Floriculture and Ornamental Biotechnology ©2012 Global Science Books

Mexican Geophytes II. The Genera *Hymenocallis*, *Sprekelia* and *Zephyranthes*

Ernesto Tapia-Campos[1] • Jose Manuel Rodriguez-Dominguez[1] • María de los Milagros Revuelta-Arreola[1] • Jaap M. Van Tuyl[2] • Rodrigo Barba-Gonzalez[1*]

[1] Centro de Investigación y Asistencia en Tecnología y Diseño del Estado de Jalisco A.C. Biotecnología Vegetal, Av. Normalistas #800. Colinas de la Normal., Guadalajara Jalisco, C.P. 44270, Mexico

[2] Plant Breeding, Wageningen University and Research Centre, Droevendaalsesteeg 1, 6708 PB Wageningen, The Netherlands

***Corresponding author*: * rbarba@ciatej.net.mx; rbarba002@hotmail.com**

ABSTRACT

Among hundreds of bulbous ornamental plants native to tropical and subtropical America, different genera from the Amaryllidaceae family such as *Hymenocallis*, *Sprekelia and Zephyranthes* present an enormous potential as ornamental crops. The genus *Hymenocallis* comprises over 60 species distributed from the north of Brazil to the south east of the United States; many of them are endemic to Mexico. The flowers are star shaped and white. The different species grow in a wide and contrasting diversity of habitats, near rivers and streams, on occasion completely submerged under water and sometimes in dry areas. The genus presents a complicated phylogeny, where in some cases it is difficult to distinguish species from hybrids. The genus *Sprekelia* is a monotypic genus native to Mexico; *Sprekelia formosissima* is cultivated as an ornamental pot plant in many countries. It presents solitary red flowers, their stems reaches up to 80 to 90 cm. The genus *Zephyranthes* comprises over 70 species distributed in tropical and subtropical America; different species are cultivated all over the world as an ornamental crop. The different species have beautiful flowers from white to yellow with various tints from lemon to sulphur and pink. In this review we will cover taxonomical, chromosomal and phenological aspects of these genera, with the aim of providing a reference of useful traits for breeding programs.

Keywords: breeding, *in vitro* culture, ornamental, perspectives, taxonomy
Abbreviations: BA, 6-benzyladenine; **GA_3**, gibberellic acid; **IBA**, indole-3-butyric acid; **ITS**, internal transcribed spacer region; **RFLP**, restriction fragment polymorphism

CONTENTS

INTRODUCTION

The Amaryllidaceae J. St.-Hil. is a cosmopolitan family (predominantly pantropical) of petaloid monocots (Meerow *et al.* 1999). Its origin is western Gondwanaland in Africa, from where it radiated to Australia, Eurasia and America (Huber 1969; Raven and Axelrod 1974; Meerow *et al.* 1999). The genera *Hymenocallis* Salisb., *Sprekelia* Heister and *Zephyranthes* Herb. are components of terminal sub-clades whose higher diversity is present in Mexico. These genera have been cultivated in some cases, for centuries; however, it is worthwhile to reconsider their potential as ornamental plants and for their pharmaceutical importance due to their alkaloid content. The aim of this work is to give an insight to the origin of the genera, their culture and propagation techniques, and to focus attention on traits of ornamental importance of the Mexican species to set a base for their use in breeding programs.

Received: 26 January, 2011. Accepted: 20 December, 2012.

Invited Review

Table 1 Mexican species of the genus *Hymenocallis*, their distribution in Mexico and some traits of ornamental interest.

