

Hyparrhenia variabilis and Hyparrhenia cymbaria (Poaceae): New for the Americas, Successful in Mexico

Authors: Vibrans, Heike, García-Moya, Edmundo, Clayton, Derek, and Sánchez-Ken, Jorge G.

Source: Invasive Plant Science and Management, 7(2) : 222-228

Published By: Weed Science Society of America

URL: <https://doi.org/10.1614/IPSM-D-13-00107.1>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Hyparrhenia variabilis and *Hyparrhenia cymbaria* (Poaceae): New for the Americas, Successful in Mexico

Heike Vibrans, Edmundo García-Moya, Derek Clayton, and Jorge G. Sánchez-Ken*

Hyparrhenia cymbaria (boat thatching grass, ipopo grass) and *Hyparrhenia variabilis* (no common name), robust African savanna grasses with complex taxonomies, have not yet been reported for the Americas. Large populations were found in central Jalisco, northeastern Michoacán, and Morelos, Mexico. The species grow in maize and sorghum fields as well as on roadsides and in old fields, but always in association with present or past sorghum cultivation; this suggests introduction through contaminated seed material from Africa. Because of the size and density of the populations, and their native ecology, they are both agricultural pests as well as a potentially dangerous invaders for the American (sub)tropical grasslands and native scrublands, including the southern United States. The invasion underlines the importance of effective phytosanitary controls of the seed supply.

Nomenclature: Boat thatching grass, *Hyparrhenia cymbaria* (L.) Stapf; *Hyparrhenia variabilis* Stapf.

Key words: Invasive grasses, invasive plants, Jalisco, Michoacán, Morelos, phytosanitary controls, new record.

Two African grasses, boat thatching grass, *Hyparrhenia cymbaria* (L.) Stapf and *Hyparrhenia variabilis* Stapf, with high invasive potential for the American subtropics and tropics have been introduced into Mexico. Mexico has a relatively low proportion and absolute number of established exotic plant species (Villaseñor and Espinosa-García 2004). However, there are two groups of plants that have a high percentage of exotic species, many of them invasive and transformers of ecosystems. One of these groups is taxonomic (grasses), and the other functional (aquatic plants) (Comité Asesor Nacional sobre Especies Invasoras 2010). Grasses are particularly damaging, as they change the fire dynamics in the more arid vegetation types.

Most of the exotic grasses have been introduced intentionally as pasture and forage; many originated in Africa (Parsons 1970, 1972; Rzedowski and Rzedowski 1990; Williams and Baruch 2000). Some have apparently arrived by accident, perhaps as seed contaminants.

DOI: 10.1614/IPSM-D-13-00107.1

*First and second authors: Professor, Postgrado en Botánica, Campus Montecillo, Colegio de Postgraduados, km 36.5 carretera federal México–Texcoco, 56230 Montecillo, Mpio. Texcoco, Estado de México, Mexico; third author: Honorary Research Fellow (retired), The Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey, United Kingdom; fourth author: Independent Researcher, 03100 México, D.F. Corresponding author's E-mail: heike@colpos.mx, heike_textcoco@yahoo.com.mx

The genus *Hyparrhenia* (Panicoideae: Andropogoneae) is mainly an African savanna genus with over 50 species (Clayton 1969; Clayton et al. 2006). It contains several species of forage grasses that are known to be invasive in tropical regions worldwide, and also in Mexico. *Hyparrhenia rufa* (Nees) Stapf (jaraguagrass or giant thatching grass), is very common in the tropical lowlands of the country and the continent. *Hyparrhenia hirta* (L.) Stapf (thatching grass) grows in several parts of Mexico, Central America, the Caribbean, and South America. *Hyparrhenia bracteata* (Humb. & Bonpl. ex Willd.) Stapf (no common name) has a few populations in Mexico and is more common further south (Beetle et al. 1983–1995; Davidse et al. 1994; Dávila et al. 2006; Tropicos database [www.tropicos.org]; herbarium specimens at MEXU). However, *H. cymbaria* (boat thatching grass, ipopo grass) and *H. variabilis* have not yet been registered for the American continent.

