Chapter 15

Genetic and Ecological Characterization of the Invasive Wetland Grasses *Arundo donax* and *Phragmites australis* in the Cuatro Ciénegas Basin

Ricardo Colin and Luis E. Eguiarte

Abstract *Arundo donax* and *Phragmites australis* are two of the most aggressive invasive grasses worldwide, both are associated with wetlands and can be very abundant, becoming dominant in these ecosystems. These two species are common in northern Mexico. Genetic and ecological characterization of *A. donax* in two populations from the state of Coahuila (North of Mexico) indicate that they are less clonal and more variable, as well as with a higher genetic diversity compared to populations in other parts of the world and suggest that their genotypes are adapted to different environmental conditions and may represent independent introductions. On the other hand, genealogical analyses show that two independent lineages of *P. australis* are present in Mexico, the Gulf Coast subspecies, *P. australis* ssp. *berlandieri*, found across Mexico, including the state of Coahuila, and the endemic native subspecies, *P. australis* ssp. *americanus*, found in a population from Cuatro Ciénegas Basin (CCB) (Coahuila, Mexico). Here, we conduct a review of the genetic and ecological characteristics of both species in the Chihuahuan Desert, mainly focusing in CCB. The aim is to provide a better understanding in the evolutionary ecology of these two closely related and ecologically similar species and determine if these species of grasses represent a risk for the ecosystem and the valley's biota.

Keywords Asexual propagation · Chloroplast haplotypes · Clonal diversity
Invasive species · ISSRs

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The Biology of Invasive Plants

The classification of plants as either native or introduced is a fundamental biological distinction, as it determines virtually all aspects of how the organisms are treated in scientific and applied contexts. For example, in ecological studies, native species are treated as vital participants in natural services and processes, whereas ecological studies of invasive plants focus on their harmful effects (D'Antonio and Vitousek 1992; Kolar and Lodge 2001; Sakai et al. 2001; Lambrinos 2004; Mack et al. 2000, and references therein). If the species is considered native, then extraction efforts will inevitably require management with a view toward conservation. On the other hand, if it is known to be invasive, then intensive use and even eradication are usually viewed as permissible and even desirable (Rejmánek 2000; D'Antonio and Meyerson 2002; Vilà et al. 2011; Simberloff et al. 2013; Blackburn et al. 2014; Latombe et al. 2016, and references therein).

It is well known that the genetic characteristics of populations will determine their capacity of establishment and range expansion (Mooney and Cleland 2001; Sakai et al. 2001; Lee 2002; Allendorf and Lundquist 2003; Dlugosch and Parker 2008; Suarez and Tsutsui 2008). Since species can evolve during their initial establishment and during their range expansion (Sakai et al. 2001), knowledge of the levels of diversity and of the genetic structure in the native and introduced range can help us to better understand the underlying demographic processes and the adaptive evolution that lead to the invasion (Mooney and Cleland 2001; Sakai et al. 2001; Lee 2002; Allendorf and Lundquist 2003; McCauley et al. 2003; Trewick et al. 2004; Kang et al. 2007; Prentis et al. 2008). That is, the genetic reshuffle at founding will determine the outcome and future impact for non-native populations (Mooney and Cleland 2001; Lee 2002; Novak and Mack 2005; Prentis et al. 2008).

Molecular markers (genetic data from the nuclear and organellar genomes) are critical to identify and study invasive species, pinpointing areas of origin of invaders, distinguishing among species in groups that are difficult to differentiate morphologically (i.e., identification of cryptic species), understanding types and distance of migration, tracking dispersal and spread, determining whether or not hybridization is occurring, and detecting introgression (Hufbauer 2004; Booth et al. 2007; Ward et al. 2008), which are crucial aspects of the basic biology of invaders that we need to know to develop an appropriate management and control strategy of these species.

Among the great diversity of flowering plants, grasses constitute a major group of invasive plants and their negative impact (e.g., they can dramatically alter native plant community structure and ecosystem processes such as fire frequency, nutrient cycling, and water circulation) has long been under great scrutiny by ecologists and conservation scientists (D'Antonio and Vitousek 1992; Strauss et al. 2006).

The Protected Area of Cuatro Ciénegas and Two Potentially Invasive Grasses

Protected natural areas constitute a valuable instrument of environmental policy to safeguard biological richness and to carry out actions for the preservation of biodiversity (SEMARNAP 1997; INE 1999; CONANP 2018). In Mexico there are 182 protected natural areas that are subject to special protection, conservation, restoration, and development regimes (CONANP 2016). However, the management of wild habitats depends almost entirely on whether dominant species are regarded as important native keystones to be protected or harmful exotics to be eradicated (Dudley and Collins 1995; SEMARNAP 1997; INE 1999; Mack et al. 2000; D'Antonio and Meyerson 2002; Hendrickson and McGaugh 2005; Vilà et al. 2011; Simberloff et al. 2013; CONABIO 2018; CONANP 2018). Despite the importance of the native versus naturalized distinction for science and applied situations, the status of many species remains ambiguous, even for some species that dominate vast areas of habitat.

The Cuatro Ciénegas Basin (CCB) (Coahuila, Mexico) is considered the most important wetland in the Chihuahuan Desert, and one of the most important wetlands in Mexico (INE 1999). At the international level, it is classified as a RAMSAR site and is considered a priority wetland for the world (INE 1999), an area of protection of flora and fauna under Mexican government, and a priority site for Conservation of Nature by the World Wildlife Fund for Nature and UNESCO (INE 1999; Souza et al. 2012). CCB is a remarkable area, having the highest endemism than any other place in North America (Stein et al. 2000), and much of the valley's biota is classified either as endangered, threatened, or in special protection status by the Mexican government and the Convention on International Trade of Endangered Species (CITES) (Minckley 1992; INE 1999; Souza et al. 2004; Souza et al. 2006; Instituto Nacional de Ecología y Cambio Climático 2016). Current threats to its biodiversity include water exploitation, species invasions, industrial development, rapidly increasing tourism and population growth. Therefore, actions have been implemented to promote the conservation of terrestrial and aquatic ecosystems in the region. One of these actions is the control and eradication of invasive species (INE 1999; Souza et al. 2004; Hendrickson and McGaugh 2005; Instituto Nacional de Ecología y Cambio Climático 2016).