Species	Distribution	Traits of interest
H. acutifolia (Herb. ex Sims) Sweet	Wide distribution	Narrow foliage, blooms from late summer through autumn
H. araniflora T.M.Howard	Sur Sinaloa, Nayarit	Clusters of long-tubed, sweet-scented blooms, pale green to grayish foliage (Ogden 2007)
H. astrostephana T.M.Howard	Guerrero	Costate leaves, two to five long-tubed flowers (Howard 2001)
H. azteciana Traub.	Jalisco, Nayarit, Zacatecas	Spreading, long-stemmed or petiolated leaves with a satiny dusting of gray overlaying dark green. Small clusters of erect blooms (Ogden 2007)
H. baumlii Ravenna	Chiapas	Erect green star-shaped leaves, ribbon-like flowers (Howard 2001)
H. choretis Hemsl.	C & SW. Mexico	Large-cupped snowy blossoms, with orange pollen. Gray foliage (Ogden 2007)
H. cleo Ravenna	Chiapas	Medium-sized white flowers, broad, glaucous, petiolated leaves (Howard 2001)
H. clivorum Laferr	Sonora	Green stamens, long and thin tepals
H. concinna Baker	Jalisco	Endangered species
H. cordifolia Micheli	Guerrero	Heart-shaped petiolated leaves, umbels of small white flowers (Howard 2001)
H. durangoensis T.M.Howard	Durango	Thick and short sepals. Blooms in early summer. Self-compatible. Endangered specie
H. eucharidifolia Baker	Guerrero, Oaxaca	Broad, green hosta-like foliage. Snowy foliage held in up-facing groups of three or more
H. galuca (Zucc.) M.Roem.	C&SW Mexico	Large-cupped upright snowy blossoms, with orange pollen with a ammonia or chlorine fragrance. Gray foliage (Ogden 2007)
H. graminifolia Greenm	Morelos	Dwarf, glaucous leaves, fragrant flowers (Howard 2001)
H. guerreroensis T.M.Howard	Guerrero	Endangered species
H. harrisiana Herb	C & SW Mexico	Small upright flowers with good sized blooms
H. howardii Bauml	SW Mexico	Small plant of glaucous foliage, blooms form mid-June through mid-July
H. imperialis T.M.Howard	San Luis Potosí, Hidalgo	Wide, snowy petals. Blooms from late April and May. The bulbs are huge and the big leaves are spear-shaped.
H. jaliscensis M.E.Jones	Jalisco, Nayarit	Big upright flowers (Borys *et al.* 2008)
H. leavenworthii (Standl. & Steyerm.) Bauml	Michoacán	Spreading long stemmed or petiolated leaves with a satiny dusting of gray overlaying dark green. Small clusters of erect blooms (Ogden 2007). Endangered species
H. lehmilleri T.M.Howard	Guerrero	Elegant white flowers with thin petals, greenish filaments
H. littoralis (Jacq.) Salisb.	Wide distribution	Slender petals attached to the cups of the blooms. Blooms in August. Filaments tipped with bright orange pollen (Ogden 2007)
H. longibracteata Hochr.	Veracruz	Presumed extinct (Castillo-Campos *et al.* 2005)
H. maximiliani T.M.Howard	Guerrero	Compact, narrow and erect foliage. Long and narrow sepals
H. partita Ravenna	Chiapas	Aquatic, pleasant fragrance
H. phalangidis Bauml	Nayarit	Daffolil-like plant with few flowered umbels (Howard 2001)
H. pimana Laferr.	Chihuhua	Flowers with yellowish-centered flat cup (Howard 2001)
H. portamonetensis Ravenna	Chiapas	Sharp lanceolate leaves, four to five flowers
H. proterantha Bauml.	SW Mexico	Wide, petiolated glaucous leaves; flowers appear as leaves go dormant (Howard 2001)
H. pumila Bauml.	Jalisco, Colima	Dwarf habit, bright green sword-like leaves (Howard 2001)
H. sonorensis Standl.	Sonora to Nayarit	Clusters of long-tubed, sweet scented blooms, pale green to grayish foliage (Ogden 2007)
H. vasconcelossi Garcia-Mend.	Oaxaca, Puebla	Few oblong-elliptical green leaves. White flowers with thin and short tepals (Garcia-Mendoza 2010)
H. woelfleana T.M.Howard	Durango, Sonora, Nayarit	Presence of a pedicel below the ovary (Howard 1978)