The genus is taxonomically difficult because of rampant polyploidy, apomixis, and hybridization. The basis for the current understanding of the genus is Clayton (1969). He adopts a relatively strict species concept in order to represent the major variations of the group. However, he says:

In *Hyparrhenia* the concept of species is peculiarly difficult, for variation is apparently continuous throughout much of the genus. Both the available cytogenetic knowledge of the genus, and its successful occupation of

an ecosystem constantly liable to disturbance, offer an explanation as to why this should be so. It should be appreciated that herbarium collections are likely to over-emphasize the degree of continuity; partly because the stable populations tend to be more distant from human occupation and therefore more trouble to collect, and also because their very uniformity renders them less interesting to the collector. To the taxonomist, who must catalogue variation in terms of discrete units, it is a thought which brings some comfort, but nevertheless he is faced with a formidable dilemma.” ... “The continuum concept, borrowed from ecology, is helpful when dealing with entities whose discontinuity is not readily ascertained. The specimens are visualized as clustered about a number of nodes in a multidimensional network. (Clayton 1969, pp. 36–37).

A subsequent multivariate analysis of differences between *Hyparrhenia cymbaria*, *H. variabilis* and some close relatives found few clear differences between these groups (Clayton 1975). However, recent floristic works retain the two species (Clayton and Renvoize 1982, Clayton et al. 2006).

Here, we report these species from the central-western part of Mexico, in the states of Jalisco, Michoacán, and Morelos. They are found mainly in disturbed habitats, but their native distribution and ecology suggest they can invade the natural vegetation of the American dry tropics and subtropics.

Discovery and Identification

The species were first noted by the second author in autumn of 2010. After the first author identified a specimen to genus (and determined that it was a taxon not yet recorded for Mexico), a field trip on February 7, 2011, yielded three numbered collections, as well as photographs and observations of numerous populations (Figure 1A–F). William D. Clayton (Kew) identified the two species from specimens in 2012. A review of grass specimens of Morelos by the fourth author and a subsequent field trip in the same year discovered several populations in Morelos (Figure 1I). The first collection had been made in the year 2006 but it was not identified until this review. The Jalisco populations were not only confirmed in the summers of 2012 and 2013 (Figure 1G and H), but found to be expanding. Dr. Irma López Muraira (Instituto Tecnológico de Tlajomulco, Jalisco, personal communication) reported large populations in the La Barca region in Michoacán in 2012, with photographs, and new populations near Tlajomulco de Zuñiga, a few km south of Guadalajara in 2013. A search of the literature, herbarium databases, the National Herbarium of Mexico (MEXU), and the herbarium of the Institute of Botany, University of Guadalajara, Jalisco (IBUG), failed to

show previous collections from Mexico or the American continent.

Taxonomy

The most striking features of *Hyparrhenia*, a member of the tribe Andropogoneae, are their compound inflorescences with bracts (spatheoles) and paired racemes. However, they share this characteristic with a number of other genera in the tribe. The diagnostic traits of the genus are the following:

- the sessile spikelet is inserted laterally on the internode, and the internode's tip is free and usually pointed;
- the lower glume of the sessile spikelet is rounded, not keeled or grooved, sometimes with some shallow striations;
- the upper glume of the sessile spikelet is obtuse to acute or mucronate;
- the fertile lemma is minutely bidentate, and its awn pubescent to hirtellous;
- the pedicelled spikelet does not have a pronounced callus; and
- the base of the racemes are no longer than 10 mm, usually shorter.

Both *Hyparrhenia cymbaria* and *H. variabilis* belong to Clayton's (1969) section *Pogonopodia* and are closely related to each other. The section is circumscribed by having only one homogamous pair of spikelets per spatheole; short, flattened lower raceme bases that are not much longer than the upper raceme bases; both raceme bases with beards and without appendages; and an acute to pungent callus of the sessile spikelet. The closely related section *Hyparrhenia* has appendages on the raceme-bases and overall narrower spatheoles and fewer awns. These differences are difficult to see and require the use of a strong hand lens or herbarium microscope.