The giant reed, *Arundo donax* and the common reed, *Phragmites australis* are considered two of the most aggressive invasive grasses worldwide and the negative ecological impact of these species is well known (Perdue 1958; Dudley and Collins 1995; Bell 1997; Dudley 2000; Saltonstall 2002; Saltonstall and Hauber 2007; Saltonstall and Stevenson 2007; Lambert et al. 2010; Meyerson et al. 2010). These two species of grasses are associated with wetlands and can be very abundant and become dominant in these ecosystems. Both species are common in northern Mexico; however, the more ecological approach has left out many of the genetic or evolutionary aspects of their introduction in the region.

In this chapter we carry out a review of the genetic and ecological characteristics of *A. donax* and *P. australis* in general and in particular for the ecological region of the Chihuahuan Desert, with special focus in the CCB. The aim is to provide a better understanding of the evolutionary ecology of these two related and ecologically similar species, and determine if these grass species represent a risk for the ecosystem and the valley's biotic diversity.

The Complex Case of the Invasive *Arundo donax*

Systematics and distribution of *Arundo donax*. *Arundo* L. (Poaceae, tribe Arundineae) is a cosmopolitan genus that includes three to five taxa distributed from tropical Asia to the Mediterranean Basin (Conert 1961; Bell 1997; Grass Phylogeny Working Group 2001; Danin 2004). The species *Arundo donax* (Fig. 15.1 a, b, and c) is the largest species in the genus and is one of the tallest herbaceous grasses (up to 10 m tall). Since giant reed has been cultivated in Asia, southern Europe, North Africa, and the Middle East for thousands of years (Perdue 1958; Zohary 1962; Bell 1997), the native range is a matter of speculations because the biogeographic and evolutionary origin of this species has been obscured through

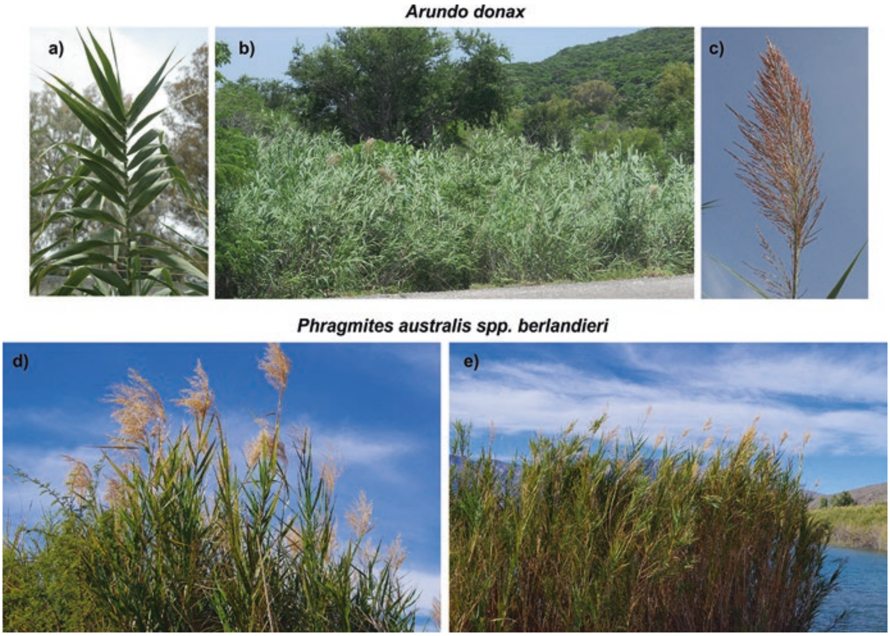

Fig. 15.1 Pictures showing inflorescences, stems, and stands of *Arundo donax* (a-c) and *Phragmites australis* (d and e). Photographs of *Arundo* by Ricardo Colin and photographs of *Phragmites* by Luis E. Eguiarte

ancient and widespread cultivation, and has been variously reported as southern Asian (Bell 1997; Dudley 2000), eastern Asian (Polunin and Huxley 1987), and from countries surrounding the Mediterranean Sea, where it occurs along the other *Arundo* species, *A. plinii* Turra, *A. collina* Tenore and *A. mediterranea* Danin (Perdue 1958). Nevertheless, a more recent study has provided evidence that *A. donax* likely originated in Asia and subsequently spread into the Mediterranean region (Mariani et al. 2010). The ancient spread of *A. donax* has been accounted mainly due to its multiple uses, including the making of baskets, mats, fishing rods, walking-sticks, fences, roof thatching, plant stakes, musical instruments such as the reeds for clarinets and saxophones, shading or as ornamental, and more recently for erosion control, paper, pulp, and rayon (viscose) (Perdue 1958; Zohary 1962). Therefore, it has become widely dispersed by humans and it is currently found growing into all of the tropical-subtropical and warm-temperate areas of the world (Dudley 2000; Lewandowski et al. 2003; Khudamrongsawat et al. 2004; Ahmad et al. 2008; Mariani et al. 2010; Tarin et al. 2013).

In the USA, giant reed is believed to have been initially introduced into southern California from the Mediterranean in the early 1800s for erosion control, with later introductions being made in Texas and Florida as late as the 1940s (Bell 1997; Perdue 1958). It was also used for roof thatching and widely cultivated for the production of reeds for musical instruments (Perdue 1958; Bell 1997). Since its introduction, *A. donax* has escaped cultivation and become a major invasive weed of riparian habitats, such as in Southern California, Florida, and along the Rio Grande in the border between Texas and Mexico (Bell 1997; Dudley and Collins 1995; Dudley 2000), where it not only displaces native species but also dramatically modifies ecological and successional processes (Bell 1997; Dudley 2000).

In Mexico, *A. donax* (Fig. 15.1 a, b, and c) is a common introduced species, growing in a variety of climates and habitats, including disturbed marshes, wetlands, rivers, lakes, riparian zones, and along roads. In the CCB, *A. donax* has been recently identified and efforts to document its invasion began in 2004 (Hendrickson and McGaugh 2005). Although it is not clear when *Arundo* arrived to the area, at present it has been documented to occur in a variety of mostly small to relatively large stands widely scattered throughout the CCB and surrounding areas (Fig. 15.2) (Hendrickson and McGaugh 2005). Nowadays, *Arundo* is regarded as one of the major threats to native riparian and aquatic ecosystems in the CCB (Hendrickson and McGaugh 2005; CONABIO 2018), and control measures have been implemented in the valley, including control using chemical herbicides, cutting and removing biomass, as well as prescribed fire (Hendrickson and McGaugh 2005; Contreras-Arquieta and Cruz-Nieto 2007).