ORIGIN

Hymenocallis, *Sprekelia* and *Zephyranthes* are bulbous genera of the monocotyledoneous family Amaryllidaceae. The systematics of the family have undergone study at several levels (Meerow *et al*. 1999) and there is a sister relationship between the Eurasian/Mediterranean clade and the American genera. The Madrean–Tethyan hypothesis notes that the initial entry of the family occurred through North America during the late Cretaceous to the early Eocene, when North America and western Europe may have shared a warm, seasonally dry climate (Axelrod 1973, 1975) which might have allowed east/west movement of species, with island chains of the mid-Atlantic ridge providing stepping stones (Meerow *et al.* 1999). However, there are members of the family in Mexico and the United States that are linked to more basal taxa endemic to South America (Meerow *et al.* 1999). The Madrean-Tethyan hypothesis has been questioned after several studies utilizing isozymes, plastid DNA, restriction fragment polymorphisms (RFLPs), and cladistic analyses of taxa considered emblematic of the disjunction (Little and Chrutchfield 1969; Kölher and Brückner 1989; Liston *et al.* 1992; Ray 1994; Meerow *et al*. 1999, 2002). Due to the distribution of Amaryllidaceae in America and the generic richness south of the equator, a massive extinction event should have occurred after migration to South America (Meerow *et al.* 1999). However, there is evidence that the movement of Amaryllidaceae has been northward from South America (Meerow 1987, 1989; Merrow *et al.* 2002). A study of the phylogeny of the genus *Hymenocallis*, based on cladistic analyses of morphology, plastids and ribosomal DNA, groups the Hymenocallidae tribe with three genera: *Hymenocallis*, *Ismene* Herb. and *Leptochiton* Sealy, being the latter sister to the *Hymenocallis*/*Ismene* clade. As the genera *Ismene* and *Leptochiton* are endemic to the central Andes and *Hymenocallis* is absent from this region, this study suggests an entry of the Amaryllidaceae through South America and a vicariance event at some point subsequent to the origin of the tribe, with a later extinction of the intervening populations of a proto-*Hymenocallis* ancestor (Meerow *et al*. 1999, 2002). Furthermore, Meerow *et al.* (1999) investigated the fact that the Eurasian sister clade has been successful in adapting to temperate habitats, whereas the American clade has not been able to adapt to those climates. There is also evidence from internal transcribed spacer regions (ITS) analyses in the genus *Zephyranthes* of the probable center of origin of the Amaryllidaceae family's extant diversity in the Americas in South America, with a later migration to North America. The results of Meerow *et al.* (2000) show two *Zephyranthes* clades having originated by different migration paths northwards from South America. The South American species *Z. flavissima* Ravenna and *Z. mesochloa* Herb. are sister to the Mexican *Zephyranthes* clade, suggesting a migration from South America northward through the Panamerican isthmus. The second clade includes species from Argentina (*Z. candida* (Lindl.) Herb., *Z. filifolia* Baker & Kraenzl.), Brazil (*Z. cearensis*

Baker), Cuba (*Z. rosea* (Sprenger) Lindl.) and North America (*Z. atamasco* (L.) Herb., *Z. simpsonii* Chapm.), suggesting that this clade entered the southeastern United States via Cuba after migrating from South America (Meerow *et al.* 2000).

Cladistic analyses of plastid DNA sequences *rbcL* and *trn-L-F* and ITS position the genus *Hymenocallis* as a monophyletic group; belonging to the *Hymenocalliade* tribe along with *Ismene* and *Leptochiton* the three genera are enclosed in the Andean clade (Meerow *et al*. 2000). The genus *Zephyranthes*, a polyphyletic group, may represent convergence of two (albeit related) lineages of North (Meso) American and South America (Meerow 1995), however, a wider sampling of the genus revealed a putative triple origin of the genus (Meerow *et al.* 2000). *Zephyranthes*, together with *Sprekelia* and *Habranthus* are nested in the Zephyranthinae subtribe of the Hippeastrae tribe, together with the genera *Hippeastrum* Herb., *Rodophiala* C. Presl and *Traubia* Moldenke, within the Hippeastroid clade.