The species of the section are mainly perennial, robust plants with brightly colored, relatively short spatheoles (Figure 1A and B). These usually enclose the raceme-pairs that have short peduncles. The racemes are reflexed within the spatheoles. There are three to eight awns per pair, and these awns have a hairy column.

The two new species share stilted roots, three to five awns (sometimes up to six) per raceme pair, and glabrous pedicelled spikelets. Both have the chromosome number $2n = 20$. However, in *Hyparrhenia cymbaria* the partial inflorescences are smaller, and the callus tends to be obtuse, square, or broader than long. *Hyparrhenia variabilis* has partial inflorescences that tend to be longer, but there is considerable overlap. The best distinguishing characteristics are the length of the awns (1.8 to 3.2 cm [0.71 to 1.26 in]

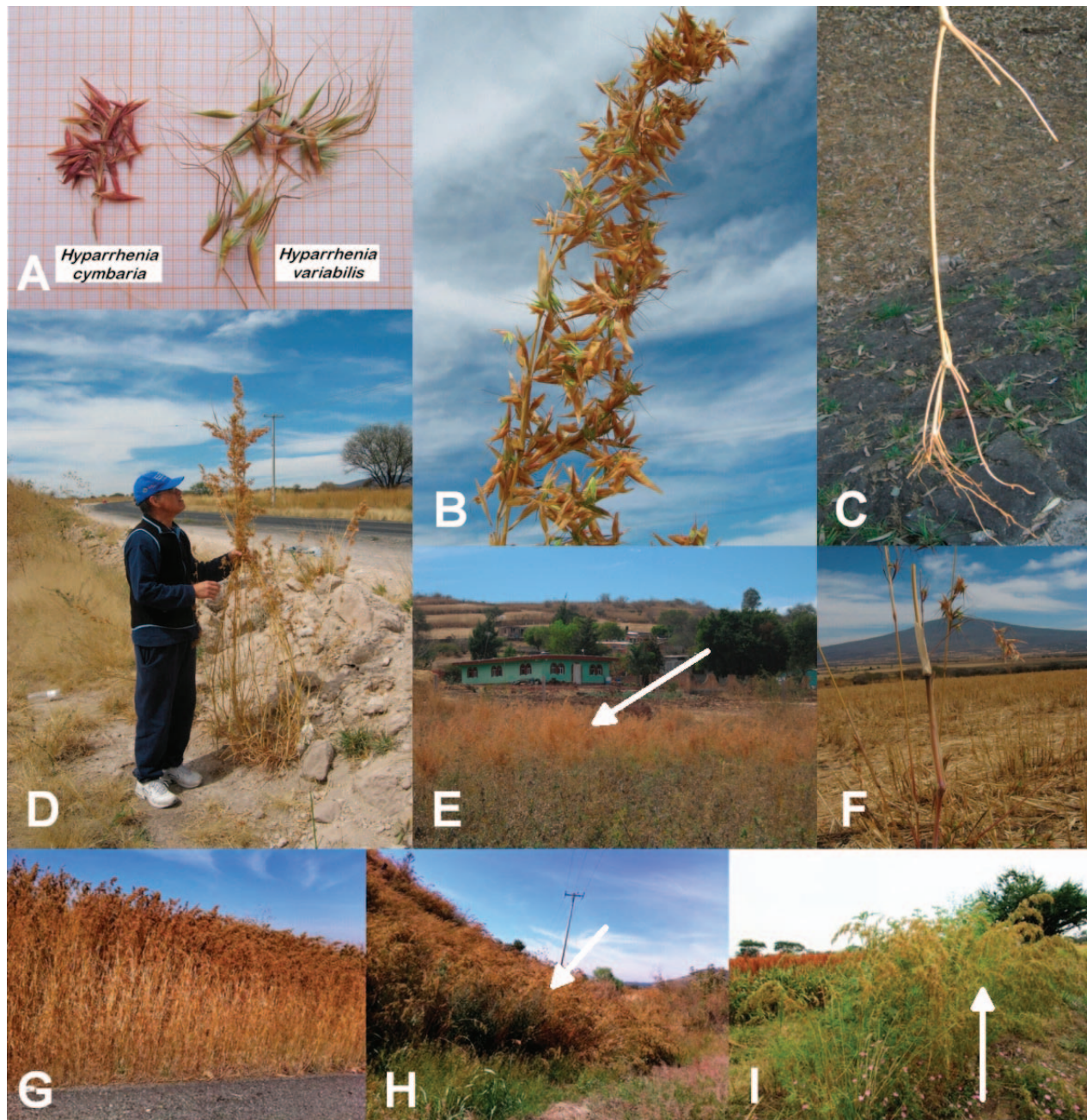


Figure 1. (A) Comparison of partial inflorescences of the two *Hyparrhenia* species; *H. cymbaria* is from the specimen H. Vibrans 8413 from Jalisco, and *H. variabilis* from the H. Vibrans et al. specimen from Morelos. (B) Inflorescence of *Hyparrhenia cymbaria*. (C) Stilted roots. (D) Habit and size of a plant in 2011, near the site of collection number H. Vibrans 8414 in Michoacán; the vegetation in the background on the other side of the road is a *Hyparrhenia* population. (E) Population in an old field, near (D), in 2011. (F) An individual in a cropped maize field near (D), in 2011. (G) A roadside population near the site of (D), but in 2013. (H) *Hyparrhenia* invading grass/bushland, 2013. (I) A field margin population of *Hyparrhenia variabilis* in Morelos, with a sorghum field in the background.

in *H. variabilis* vs. 0.5–1.6, sometimes up to 2.0 cm, in *H. cymbaria*) and the oblong or cuneate, obtuse or acute callus (if the callus is square, then the spatheole is longer).

The two species cannot be separated absolutely; Clayton (1969) presents a scatter diagram to show the differences.

The author comments extensively on the difficulties of separating species in the complex genus *Hyparrhenia*; he asserts that the choice is either to recognize imperfectly separated species, or to recognize only one, an extremely variable one. He states:

H. variabilis and *H. cymbaria* are obviously very closely related, for not only do the dimensions of their floral parts intergrade almost completely, but they share the same habit, distribution and chromosome number. The decision to maintain both species is guided chiefly by the fairly sharp difference in the shape of the callus, but also, let it be admitted, by an intuitive feeling that the distinctive little ovate spatheoles of typical *H. cymbaria* merit separation. (Clayton (1969)