Genetic characterization. In Mexico, Colin et al. (unpublished) used Inter Simple Sequence Repeats (ISSRs) to estimate the current geographic distribution of genetic diversity of *A. donax* in 20 natural populations across different geographic regions, and found a total of 77 different genotypes (clones) along the Mexican territory evidencing that all the Mexican populations are multiclonal (including from 3 to 9 different genotypes). In the case of northern Mexico, they analyzed 60 individuals from two populations of the state of Coahuila (CCB, $N = 32$ and Valle Cruya,

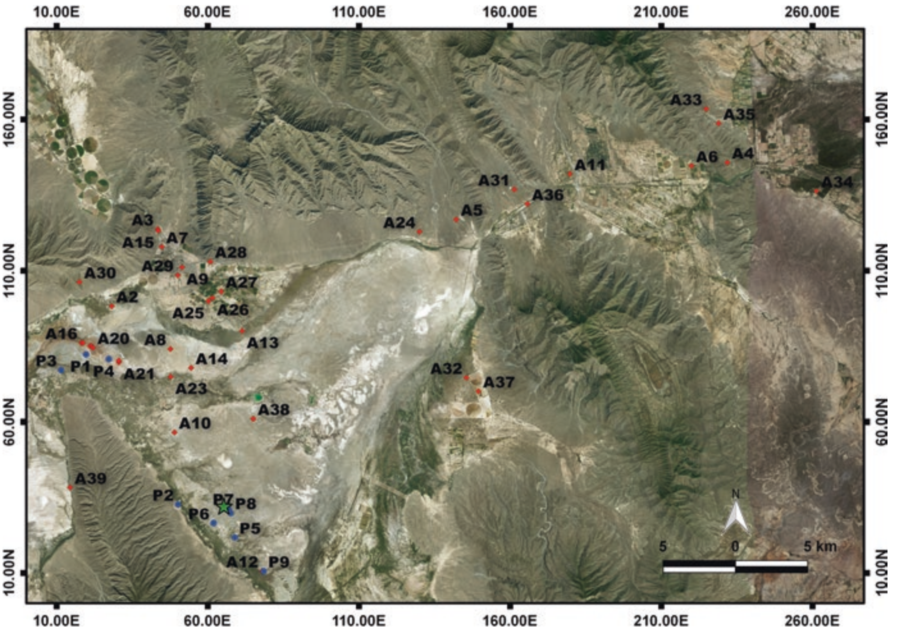

Fig. 15.2 Known localities of *Arundo donax* and *Phragmites australis* stands. Diamonds in red indicate *Arundo* locations in the CCB and surrounding areas. Circles in blue show the *Phragmites australis* ssp. *berlandieri* localities and the green stars indicate the locations of *Phragmites australis* ssp. *americanus*

N = 28), detecting 13 unique genotypes not found in any other populations (five and eight genotypes in the CCB and Valle Cruya, respectively; Fig. 15.3). In addition, they found high values of clonal diversity (Table 15.1), as suggested by the proportion of distinguishable genotypes (G/N, where G= unique genotypes, and N= number of analyzed individuals (Ellstrand and Roose 1987)). We can conclude that Mexican populations are less clonal and genetically more variable than many populations in other parts of the world (Table 15.1).

Reproduction. *Arundo donax* has been observed flowering annually between August and October, and although it produces abundant flowers, viable seeds have not been observed in most areas where it has been introduced (Perdue 1958), including North America, Europe, and Australia (Dudley 2000; Di Tomaso and Healey 2003; Lewandowski et al. 2003; Williams et al. 2008). Thus, asexual propagation through stem layering and rhizome proliferation is believed to be the primary mode of reproduction (Dudley 2000; Boland 2006; Johnson et al. 2006; Williams et al. 2008; Mariani et al. 2010; Haddadchi et al. 2013; Lewandowski et al. 2003).

In Mexico, genetic analyses of random mating by evaluating linkage disequilibrium among loci showed evidence of linkage disequilibrium for the population of CCB, suggesting an asexual mode of propagation (Colin et al. unpublished), in accordance to findings in previous studies (Khudamrongsawat et al. 2004; Ahmad et al. 2008; Mariani et al. 2010; Haddadchi et al. 2013). In contrast, no evidence of

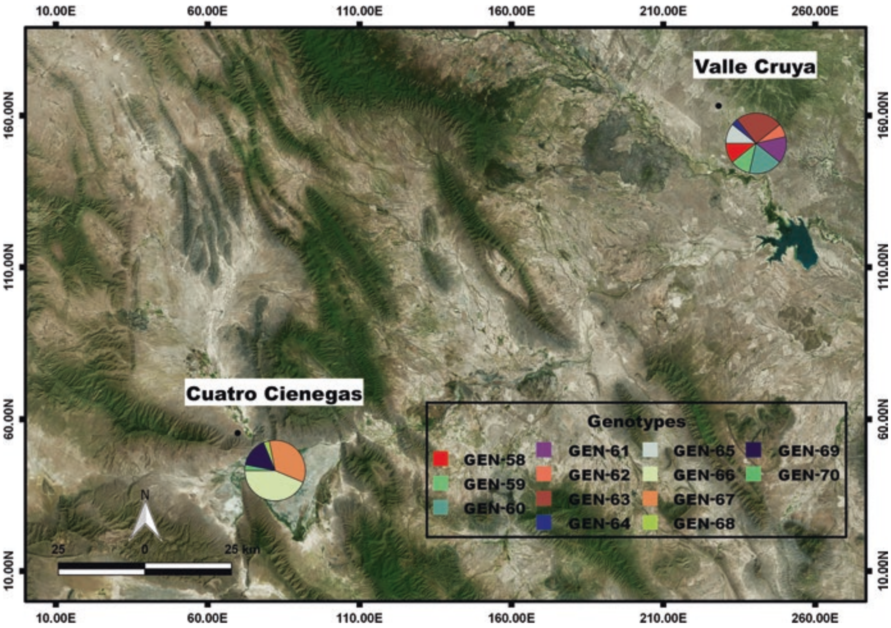

Fig. 15.3 Populations of *Arundo donax* depicting the frequency of genotypes found in northern Mexico. Data were obtained from Colin et al. (unpublished). Colors indicate different genotypes