HYMENOCALLIS

Biology and morphology

The genus *Hymenocallis* Salisb. comprises about 70 species distributed from the southeastern United States to northern South America, and present in Mexico, Central America and the Caribbean Islands (Grossi 2007). Mexico possess the highest number of species of the genus (32, many of them endemic) (**Table 1**) with a secondary area of diversity in the U.S. (Bauml 1979; Smith and Flory 1990, 2001; Smith *et al.* 2001).The chromosome number of the genus has been reported as 2n = $2x$ = 46 and 40; however, many aneuploid accessions that have been reported showing a derivation of these numbers; *H. henryae* Traub. possesses a chromosome number of 2n = $2x$ = 38, being the lowest reported for the genus (Smith and Flory 1990). Different species have been cultivated worldwide for two main purposes, their alkaloid content and ornamental value.

'Spider lily' is the common name for the genus *Hymenocallis* (from Greek "beautiful membrane"); they are bulbous and perennial herbaceous plants, with elegant, long-tubed, snowy white flowers, some of them with a pleasant fragrance. Their bulbs are roundish or oblong, from which thick whitish roots emerge, covered by a tunic. The most outstanding trait is the pancratioid morphology of the flowers, with the stamens united into a distinctive corona and the long and narrow tepals which give them their characteristic "spidery" look. They have a variable number of distichous leaves, except *H. eucharidifolia* Baker, which has a rosette. The leaves range from 5-7 mm wide and are sessile, linear and glaucous in *H. graminifolia,* Greenm. to 15 cm wide, petioled, lanceolate and bright green in *H. speciosa* Salisb. (Preuss 2002; Grossi 2007).

Spider lilies grow in a wide diversity of habitats. The North American spider lilies grow in or on the margins of wetlands habitats, and less often in dry, flat woods or in disturbed sites, whereas the Mexican spider lilies grow in most of the climatic conditions of Mexico, from the north to the south, from xeric to aquatic conditions and from arid climates with increased elevation to tropical coastal areas (Preuss 2002).

Hymenocallis 'traditional' classification

Traub (1962) grouped the *Hymenocallis* species into six alliances based on morphological characteristics. These are: I. *Speciosa*, which comprises species with petiolate leaves, distributed in Brazil, Mexico and the Caribbean. II. *Mexicana*, with sessile leaves or sub-petiolate that are oblong, oblong-lanceolate, ensiform or caduceus, native to Mexico. III. *Caribeae*, with slightly lanceolate leaves, evergreen, with free perigonium segments in relation to the staminal corona. Species of this alliance are distributed in Central America, the Caribbean and Florida. IV. *Littoralis*, species of this alliance have slightly lanceolate leaves, are usually evergreen, with shortly joined perigonium segments to the stamina corona. It is distributed in Colombia, Ecuador and Mexico. V. *Caroliniana*, which have introrse anthers, caduceus leaves and a globular ovary with less than four ovules per locule. These species are native to the southern U.S. VI. *Henryae*, distributed in Florida and Cuba, with caduceus leaves, introrse anthers, oblong ovaries and more than four ovules per locule.

Hymenocallis propagation and culture

Most of the cultivated *Hymenocallis* are old heirloom flowers spread widely by sailors in the 16th century; they were originally brought from the tropical shores of the Antilles and the Spanish Main. The identities of these plants are hidden in a tangled horticultural history. These beautiful flowers are sold in nurseries as *H. littoralis* Salisb., *H. caribbaea* Herb., *H. rotata* (Ker Gawler) Herb., or *H. tenuiflora* Herb. (Ogden 2007). In Mexico, *H. laevenworthii* (Standl. & Steyerm.) Bauml, *H. proterantha* Bauml. and *H. harrasiana* Herb. are planted in home gardens and open areas (Borys *et al*. 2005a).

Hymenocallis is a very minor component in the bulb trade, however, the beauty of the spider lily flowers, their fragrance and their vigorous growth hint at the potential value of the genus (Hanks and Jones 1987). Some of the Mexican species are shown in **Fig. 1**, and a list of traits of ornamental importance is given in **Table 1**.