As mentioned in the introduction, a subsequent analysis involving several traits did not resolve the problem (Clayton 1975). Table 1 shows Clayton's descriptions of the species in comparative form, and Figure 1A shows partial inflorescences of the two taxa.

The other Mexican species of *Hyparrhenia* can be distinguished easily. Neither *H. rufa* nor *H. hirta* have the conspicuous spatheoles of our two species, which are bicolored to reddish when dry. *Hyparrhenia bracteata* has hairy spatheoles—in *H. variabilis* and *H. cymbaria* these structures are glabrous.

Distribution and Ecology

In Africa, *Hyparrhenia cymbaria* is found mainly within a broad corridor along the eastern half of the continent, from southern Sudan, Kenya, and Tanzania to KwaZulu-Natal and the western coastal region of South Africa. There are also some populations in West Africa (Cameroon), Madagascar, and the Comoro Islands. *Hyparrhenia variabilis* occupies the same East African corridor, without the West African and island sites (Clayton 1969). It is also known in Java, where it is presumably exotic. The Atlas of Living Australia (cited 2012) records some specimens in cultivation and at agricultural research stations, but also one from a wild population (Queensland, 1982, on bauxite mining tailings). The southernmost sites in South Africa are at approximately 33°S for *H. cymbaria* and 29°S for *H. variabilis* (Clayton 1969; SANBI-SIBIS database 2013).

Ecological information is relatively scarce for such an important and dominant species. Clayton (1969) indicates that *H. cymbaria* is “a common species in tall grass savanna, with a preference for the upland regions,” and *H. variabilis* is “... commonly a dominant constituent of tall grass savanna, occurring on a wide range of soil types.” According to the Flora Zambesiaca (Cope 2002), *Hyparrhenia cymbaria* grows in “wooded grassland, on open hillsides, on the edges of evergreen forest and along stream banks, 480 to 1,680 m” (1,575 to 5,512 ft), and *Hyparrhenia variabilis* in “tall grassland and open woodland on a variety of soils, also common on roadsides and in areas of abandoned cultivation, 700 to 1,560 m.” The Flora of Tropical East Africa (Clayton and Renvoize 1982)

widens the altitudinal range of *Hyparrhenia cymbaria* to 1,000 to 2,800 m and of *H. variabilis* to 600 to 2,200 m.