linkage disequilibrium among loci was found in Valle Cruya, being consistent with (at least partially) sexual recombination (Colin et al. unpublished). Although the frequency at which rare sexual reproductive events may occur in *A. donax* remains unclear, viable seeds (Perdue 1958) have been reported in Asian populations (Afghanistan, South Western Pakistan, and Iran), and more recently, Johnson et al. (2006) found a low frequency of ovules that may have been viable in florets collected in the USA (California, Nevada, Colorado, New Mexico, Texas, Georgia, and Washington D. C.), as well as in northern Mexico, particularly in the state of Nuevo Leon. Thus, the evidence for sexual reproduction that was detected in Valle Cruya is not surprising, but it should be taken with caution (Colin et al. unpublished), since there is no knowledge about the biological reproduction in the Mexican *A. donax* populations.

Eventually, it will be important to conduct studies on the fruit production, seed set rates, viability, and germination of seeds as well as on their ability to spread in the different Mexican populations of *A. donax*. These analyses of reproductive biology along with molecular markers should allow us to better disentangle the roles of seed and asexual propagation, and to understand the importance of the reproductive systems in governing the organization and levels of genetic diversity within the species.

Genetic structure and genetic relationships. It is important to describe the genetic differentiation (also called genetic structure) of populations because it

Table 15.1 Genetic diversity in northern Mexican populations and other regions for *Arundo donax*

Country	Genetic markers	N	G	G/N	References
United States	Isozyme	87	8	0.092	Khudamrongsawat et al. (2004)
United States	RAPD	87	40	0.460	Khudamrongsawat et al. (2004)
United States	SRAP	185	2	0.011	Ahmad et al. (2008)
United States	TE-based	185	3	0.016	Ahmad et al. (2008)
Southern France	SRAP	20	1	0.050	Ahmad et al. (2008)
Southern France	TE-based	20	1	0.050	Ahmad et al. (2008)
Italy	ISSRs	12	1	0.083	Mariani et al. (2010)
Mediterranean Basin	AFLP	16	1	0.062	Hardion et al. (2012)
Australia	ISSRs	58	38	0.655	Haddadchi et al. (2013)
New World[a]	microsatellites	159	6	0.038	Tarin et al. (2013)
Old World[b]	microsatellites	203	129	0.635	Tarin et al. (2013)
Italy	microsatellites	86	8	0.093	Pilu et al. (2014)
Mexico					
Cuatro Ciénegas, CCB	ISSRs	32	5	0.156	Colin et al. (unpublished)
Valle Cruya	ISSRs	28	8	0.285	Colin et al. (unpublished)
North Region[c]	ISSRs	60	13	0.216	Colin et al. (unpublished)

[a] List of the countries sampled and number of analyzed plants in New World: Texas/ Rio Grande Basin = 105, Southeast U.S = 12, California/Nevada = 8, Mexico = 29, Argentina = 5 (Tarin et al. 2013). [b]List of the countries sampled in Old World and number of analyzed plants: Spain = 132, Turkey = 6, Israel = 3, Greece = 6, Italy = 24, Portugal = 11, Morocco = 3, France = 6, Algeria = 12 (Tarin et al. 2013). [c]North region is constituted by the Cuatro Ciénegas (CCB) and Valle Cruya populations (Colin et al. unpublished).

N = Sample size, *G*= Number of detected genotypes, *G/N* = Proportion of distinguishable genotypes (Ellstrand and Roose 1987)

reflects the biological processes of the past that modeled the evolution of the species (Templeton 2006; Pleines et al. 2009; Zhao et al. 2013). In addition, analyzing how variation is partitioned within and between populations in introduced species is critical to understand their potential to establish and spread in a novel range (Sakai et al. 2001; Facon et al. 2006; Marrs et al. 2008).

Genetic structure analyses of *A. donax* in Mexico, carried out by means of several methods (i.e., principal coordinate analysis, agglomerative hierarchical clustering analysis, and AMOVA), suggest the existence of four genetic groups showing a clear genetic differentiation (coancestry coefficient $\theta = 0.830$), and low levels of gene flow between clusters (Colin et al. unpublished). In the particular case of the populations from the state of Coahuila, the analysis indicates that the Valle Cruya population is more similar to populations near the coasts of the Pacific and of the Gulf of Mexico, while all the plants from CCB remained separated, forming a distinct group (Colin et al. unpublished). In addition, these authors also identify that these two populations are genetically very different, as they do not share genotypes between them (Fig. 15.3) (Colin et al. unpublished).

Ecological and genetic characterizations. To evaluate the role of environmental conditions and to detect climate differences and/or similarities between the two populations located in the state of Coahuila, a canonical correspondence analysis was carried out using the genotype distribution data and the environmental variables (Hijmans et al. 2005) (Colin et al. unpublished). The ecological characterization indicates that the distribution and abundance of genotypes are influenced by environmental factors. Temperature seasonality appeared as the strongest environmental variable correlated with the North region, and it is directly associated with genotypes distributed in the area, suggesting that the Northern genotypes are adapted to stronger seasonality with scarce rainfall.

On the other hand, the comparisons in the global distribution of the species indicate that the Valle Cruya population is associated with the bioclimatic space occupied by the invasive occurrence records from the USA and some areas from Europe, while the population of Cuatro Ciénegas was more similar to the environmental space occupied by native records from Asia and some areas from Australia and Africa (Colin et al. unpublished).

General observations and perspectives on *Arundo donax*. The apparently obligate asexual propagation of *A. donax* in introduced ranges of Mediterranean region, Europe, and the USA may keep their genetic diversity low (Ahmad et al. 2008). On the other hand, in the case of Mexican *A. donax* populations, the higher genetic diversity could be likely maintained by different modes of dispersal (i.e., asexual propagation by means of broken stems or rhizome fragments, and some levels of sexual reproduction), suggesting that the frequency at which rare sexual reproductive events may occur in *A. donax* may be variable among populations (Colin et al. unpublished).

