.e., growth, survival and fecundity) (Díaz et al., 2004; Møller, 1999; but see Clarke 1998). In this way, plants with high levels of FA could also be more susceptible to herbivores (e.g., Lempa et al., 2000; Cornelissen and Stiling, 2005; Cuevas-Reyes et al., 2011a), because of underlying differences in leaf nutritional quality and chemical defenses (Cornelissen and Stiling, 2005, 2011). However, other authors have proposed that herbivory can directly act as a plant

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stressor, modifying the patterns of leaf symmetry and increasing FA levels (Díaz et al., 2004; Santos et al., 2013; Alves-Silva and Del-Claro, 2016).

Fluctuating asymmetry may also increase as a result of hybridization because of the disruption of coadapted gene combinations (Leary and Allendorf, 1989). Natural hybridization is an important process in plant evolution that results in new genetic combinations by the introduction of semicompatible genes into another genome as consequence of interbreeding between two or more different species, which can produce fertile or infertile individuals called hybrids (Rieseberg, 1997; Martinsen et al., 2001). It has been proposed that insect herbivory on hybrid plants can potentially affect plant evolution modifying gene flow between hybrids (Pearse and Baty, 2012). In turn, other studies suggest that herbivore communities and herbivory levels can be affected by high genetic variation of hybrid plants that show a mosaic of phenotypic traits in comparison with their parental species (Rieseberg and Ellstrand, 1993; Arnold, 1997; Whitham et al., 2003; Floate et al., 2016). Therefore, differences in genetic, morphological and chemical traits among parental species and hybrids can influence insect herbivore communities, insect incidence and herbivory patterns in the hybrid plant complex (Driebe and Whitham, 2000; Cattell and Stiling, 2004; Bangert et al., 2006).

Despite the high frequency of hybridization among *Quercus* species (González-Rodríguez et al., 2004; Tovar-Sánchez and Oyama, 2004; Pérez-López et al., 2016; Ramos-Ortiz et al., 2016) these usually remain distinct, suggesting that selection may act to decrease the number of hybrids that survive to reproduction (Howard et al., 1997; William et al., 2001). Because higher levels of herbivory on hybrids have been reported in many plant systems (Strauss, 1994; Whitham et al., 1999), herbivory may select against hybrid genotypes to maintain species integrity. However, several studies in sympatric oaks species indicated high levels of hybridization with viable and fertile offspring (Dodd and Afzal-Rafi, 2004; Hipp and Weber, 2008). A longer-term observation of the success of hybrids considering environmental filters as well as their interactions with natural enemies, such as herbivores, is crucial. Hence, to understand the ecology and evolution of hybrid complexes it is necessary to consider the negative effects of herbivory on plant growth and fitness (Maldonado-López et al., 2015) and, therefore their plant stressors.

The formation of hybrid zones between *Quercus* species in Mexico is very common (González-Rodríguez et al., 2004; Tovar-Sánchez and Oyama, 2004; Albarrán-Lara et al., 2010; Pérez-López et al., 2016; Ramos-Ortiz et al., 2016). Depending on the introgression levels, hybrids may present a continuum of leaf shapes (Whitham, 1989); hence we postulate that it would also lead to different levels of FA on such areas. Therefore, hybrid oak complexes represent an ideal system to understand the relationship between plant-herbivore interactions and FA. In our study, we determined the patterns of herbivory, leaf morphology and fluctuating asymmetry in two previously genetically characterized hybrid oak complexes (*Quercus affinis* × *Quercus laurina*, and *Quercus magnoliifolia* × *Q. resinosa*) that occur in different regions of Mexico. We addressed the following questions: (1) Does leaf morphology differ between parental and hybrid plants in each hybrid complex? (2) Are hybrid plants more susceptible to herbivory in both hybrid complexes, and (3) Is leaf FA associated with the levels of herbivory?