Comparing the maps and some of the specimen citations in Clayton (1969) with the Koeppen–Geiger climate types (Kottek et al. 2006), the species occur in a wide range of climates. The majority of the sites have an Aw climate (equatorial, winter dry), but also Am (equatorial, monsoonal), BSh (hot-arid, summer dry), as well as Cwa/Cwb (warm-temperate with hot or warm summers), and Cfa/Cfb (warm-temperate, humid, with hot or warm summers). The species grow in hot or warm places, usually with a dry season. No appreciable difference appears to exist between the two taxa.

Both species are described as weedy and common in secondary, fire-dependent riverside grasslands in Central Africa, as well as in vegetation derived from degraded forests and cultivated soils, and *H. variabilis* also colonizes termite hills (Vesey-Fitzgerald 1963). Stromgaard (1986) found *Hyparrhenia variabilis* in somewhat older (> 10 yr) successional stadia of swidden agriculture. He references older literature reporting very dense root layers for grasslands dominated by the species, which make cropping impossible. Also, an earlier work (Boughey et al. 1964) indicates that *Hyparrhenia variabilis* excretes allelopathic substances that impede the growth of nitrogen-fixing bacteria. Stromgaard (1986) suggests that the dense root system together with the toxins might impede succession by woody plants. However, more recent literature is ambivalent in attributing low-nitrogen grasslands to either competition or inhibition (see introduction and results of Lata et al. 2004).

The species are used for thatching roofs in their native area, as the names indicate. They are palatable for livestock when young.

In Mexico, the western populations occur more or less between La Piedad de Cabadas in Michoacán, to a point approximately 60 km (37 mi) east of Guadalajara, at altitudes between 1,500 and 1,700 m, a belt about 100 km long. The area of the Morelos populations is still small and is located east of the capital Cuernavaca, between 1,300 and 1,400 m. All of the populations found were near present or past sorghum cropland, and grow in disturbed habitats: in maize and sorghum fields as agrestal weeds, as well as on roadsides, in plantations, and around human settlements as ruderals. The two species appear to be naturalized. The region has BSh and Cwa climates, which coincide with the data from Africa.

The following voucher specimens were collected:

Hyparrhenia cymbaria

MEXICO. MICHOACÁN. Mpio. Yurecuaro: Federal Highway # 110 from La Piedad towards Vista Hermosa. 20°20'25.3"N, 102°10'27.7"W, 1,667 m. Along the

Table 1. Comparison of the morphological characteristics of *Hyparrhenia cymbaria* and *H. variabilis*; the data were taken from Clayton (1969). The most important differentiating characteristics are in boldfaced letters.