Another alternative to sexual reproduction that can explain the level of variation observed in *A. donax* could be multiple introductions from different source regions, as suggested by Khudamrongsawat et al. (2004) and evidenced by Tarin et al. (2013) in the USA. Somatic mutations could also be contributing to the genetic variation in *A. donax* (Khudamrongsawat et al. 2004) and to determine the importance of this type of mutations on the genetic variation found in the Mexican populations of *Arundo*, it would be necessary to compare the genetic composition of plants with known rhizome connections (Khudamrongsawat et al. 2004; Haddadchi et al. 2013).

However, the differences in the values in a given geographic area may be simply due to different sampling schemes and the use of different genetic markers (Mohammadi and Prasanna 2003; Zhao et al. 2006). It will be important to use a standardized method to study the species worldwide (Colin et al. unpublished). It is also important to include in the future large samples from more areas in Asia, where the species apparently originated (Mariani et al. 2010) and that have been poorly studied.

As mentioned above, multiple introductions or a single introduction of multiple genotypes from diverse source populations can result in enhanced genetic diversity in the introduced range (e.g., Simberloff 2009; Lavergne and Molofsky 2007; Kelager et al. 2013), and this may result in the development of locally adapted genotypes (or ecotypes) through natural selection (Sexton et al. 2002; Lavergne and Molofsky 2007; Prentis et al. 2008). In relation to this, the ecological characterization of genotypes of *A. donax* in the North region of Mexico suggests that the genotypes in these populations are influenced by fluctuations in temperature and altitude ranges (Colin et al. unpublished), and point out that *A. donax* may have been introduced different times from disjunct regions (perhaps from the USA and Asia).

The use of genetic data to reconstruct invasion histories, and reveal how a non-native plant adapts and expands into new territory, can also lead to more effective management strategies (Sakai et al. 2001; Allendorf and Lundquist 2003; Prentis et al. 2008). That is, populations having high genetic variation may be more difficult to control because of naturally variable genotypes within the introduced population or the possibility of newly emerged resistant plants, as a result of ongoing natural selection (Sexton et al. 2002; Sterling et al. 2004; Prentis et al. 2008).

In recent years efforts have been made to identify specific phytophagous insects in giant reed as biocontrol agents in the USA (Goolsby and Moran 2009; Goolsby et al. 2009; Goolsby et al. 2013; Goolsby et al. 2015). However, the high regional differentiation of giant reed in Mexico and the multiple genotypes detected in the North region of Mexico imply that these diverse populations may show different levels of susceptibility or resistance to pathogen or other biocontrol agents (Burdon et al. 1981; Sexton et al. 2002; Bruckart et al. 2004**;** Sterling et al. 2004; Prentis et al. 2008**).** Therefore, the genetic diversity among populations may be sufficiently great to warrant different control strategies. Differential responses to the same management method have been observed in genetically diverse populations (Sexton et al. 2002**;** Sterling et al. 2004; Goolsby et al. 2006), so knowledge of existing genetic diversity in the populations provides further insight into the responses of populations to specific management strategies, including the use of chemical control and biocontrol programs (Burdon and Marshall 1981; Chapman et al. 2004; Gaskin et al. 2005; Ward et al. 2008).

Further research of biogeographic relationships in *A. donax* should include populations across a broader range from North America (USA and Mexico), Europe (mainly from Mediterranean basin), and Asia in order to address the question of multiple introductions. Other molecular tools, for instance, chloroplast DNA, could be used in conjunction with ISSR or microsatellite data (Tarin et al. 2013) coupled with ecological analysis to identify if there are different lineages through the global distribution and to determine the possible divergences between those lineages. Additionally, potential source populations of the invader can also be identified, and these populations may help to further locate associated natural enemies, which may be useful later as biological control agents (Ellstrand and Schierenbeck 2000; Clark et al. 2013; Kelager et al. 2013; Ndlovu et al. 2013).

Phragmites australis, an Important Native Species with Invasive Potential

Systematics and distribution of *Phragmites australis* The genus *Phragmites* Adans. (Poaceae, tribe Arundineae) has a worldwide distribution, from the Arctic regions to the tropics (Den Hartog et al. 1989). Historically a number of species, subspecies, and varieties in the genus have been described; currently four species are recognized: *P. australis* (Cav.) Trin. ex Steud., *P. karka* (Retz.) Trin. ex Steud., *P. mauritianus* Kunth and *P. japonicus* Steud (Clevering and Lissner 1999; Saltonstall et al. 2004; Lambertini et al. 2006).

Within the genus, the species *Phragmites australis* (Fig. 15.1 d and e) is the most widely distributed, as it is found in Europe, Asia, Africa, America, and even Australia (Conert 1961; Bjôrk 1967; Clevering and Lissner 1999; Saltonstall 2003a). *Phragmites australis* has been present for at least 40,000 years in southwestern United States (Hansen 1978) and chloroplast genetic data from (cpDNA) indicate that three distinct lineages are found in North America. *P. australis* ssp. *americanus* (comprising thirteen native North American haplotypes: A–H, AA, AB, AC, S, and Z) found throughout the USA and called the "Native North America" lineage (Saltonstall et al. 2004). *P. australis* ssp. *berlandieri*, with only one haplotype I, that grows in Southern United States (from Florida to California), Mexico, Central America, and Asia, named the "Gulf Coast" lineage, (Saltonstall 2002; Saltonstall and Hauber 2007; Saltonstall and Stevenson 2007); this lineage is usually not considered invasive (Meyerson et al. 2009; Meyerson et al. 2010). The third lineage is the haplotype M of *P. australis*, considered an invasive lineage that was probably introduced from Eurasia to North America since ca. 1600 and now is the most common *P. australi*s found from the south of Canada and most USA (Saltonstall 2002, 2003a, 2003b; Saltonstall et al. 2004; Saltonstall and Hauber 2007; Saltonstall and Stevenson 2007; Meyerson et al. 2010).

*Phragmite*s *australis* in Mexico (Fig. 15.1 d and e) is a common species, growing in different environments from disturbed to well-preserved, along roads rivers, marshes, wetlands, and lakes. In the CCB *P. australis* (Fig. 15.1 d and e) is a very common species, however, as in *Arundo*, it is not clear when *Phragmites* arrived to the region. Presently, it is found in different stands widely scattered throughout the CCB (Fig. 15.2), and it is considered a native species of the valley (Colin and Eguiarte 2016).