There is little information regarding reproductive capacity of the genus and it is mainly propagated by seeds produced by self pollination and by bulb offsets (Borys *et al.* 2005a). Two groups of *Hymenocallis* can be identified by their ecology; xerophytes and meso-hydrophytes (Borys *et al*. 2005a, 2008). In both groups the seeds lack dormancy; the xeric group (caduceus leaves) is polyembryogenic, their seeds show a sequential emergence of embryogenic roots followed by rapid formation of small rooted, leafless bulbils, which are forced by contractile roots into deep soil layers and enter a deep dormancy period. During the following rainy season the bulbs forms feeder roots and primary leaves. The meso-hydrophyte group is evergreen and their seeds produce only one embryogenic root, terminating in a leafy and rooted bulbil of continuous growth (Borys *et al.* 2005a).

As mentioned before, traditional propagation of *Hymenocallis* is done by seeds or by bulb offsets; however, Leszczynska *et al.* (2005) utilized scales and rooted basal plates for the propagation of Mexican spider lilies. Both scales and the rooted basal plates were able to form bulbils in a variable number and size per scale or bulb. The bulbs were produced in different positions, the scales formed bulbils at the basal end of veins, while in the rooted basal plates the bulbils were produced either between scales or on the upper parts of the remaining scales. In the latter case, the central part had to be removed to avoid the reappearance of the dominant meristem and the bulbils were separated when the basal plate decomposed.

Micropropagation of *H. littoralis* has been described by Backhaus *et al.* (1992). Bulb scales of *H. littoralis* were utilized as explants, surface-sterilization was made by submerging the bulbs in a 1% solution of NaOCl, 0.1% Tween® 20 for 20 min, followed by three washes in sterile distilled water. The scales with a small portion of the basal plate attached were cultured in darkness in a basal medium (BM) composed by Murashige and Skoog (1962; MS) salts, supplied with 3% sucrose, 100 mg/l *myo*-inositol, 0.4 mg/l thiamine-HCl and 7 g/l TC agar; 1-9 bulblets were formed after 5 weeks and were sub-cultured in a proliferation medium containing the BM medium to which 2 mg/l 6-benzylaminopurine (BA) and 00.02 mg/l indole-3-butyric acid (IBA) were added. On average, 8 new shoots/bulblet were produced. After proliferation, the bulbs were placed in a rooting medium composed of the BM medium plus 6 g/l agar. The rooted bulbs were successfully transferred to an