	<i>Hyparrhenia cymbaria</i>	<i>Hyparrhenia variabilis</i>
Life form	Robust perennial, grows in tufts	
Rhizome	Slender and creeping, with small cataphylls	Short, clad in hard cataphylls
Height	2–4 m	1.5–3 m
Culms	Initially slender and rambling, later erect and stout, up to 8 mm (0.31 in) in diameter, with stilt roots at the base	Often initially decumbent, supported by stilt roots
Leaf sheaths	Usually glabrous, but can be ciliate on the margins and/or pubescent at the base	Glabrous, sometimes pubescent at the base
Ligule	Up to 1 mm long	Up to 2 mm long
Leaf blade	Up to 45 cm long and 6–20 mm wide, rigid to subflaccid, dull green, glabrous or hirsute at the base	Up to 45 cm long and 15 mm wide, firm, glabrous or rarely hirsute at the base
Spathate panicle	Large, typically 20–40 cm long, dense, much-branched	
Spatheoles	Boat-shaped, narrowly ovate in profile, 0.8–1.8 (–2.1) cm long and 3–4 mm wide, glabrous, enclosing shortly awned racemes	Boat-shaped, lanceolate in profile, 1.4–2.4 cm long and 3–4 mm wide, glabrous
Color of spatheoles	Beautiful colored, turning a bright russet red at maturity	At maturity russet red, tinged with yellow and green
Peduncle of spatheoles	Short, 3–8 mm long, 1/3 to 1/2 as long as the spatheole, bearded above with white or yellowish hairs	Short, 3–9 mm long, up to about 1/3 as long as spatheole, bearded above with white hairs
Racemes	0.7–1.3 cm long, 3–5(–6)-awned per pair, projecting laterally from the spatheole.	0.8–1.3 cm long, 3–5-awned per pair, projecting laterally from the spatheole
Raceme bases	Subequal, very short, up to 0.5 mm long, the tip with or without a scarious frill up to 0.2 mm long	Subequal, short, the upper about 1 mm long, with a scarious rim up to about 0.2 mm long at the tip.
Homogamous spikelets	4–6(–7) mm long, glabrous to puberulous, ciliate on the margins	7–9 mm long, glabrous to puberulous, ciliate on the margins
Sessile spikelets	3.8–4.5 mm long, glabrescent to sparsely and shortly pubescent, often becoming purplish	4–5 mm long, glabrescent to sparsely and shortly pubescent
Callus	Square or broader than long, 0.2–0.3 mm long, broadly rounded at the base	Cuneate, 0.5–1 mm long, narrowly obtuse to subacute at the base
Apex of sessile spikelet	With an awn 0.5–1.6(–2.0) cm long, rarely almost suppressed (note: in the description by Clayton it says 0.5–1.6[–2.0] mm, but this is an error)	With an awn 1.8–3.2 cm long
Caryopsis of sessile spikelet	Cylindrical, 3 mm long	No information
Pedicelled spikelets	4–5 mm long, glabrous to puberulous, ciliate on margins	5–8 mm long, glabrous to puberulous, ciliate on margins
Apex of pedicelled spikelets	Acuminate or sometimes with an awn point up to 1.5 mm long	With an awn point 1–4 mm long
Habitat	A common species in tall grass savanna, with a preference for the upland regions	Commonly a dominant constituent of tall grass savanna, occurring on a wide range of soil types
Chromosome numbers	2n = 20, 30	2n = 20
Distribution	The eastern half of Africa from Eritrea to KwaZulu–Natal in South Africa, reaching the west coast in the Cameroon area and in northern Angola, also Madagascar and the Comoro Islands	Eastern Africa from Ethiopia to Transvaal (northeastern South Africa); also in Java
Altitude (from the Flora Zambesiaca, Kew)	480–1,680 m	700–1,560 m

highway, several 100 m, several specimens, sparse, 7 Feb 2011, *H. Vibrans* 8413 (MEXU, CHAPA).

Hyparrhenia variabilis

MEXICO. MICHOACÁN. Mpio. Yurecuaro: Federal Highway #110 from La Piedad towards Vista Hermosa, Municipality of Yurecuaro, near the small village of Cerro Blanco, 20°20'23.3"N, 102°12'20.3"W, 1,690 m, abundant in a nearby field with winter vegetation; the specimens were taken from green plants near the highway that had recently been cut, 7 Feb 2011, *H. Vibrans* 8414 (MEXU, CHAPA). **JALISCO:** Federal Toll Highway #15 from La Barca to Guadalajara, 20°23'21.4"N, 102°42'50.5"W, 1,535 m, abundant in an abandoned *Agave* plantation, 7 Feb 2011, *H. Vibrans* 8415B (MEXU, CHAPA). **MORELOS. Mpio. Zacualpan de Amilpas:** Tlacotepec, roadside, 11 Oct 2006, *R. Cerros T., A. Flores et al.* 2693 (HUMO, MEXU). **Cuautla:** Highway near the entrance from Cuautla towards Amacuzac, 18°51'00"N, 98°56'09"W, 1,390 m, on both sides of the road, several populations, 12 Oct 2012, *J. G. Sánchez-Ken, H. Vibrans, and E. García w/o number* (MEXU). **Cuautla:** Federal Highway 115D Jantetelco–Cuautla, east of Cuautla, approximately 2 km south of the interchange with highway 115/160, 18°50'00.5"N, 98°55'22.1"W, 1,358 m, abundant on roadsides and edges of fields in the area, 20 Oct 2012, *H. Vibrans, J. G. Sánchez-Ken, and E. García w/o number* (MEXU, CHAPA).