Genetic characterization. Two lineages of *Phragmites* are present along Mexico: The Gulf Coast lineage, *P. australis* subsp. *berlandieri* found across of Mexico, and the Native North America lineage *P. australis* subsp. *americanus,* found in north of Mexico, in the state of Coahuila (Colin and Eguiarte 2016).

Phragmites australis subsp. *berlandieri* has been characterized by a single cpDNA haplotype (haplotype I) and low genetic diversity in the USA, Central America, and northern South America (Saltonstall 2002, 2003a). Nevertheless, 13 new haplotypes (BH, BM- BX) were found in Mexico, strongly suggesting expansion and diversification in this country (Colin and Eguiarte 2016). From this subspecies four populations were analyzed in the CCB, (Mojarral, Vereda, Desviación, and Mezquite) for a total of 58 individuals (Colin and Eguiarte 2016). Chloroplast haplotype diversity (H_d) in these populations ranged from zero to 0.5333, and nucleotide diversity (π) among these populations ranged from zero to 0.0003 (Table 15.2).

Phragmites australis subsp. *berlandieri* populations in CCB are characterized by a lower genetic variation when compared with central and southern regions of Mexico (Table 15.2), and by the presence of two haplotypes (BH and BM). The

Table 15.2 Genetic variation of *Phragmites australis* in the Cuatro Ciénegas Basin (CCB), Central, and Southern regions of Mexico

Lineages	Population	N	H_d	π	S	h
Gulf Coast	Mojarral	14	0	0	0	1
Gulf Coast	Vereda	15	0.34286	0.00019	1	2
Gulf Coast	Desviacion	15	0.5333	0.00029	1	2
Gulf Coast	Mezquite	14	0.49451	0.00027	1	2
Native North America	Poza X	13	0.65385	0.00042	3	4
Regions						
Cuatro Ciénegas Basin CCB[a]	4	58	0.44828	0.00025	1	2
Central[b]	8	125	0.64503	0.00051	8	8
Southern[c]	14	215	0.66712	0.00051	5	9

[a] Cuatro Ciénegas Basin (CCB): 4 populations in de valley (Mojarral, Vereda, Desviacion, and Mezquite). [b]Central: 8 populations from the states of Guanajuato, Michoacan, and Jalisco. [c]Southern: 14 populations belonging to the states of Veracruz, Tabasco, Campeche, Yucatan, Quintana Roo, and Oaxaca (Colin and Eguiarte 2016)

N = sample size, H_d = haplotype diversity, π = nucleotide diversity, S = segregating sites, and h = number of haplotypes. Data were obtained from Colin and Eguiarte (2016)

Mojarral population presented only one haplotype (BH; Fig. 15.4), whereas the remaining populations had two haplotypes, with greater predominance of haplotype BM in the populations Desviación and Mezquite, while the haplotype BH was more frequent in the Vereda population (Fig. 15.4). It is interesting to mention that the haplotype I has been reported in the Texas side of the Rio Grande and even in the Cuatro Ciénegas Valley (K. Saltonstall, Smithsonian Tropical Research Institute, personal communication). Nevertheless, Colin and Eguiarte (2016) sampling did not detect this haplotype in the CCB (Fig. 15.4), and it was detected only in populations from southern and central Mexico, being more common in the southern areas.

On the other hand, *P. australis* subsp. *americanus* includes thirteen native North American cpDNA haplotypes (A–H, AA, AB, AC, S, and Z), showing high genetic diversity (Saltonstall 2002, 2003a, 2003b). In Mexico, four new haplotypes (BI–BL) were found in the Poza X population from CCB (Fig. 15.4); these haplotypes are related to the native lineage of North America, particularly to haplotype B (Saltonstall 2002, 2003a), increasing the range of *P. australis* subsp. *americanus* (Colin and Eguiarte 2016). As in the USA, this Mexican population (Poza X) showed high genetic variation compared with the populations of *P. australis* subsp. *berlandieri* (Table 15.2). The finding of these haplotypes in the CCB may be related to the high diversity and levels of endemism of the basin (Souza et al. 2012; Carson et al. 2015).

Reproduction. Previous studies in *P. australis* (Rice et al. 2000; Ishii and Kadono 2002; Saltonstall 2002, 2003a; Brisson et al. 2008; Howard et al. 2008; Fer and Hroudova 2009; Baldwin et al. 2010; Belzile et al. 2010; McCormick et al. 2010; Kirk et al. 2011) have documented both sexual and asexual (e.g., lateral rhizome extension, rhizome fragments, and tillering) propagation. Flowers are

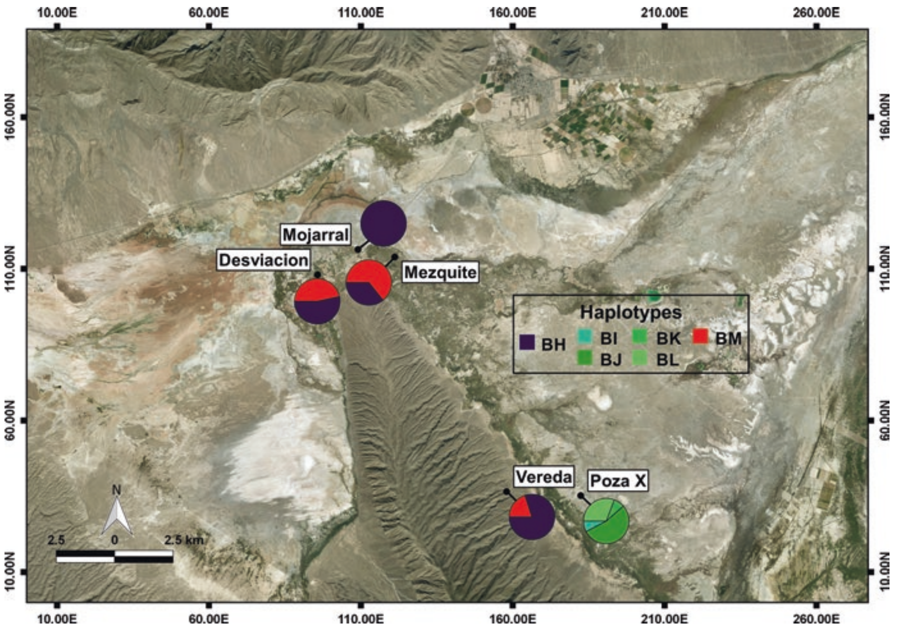

Fig. 15.4 Populations of *Phragmites australis* depicting the frequency of haplotypes found in Cuatro Ciénegas Basin (CCB). Haplotypes BH and BM (violet and red colors, respectively) belong to *Phragmites australis* ssp. *berlandieri*. Haplotypes BI, BJ, BK, and BL (green color gradient) depicting haplotypes that were more closely related to the native North American lineage *Phragmites australis* ssp. a*mericanus*. Data were obtained from Colin and Eguiarte (2016)