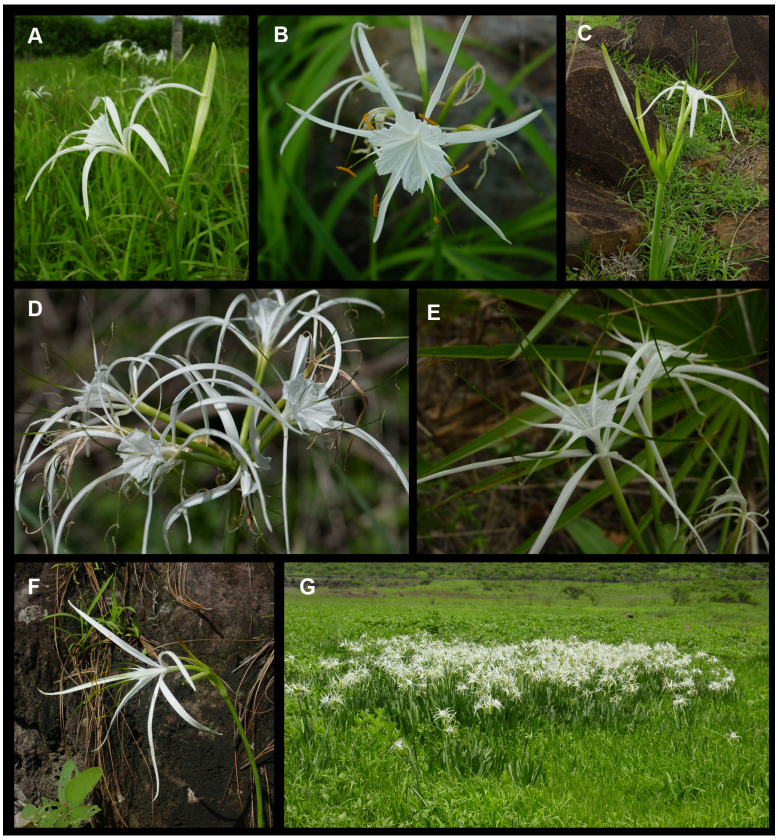

Fig. 1 Some *Hymenocallis* species present in Mexico. (**A**) *H. howardii*; (**B**) *H. concinna*; (**C**) *H. acutifolia*; (**D**) *H. jaliscensis*; (**E**) *H. protheranta*; (**F**) *H. laevenworthii*; (**G**) *H. concinna* in its natural habit. Photos: A. Rodriguez.

intermittent mist greenhouse.

With the application of these techniques it is possible to achieve massive production for commercial purposes.

Spider lilies are not hardy. *H. littoralis* prefers a well-drained soil with organic matter and abundant irrigation. In a study performed by Isdo *et al.* (2007), 2-year-old bulbs of *H. littoralis* were cultivated in a natural field soil (a fine-loamy, mixed (calcareous), hyperthermic Anthropic Torrifluvet), in the Sonoran Desert environment of central Arizona, and the plants exposed to two different levels of ambient air of 400 and 700 ppm CO_2. This increase in atmospheric CO_2 resulted in 48% increase in above ground growth and 56% increase in bulb growth. Additionally, it also increased the concentrations of five bulb constituents that possess anticancer, and antiviral properties.

There have been some attempts to control forcing in *H. x festalis* (Worsley) Schmarse (=*Ismene x festalis* Worsley); unfortunately, unsuccessfully (De Hertogh and le Nard 1993). Hanks and Jones (1987) stored bulbs of *H. x festalis* over winter at 5°C, promoting less flowering. Flower formation in *H. speciosa* is inhibited in plants held at 25°C but prompted in plants transferred to 15° or 20°C after 1 July (Mori *et al.* 1991). Borys *et al.* (2009) in an attempt to break dormancy in *H. harrasiana* and *H. jaliscensis* M.E. Jones stored the bulbs at 18 to 22°C for 5 to 7 months and planted them in soil at temperatures that ranged from 10 to 35°C. Their results showed that with a longer storage the time to initiate the emission of leaves decreased, but also the number of scapes. Anyway, the results varied when the bulbs were grown in open fields, concluding that neither clone is suited for forced flowering.

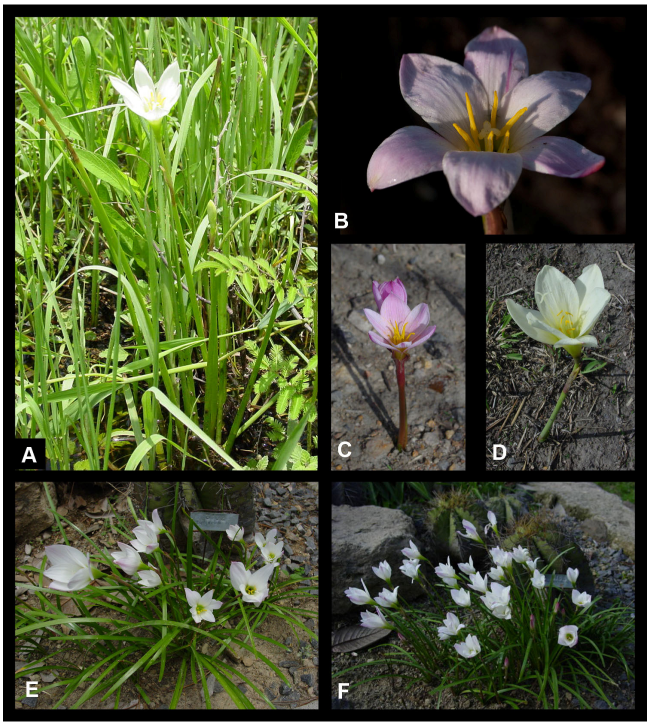

Fig. 2 Some *Zephyranthes* species present in Mexico. (**A**) *Z. nymphaea*; (**B**) *Z. latissimifolia*; (**C**) *Z. fosteri*; (**D**) *Z. concolor*; (**E**) *Z. macrosiphon*; (**F**) *Z. clintiae*. Photos: A. Rodriguez