Several populations were large—many thousands of individuals—and often dominant, even monospecific (Figure 1G). They generally formed patches. From observations, the species appear to be serious weeds in sorghum and maize, and probably difficult to control.

Discussion

These species are new records for Mexico and the Americas. They are widespread in their home range, covering an ample spectrum of warm-temperate and tropical climate types, which suggests adaptation to variable ecological conditions. They are known to be intolerant, either because of their dense root network or through chemical inhibition. As such, the species have potential for becoming serious invasive plants and agricultural weeds in most of the warmer regions of the Americas, including the southern United States and the cerrado regions of Brazil.

We do not know the pathway of introduction for certain. Intentional introduction is unlikely, because these species are not prime pasture grasses; some reference would presumably have turned up in the agricultural literature and a purposeful introduction would probably only involve a single genotype. However, the fact that a mixture of genotypes/species was introduced, and that all

of the sites were associated with present or past sorghum cultivation, points to introduction with contaminated sorghum seeds from Africa. This underlines the importance of phytosanitary controls of the seed supply; these exist in Mexico but the legal basis is a negative list of regulated species in the Mexican Official Norm (Norma Oficial Mexicana) NOM-043-FITO-1999, which does not contain the species reported here. We suggest amending national regulations to include the species as soon as possible, both in Mexico and in other countries of the Americas. However, the example of this invasion also showcases the limits of these negative lists, which cannot possibly include all potential invaders.

These plants are quite conspicuous, and several large populations are easily visible from a major highway, the Mexico City–Guadalajara toll road (Autopista de Occidente). The species must have existed in the region for some time, and it is surprising that it has not been collected and described previously. We suggest that this might be due to a precipitous drop in general botanical collections in Mexico in the last 15 yr after the completion of some large floristic projects, and the dearth of competent general florists interested in weedy species.

Considering the experience with the eradication of invasive plants in other regions (e.g., Pluess et al. 2012; Rejmanek and Pitcairn 2002), we do not think these species can be eradicated easily from their present area. However, they can be prevented from reaching other regions. No information on management or eradication measures was found in the literature. Because of their (apparent) similarity in ecology, we suggest that the two species can be treated as a single taxon for management purposes, pending the availability of better data.

A more detailed mapping of their distribution in Mexico and investigation on the biology/ecology of the two species is urgently needed in order to evaluate the possibilities of containment. Do the two species reported here form separate populations? Do they interbreed? Are there differences in their ecology and invasiveness? What measures can be taken to avoid their expansion into natural areas? Do they require additional measures of control in agriculture, or can they be controlled with the conventional weed management of the region? Outreach to farmers of the region would be a useful and rapid method of slowing further expansion.

Literature Cited

- Atlas of Living Australia (no date) <http://bie.ala.org.au/species/Hyparrhenia+variabilis>. Accessed July 30, 2012
- Beetle AA, Miranda-Sánchez JA, Jaramillo-Luque V, Rodríguez-Rodríguez AM, Aragon-Melchor L, Vergara-Batalla MA, Chimal-Hernández A, Domínguez-Sepulveda O (1995) Las Gramíneas de México IV. México, D.F.: Secretaría de Agricultura, Ganadería y Desarrollo Rural. 372 p