2. Materials and methods

2.1. Study system

This study was conducted in different regions of Mexico where the two hybrid oak complexes are located. Both regions are characterized for the presence of deciduous or brevideciduous oak species that occur in seasonal temperate forests (Hernández-Calderón et al., 2013; Pérez-López et al., 2016; Ramos-Ortiz et al., 2016). For both hybrid

complexes, individuals analyzed here were the same used in previous genetic characterizations of the hybrid zone structure (Pérez-López et al., 2016; Ramos-Ortiz et al., 2016). The first hybrid complex is formed by the red oaks *Quercus affinis* × *Quercus laurina*. *Quercus affinis* Scheidweiler occurs along the Sierra Madre Oriental and is distributed along an altitudinal gradient from about 1600 to 2800 m (González-Rodríguez et al., 2004). This tree can reach 30 m in height, and its leaves are oblong lanceolate, 4.5–9 cm long, 1.5–2 cm wide, smooth on both sides, with toothed margin from the mid region to the apex (Rzedowski, 1978). *Quercus laurina* Humboldt et Bonpland is distributed along the Sierra Madre del Sur and in the Trans-Mexican Volcanic Belt. It is a tree growing up to 25 m with deciduous leaves, broadly lanceolate or oblanceolate, 7–10 cm long, 2.5–3 cm wide, smooth and shiny on the adaxial surface, undersides with woolly pubescence (Rzedowski, 1978). The hybrid zone between these two species is located in the eastern portion of the Trans-Mexican Volcanic Belt and northern Oaxaca (González-Rodríguez et al., 2004; Ramos-Ortiz et al., 2016).

The second hybrid complex is composed by the white oaks *Quercus magnoliifolia* × *Q. resinosa* and is located at the Tequila volcano, Jalisco state, Mexico (20°50' N, 103°5' W). At this site, both plant species are distributed along an altitudinal gradient from about 1400 to 2100 m. *Quercus magnoliifolia* Née occurs between 1400 and 1800 m. It is a tree, growing up 25 m, with obovate leaves from 7.5 to 23 cm long and 3.5 to 13 cm wide. The adaxial surface is lustrous and almost glabrous, tomentose on the abaxial surface and with glabrescent petioles (Arizaga et al., 2009). *Quercus resinosa* Liebm occurs from 1700 to 2100 m. This tree can grow up to 20 m in height, it has large leaves 15–25 cm long and 5–16 cm wide. The leaves are obovate, rugose on the adaxial surface and pale-green or yellowish, tomentose on the abaxial surface and with densely tomentose petioles (Arizaga et al., 2009). The hybridization zone between the two species is located between 1600 and 1800 m at the Tequila volcano (Albarrán-Lara et al., 2010; Pérez-López et al., 2016).

Herbivorous insect species attacking the plant species studied here have not been previously documented in the literature. However, during the study, we observed at least nine free-feeders insect species of different families such as Lepidoptera (Geometridae), Orthoptera (Acrididae) and Coleoptera (Chrysomelidae) responsible for most of the apparent damage in the *Q. affinis* × *Q. laurina* hybrid complex. In the case of the *Q. resinosa* × *Q. magnoliifolia* hybrid complex, we detected the presence of some free-feeders species of Lepidoptera (Geometridae, Noctuidae, Pyralidae, Phalonidae, Gelechiidae, Lymantridae, Thyridiidae, Limacodidae, Arctiidae), Coleoptera (Chrysomelidae), Hymenoptera (Formicidae, Pergidae) and Orthoptera (Gryllidae).

2.2. Sample collection

The studied individuals of the *Quercus affinis* × *Quercus laurina* complex were the same analyzed genetically by Ramos-Ortiz et al. (2016) in seven different localities: Tizapán, Hidalgo state (20.62° N, 98.6° W); Zacatlán, Puebla state (19.9° N, 97.95° W); Tonayán, Veracruz state (19.72° N, 96.9° W); Zoquitlán, Puebla state (18.28° N, 97.08° W); Pápalo, Oaxaca state (17.85° N, 96.8° W); Lachao, Oaxaca state (16.22° N, 97.13° W) and Suchixtepec, Oaxaca state (16.06° N, 96.48° W). In each population, 15 trees were studied. After the previous genetic analysis, individuals in the Tizapán and Zacatlán populations were assigned as *Q. affinis* except for one and two individuals, respectively, that were assigned as hybrids. In Tonayán population there were six *Q. affinis* individuals, four *Q. laurina* individuals and five hybrids, while in population Zoquitlán there were 12 *Q. laurina* individuals and three hybrids. In the three southernmost populations all individuals were assigned as *Q. laurina* (see Ramos-Ortiz et al., 2016 for more details).

In the second oak hybrid complex, from the individuals analyzed genetically by Pérez-López et al. (2016), we randomly selected a set of 30 trees at each of three different altitudes, 1400–1500, 1600–1800 and

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