monoecious and wind-pollinated. Each infructescence can contain thousands of seeds, which have long silky hairs on the rachilla, facilitating wind dispersal. It was originally suggested that the species is self-incompatible (Clevering and Lissner 1999), but more recent evidence suggests that self-pollination is possible (Lambert and Casagrande 2007). In addition, environmental conditions can affect production and seed viability; seeds require high exposure to light, as well as diurnal temperature fluctuations (range 10° to 30° C) to germinate (Marks et al. 1994; Campbell 2007; Meyerson et al. 2010).

Phragmites australis subsp. *berlandieri* flowers annually from late October to November, and although it produces abundant flowers, viable seeds have not been observed in most areas from the USA, Mexico, Central America, and northern South America, and vegetative propagation through stem layering and rhizome proliferation is believed to be the primary mode of reproduction (Pellegrin and Hauber 1999; Saltonstall 2002, 2003a; Meyerson et al. 2009: Meyerson et al. 2010). Colin and Eguiarte (2016), working with populations across the species' geographical range in Mexico, found that some populations contain only a single haplotype (such as the population Mojarral; see Table 15.2 and Fig. 15.4), suggesting that in some cases the populations may derive from a single founder, and subsequently spread by asexual propagation. In contrast, in the majority of the populations—as in

Desviación, Mezquite, and Vereda in CCB (see Table 15.2 and Fig. 15.4)—different haplotypes were detected, indicating that different individuals originated these populations (Colin and Eguiarte 2016).

Phragmites australis subsp. *americanus* flowers earlier, between June and October (Meyerson et al. 2009; Meyerson et al. 2010). It propagates both by seed, mainly dispersed by wind, and by vegetative propagules likely dispersed by water and maybe by animals. However, apparently this lineage has lower seed germination rates (Meyerson et al. 2010). In Mexico, genetic diversity for this subspecies was high (see Poza X population in Table 15.2 and Fig. 15.4). Again, as in the other subspecies, this indicates either that dispersal events involved multiple founders by vegetative propagules or that dispersal by seeds is important for the establishment of new populations (Colin and Eguiarte 2016).

These findings suggest that in Mexico the genetic composition of the populations from both lineages is likely the result of different modes of spread and dispersal, including at least some sexual reproduction. However, as discussed by Colin and Eguiarte (2016), it is important to conduct future studies including aspects of the reproductive ecology, seed germination, and dispersal that shall help us to determine the importance of reproductive systems in the life history of the species. In addition, it will be relevant to use nuclear DNA (e.g., microsatellites or SNPs) to understand the roles of seed and asexual propagation and to better describe the evolutionary genetics of *P. australis* in the CCB and Mexico (Colin and Eguiarte 2016).

Genetic structure and genetic relationships. Using a representative set of samples from the Mexican range, Colin and Eguiarte (2016) investigated the genetic structure patterns within and between the introduced *P. australis* subsp. *berlandieri* populations by conducting a spatial analysis of molecular variance (SAMOVA). Colin and Eguiarte (2016) found seven genetic groups ($K= 7$) in Mexico. The CCB was characterized by the presence of two genetic groups ($K1$ and $K2$). The first cluster ($K1$) included the Mojarral and Vereda populations that were grouped together with populations belonging to the states of Michoacán, Veracruz, Tabasco, Jalisco, Campeche, Yucatán, and Quintana Roo. The second cluster ($K2$) comprises only the Desviacion and Mezquite populations.

The historical demography of these groups was inferred by examining hypotheses of demographic expansion (Colin and Eguiarte 2016). For the first cluster, $K1$ a recent range expansion was inferred and the estimate of the age of population expansion was older (ca. 0.73 Myr before the present) for $K1$. In contrast, the analysis for the $K2$ cluster suggests that these populations have maintained a constant population size (Colin and Eguiarte 2016).

Ecological and genetic characterizations. At present, there is no data available on whether or not environmental factors affect the distribution and abundance of haplotypes for both lineages in the CCB. However, the patterns of genetic diversity found across the species' geographical range in Mexico suggest that dispersal was from the South towards the North, with a reduction of genetic diversity in the process (Table 15.2) (Colin and Eguiarte 2016). This gradient of genetic diversity suggests that the Pleistocene climatic changes were relevant for the historical dynamics of *P. australis* in Mexico. In consequence, the populations in the CCB may be relatively recent, and this may also explain why the *P. australis* populations from Mexico—even in the northern areas— are so different from the populations in the USA (Colin and Eguiarte 2016).

General observations and perspectives on *P. australis*. As found by Colin and Eguiarte (2016) in the CCB we can find two independent and native lineages of *Phragmites*: *P. australis* subsp. *berlandieri* and *P. australis* subsp. *americanus*, we provided insights into the dynamic of the populations of *P. australis* subsp. *berlandieri* in the CCB, and Colin and Eguiarte (2016) also demonstrated that the invasive lineage of *P. australis* (haplotype M) is absent in the CCB.

The CCB is characterized by the presence of two (Fig. 15.4) of the thirteen haplotypes belonging to *P. australis* subsp. *berlandieri* found in Mexico, and by a low genetic variation (Table 15.2). The detection of new haplotypes in the Poza X population from *P. australis* subsp. *americanus* increased the proposed range of this lineage (Fig. 15.4) (Colin and Eguiarte 2016).

Populations in the CCB have significantly lower genetic variation when compared with populations from the central and southern Mexican regions (Colin and Eguiarte, personal observation). Genetic diversity can be reduced in expanding populations, as only a few individuals contribute with genetic variation to the newly colonized populations (Buckley et al. 2012; Hallatschek and Nelson 2008). Previous studies have shown that there is a correlation between genetic diversity and environmental heterogeneity *in P. australis* (Curn et al. 2007; Hansen et al. 2007; Engloner 2009), but whether or not climatic factors affect the distribution and abundance of haplotypes in *P. australis* subsp. *berlandieri* in Mexico has yet to be determined (Colin and Eguiarte in preparation).