- Boughey AS, Munro PE, Meiklejohn J, Strang RM, Swift MJ (1964) Antibiotic reactions between African savanna species. *Nature* 203: 1302–1303
- Clayton WD (1969) A revision of the genus *Hyparrhenia*. Kew Bull Additional Series II. Kew, UK: Kew Botanical Garden. 196 p
- Clayton WD (1975) Some discriminant functions for *Hyparrhenia*: studies in the Gramineae: XLI. Kew Bull 30:511–520
- Clayton WD, Renvoize SA (1982) Flora of Tropical East Africa. Gramineae (Part 3). Kew, UK: Kew Botanical Garden. <http://plants.jstor.org/flora/fta008991>. Accessed July 30, 2012
- Clayton WD, Vorontsova MS, Harman KT, Williamson H (2006) GrassBase—The Online World Grass Flora. <http://www.kew.org/data/grasses-db.html>. Accessed July 27, 2012
- Comité Asesor Nacional sobre Especies Invasoras (2010) Estrategia Nacional sobre Especies Invasoras en México, Prevención, Control y Erradicación. México, D.F.: Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Comisión Nacional de Áreas Protegidas, Secretaría del Medio Ambiente y Recursos Naturales. 91 p
- Cope TA (2002) Gramineae (*Hyparrhenia variabilis* and *Hyparrhenia cymbaria*). In Pope GV, Martins ES, eds. Flora Zambesiaca, Volume 10, part 4, online version. <http://apps.kew.org/efloras/namedetail.do?flora=fz&taxon=8887&nameid=23353> and <http://apps.kew.org/efloras/namedetail.do?qry=namelist&flora=fz&taxon=8886&nameid=23337>. Accessed July 30, 2012
- Davidse G, Sousa-Sánchez M, Chater AO (1994) Alismataceae a Cyperaceae. Flora Mesoamericana 6. México, D.F.: Instituto de Biología, Universidad Nacional Autónoma de México. 543 p
- Dávila P, Mejía-Saules MT, Gómez-Sánchez M, Valdes-Reyna J, Ortiz JJ, Morin C, Castrejon J, Ocampo A (2006) Catálogo de Gramíneas de México. México, D.F.: Universidad Nacional Autónoma de México. 671 p
- Kottek M, Grieser J, Beck C, Rudolf B, Rubel F (2006) World Map of the Köppen-Geiger Climate Classification Updated. *Meteorol Z* 15: 259–263 <http://koeppen-geiger.vu-wien.ac.at/present.htm>. Accessed February 17, 2014
- Lata JC, Degrange V, Raynaud X, Maron PA, Lensi R, Abbadie L (2004) Grass populations control nitrification in savanna soils. *Funct Ecol* 18:605–611
- Parsons JJ (1970) The “Africanization” of the New World tropical grasslands. *Tübinger Geogr Stud* 34:141–153
- Parsons JJ (1972) Spread of African pasture grasses to the American tropics. *J Range Manag* 25:12–17
- Pluess T, Cannon R, Jarošík V, Pergl J, Pyšek P, Bacher S (2012) When are eradication campaigns successful? A test of common assumptions. *Biol Invasions* 14:1365–1378
- Rejmanek M, Pitcairn MJ (2002) When is eradication of exotic pest plants a realistic goal? Pages 249–253 in Veitch CR, Clout MN, eds. *Turning the Tide: The Eradication of Invasive Species*. Proceedings of the International Conference on Eradication of Island Invasives. Gland, Switzerland and Cambridge, UK: IUCN, Invasive Species Specialist Group
- Rzedowski J, de Rzedowski GC (1990) Nota sobre el elemento africano en la flora adventicia de México. *Acta Bot Mex* 12:21–24
- SANBI (South African National Biodiversity Institute (2013) Integrated Biodiversity Information System (SIBIS). <http://sibis.sanbi.org/faces/SearchSpecies/Search.jsp?1=1>. Accessed December 5, 2013
- Stromgaard P (1986) Early secondary succession on abandoned shifting cultivator's plots in the miombo of South Central Africa. *Biotropica* 18:97–106
- Vesey-Fitzgerald DF (1963) Central African grasslands. *J Ecol* 51: 243–274
- Villaseñor JL, Espinosa-García FJ (2004) The alien flowering plants of Mexico. *Divers Distrib* 10:113–123
- Williams DG, Baruch Z (2000) African grass invasion in the Americas: ecosystem consequences and the role of ecophysiology. *Biol Invasions* 2:123–140

Received December 21, 2013, and approved February 25, 2014.