The genetic structure of populations is not always reflected in the geographical proximity of individuals, and individuals with different geographical locations are not necessarily genetically differentiated (Evanno et al. 2005). Among multiple-population clustering of the Mexican population, group *K1* included different populations separated by long distances, and this cluster included the Mojarral and Vereda CCBs populations, that were grouped together with populations from Michoacán, Veracruz, Tabasco, Jalisco, Campeche, Yucatán, and Quintana Roo states. In contrast, the cluster *K2* that included Desviación and Mezquite was restricted to a small area within CCB (Colin and Eguiarte, personal observation). These results suggest that genetic clustering in *P. australis* in Mexico is best explained as a function of genetic divergence rather than of geographical distance, in contrast to what happens in the USA (Saltonstall 2003a) and, perhaps in China (An et al. 2012).

Finally, results suggest that haplotype U distributed in Australia and Asia (Saltonstall 2002, 2003a) is the closest relative to haplotypes of *P. australis* subsp. *berlandieri* found in Mexico (Colin and Eguiarte 2016); however, their history is complex. Genetically, it has been shown that the haplotype I has affinity to different geographic regions (Saltonstall 2002, 2003a; Lambertini et al. 2006) and has been reported to have a closer relationship with *Phragmites* in Asia (Saltonstall 2002, 2003a), as well as with the African species *P. mauritianus* (Lambertini et al. 2006); also morphological analyses indicate that haplotype I may correspond to *P. karka*, from tropical Africa (Saltonstall and Hauber 2007; Ward 2010). Future genetic and morphological analyses of plants from Africa and South America will be needed to understand the origin and evolution of *P. australis* in Mexico and of the *Phragmites* genus in general.

Concluding Remarks: *A. donax* Is an Aggressive Invasive Plant, But *P. australis* Is Native to CCB

Here we presented a review of the evolutionary biology and invasive potential of two related and ecologically similar grasses (*A. donax* and *P. australis*) in the Chihuahuan Desert, with special emphasis in the CCB. In general, in the state of Coahuila there are 13 genotypes of *A. donax* and two independent native lineages of *Phragmites* (*P. australis* subsp. *berlandieri* and *P. australis* subsp. *americanus*), although the invasive lineage (M) was not found. We hope that this review will shed new light on the understanding of ecological, evolutionary, and biogeographic aspects of the complex studied species and can also assist in the development of conservation, management, and policy strategies of these species in the region, and in particular in the CCB.

The genetic data available for *A. donax* and *P. australis* reflect that both sexual and asexual propagation seem to be relevant but the role of each reproductive mode varies in each species. Gaps in our knowledge are particularly apparent in the dispersal and establishment phases of the life cycle of these two species, for example rates of seed set and germination have not yet been determined in Mexico. Indeed, it will be important to conduct studies on the viability and germination of seeds as well as on their ability to spread in native and introduced environments to assess the fecundity of these species and of their different genetic lineages. At the same time, as we mentioned above, it will be relevant to use nuclear DNA (in particular microsatellites or SNPs) markers to better understand the roles of seed and asexual propagation and evaluate their importance to determine genetic diversity within and among populations.

Recent studies have shown that when species with a broad climatic and geographical range colonize or invade a new environment or spread over large geographical ranges, they may come upon suitable habitats to colonize and can establish in contrasting climatic regions, displaying environmental tolerances and physiological plasticities that promote their potential to adapt and invade these environments (Lee 2002; Sax et al. 2007; Vellend et al. 2007; Prentis et al. 2008). Thus, the novel environmental conditions found in the range of introduction may act as strong selection forces and can lead to rapid evolution (in centuries, decades, or even just in years) during the establishment and spread of invasive species (García-Ramos and Rodríguez 2002; Colautti and Lau 2015).

In *A. donax* the data shown here suggest that the genotypes distributed in the Northern region are adapted to stronger seasonality with scarce rainfall, and point out that *A. donax* may have been introduced in different occasions from disjunct regions. On the other hand, for *P. australis*, we cannot say at this time whether the haplotypes are influenced by fluctuations in temperature, rainfall, and/or altitude ranges; however, evidence suggests a post-glacial colonization or recolonization of *P. australis* in the CCB. Thus, more research is needed to evaluate whether or not the environmental factors play an important factor in the distribution of haplotypes in the region.

Besides natural selection, lack of gene flow between the native and introduced ranges can generate genetic differentiation and divergence between them and may eventually lead to allopatric speciation (García-Ramos and Rodríguez 2002; Lee 2002; Sax et al. 2007; Vellend et al. 2007; Prentis et al. 2008; Futuyma 2013; Colautti and Lau 2015). In Mexico, for *A. donax* 77 different genotypes were detected by Colin et al. (unpublished), among which 13 unique genotypes were found in northern Mexico (5 and 8 genotypes in the CCB and Valle Cruya, respectively (Fig. 15.3), but we still do not know if they are the same or different haplotypes from those found in the Mediterranean region, Europe, Australia, and/or the USA. Thus, we need to use a standardized method (e. g., chloroplast DNA, in conjunction with microsatellite markers or SNPs) to evaluate if there are different lineages and to determine their biogeographical ranges in the species worldwide distribution.

Phragmites australis in Mexico seems to still be in the process of differentiation and diversification (Colin and Eguiarte personal observation). Of the thirteen (BH, BM- BX) new haplotypes found now in Mexico, two of them (BH and BM) were found in the CCB. Furthermore, 4 new haplotypes belonging to the native North America Lineage were also found in the CCB (Fig. 15.4). Experimental and ecological data including viability and germination of seeds information are needed to determine the importance of the propagation mode (sexual vs. asexual) in the life history of the different lineages of *P. australis* in Mexico.

Further research in morphology, ecology, and genetics of more samples from *A. donax*, especially from the USA, Europe, Asia, and the Mediterranean region and from *P. australis* in particular from South America, and Africa, are still needed to link the observed patterns in genetic variation with the environmental factors in order to determine more clearly the evolutionary processes in both species and address in detail their origin, ecology, and invasive potential in Mexico and in particular in the CCB.

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