ZEPHYRANTHES

Biology and morphology

The genus *Zephyranthes* Herb. is a bulbous perennial of the Amaryllidaceae family. It comprises about 90 species, of which at least 37 are native to Mexico (**Table 2; Fig. 2**), many of which are endemic. Together with the genus *Habranthus* they are commonly known as 'rain lilies' because the flowers appear in spring through fall after the first rains (Knox 2009). The genus takes its name after the Greek god of the west wind that typically brought the rainfall 'Zephyrus'. Rain lilies are noteworthy for the wide ecological

Table 2 Mexican species of the genus *Zephyranthes*, their distribution in Mexico and traits of ornamental interest.

Species	Distribution	Traits of interest
Zephyranthes arenicola Brandegee	Baja California, Isla Guadalupe	Bloom color: white / near white Bloom time: late summer / early fall; mid fall.
Zephyranthes bella T.M.Howard & S.Ogden	Zacatecas, San Luis Potosí	Bloom color: pink; white / near white Bloom time: late summer / early fall; mid fall.
Zephyranthes brevipes Standl.	Chiapas, Coahuila, Hidalgo, Morelos	Bloom color: pink Ovary almost sessile
Zephyranthes carinata Herb.	Mexico to Colombia	Scape bearing a single pink flower
Zephyranthes chichimeca T.M.Howard & S.Ogden	NE Mexico	Bloom color: pink or rose blushed petals, clustering habit and obovate to spatulate petals Bloom time: late spring / early summer.
Zephyranthes chlorosolen (Herb.) D.Diettr	Kansas to E. Mexico, Yucatan	Flowers erect; perianth white, sometimes tinged or veined pink Bloom time: late spring / early fall (May-Oct).
Zephyranthes chrysantha Greenm. & C.H.Thomps	Texas to Tamaulipas and Nuevo Leon	Bloom time: late summer / early fall; mid fall
Z. citrina Baker	SE Mexico, Cuba to haiti	Flowers erect; perianth lemon yellow, funnelform, 3.1–5 cm; perianth tube green. Bloom time: summer (Jul-Sep)
Zephyranthes clintiae Traub	Querétaro, San Luis Potosí	Bloom color: pink
Zephyranthes concolor (Lindl.) Benth. & Hook.f	Mexico	Bloom color: chartreuse (yellow-green); white / near white Bloom time: late summer / early fall; mid fall
Zephyranthes conzattii Greenm.	Oaxaca	Endangered specie
Zephyranthes crociflora T.M.Howard & S.Ogden	Coahuila	Bloom color: pale pink; white / near white Bloom time: late summer / early fall; mid fall
Zephyranthes dichromantha T.M.Howard	San Luis Potosí	Bloom color: pale yellow Bloom time: mid summer; late summer / early fall
Zephyranthes drummondii D.Don in R.Sweet	NW. Florida to NE. Mexico	Flowers erect; perianth white, sometimes flushed pink abaxially, more so with age, broadly funnelform. Flowering mid spring--mid summer (Mar--Aug).
Zephyranthes erubescens S.Watson	NE. Mexico	Bloom color: red; white / near white Bloom time: late summer/early fall; mid fall.
Zephyranthes fosteri Traub	San Luis Potosi and Jalisco to Guerrero, Puebla and Oaxaca.	Bloom color: flowers erect or slightly inclined, white, pink or red Bloom time: late summer / early fall; mid fall.
Zephyranthes howardii Traub	Nuevo Leon, San Luis Potosi	Bloom color: yellow
Zephyranthes katheriniae L.B.Spencer	Hidalgo	Bloom color: pink; rose / mauve; red; bright yellow Bloom time: late summer / early fall; mid fall
Zephyranthes latissimifolia L.B.Spencer	Jalisco	Bloom color: pink; white / near white Bloom time: late spring / early summer
Zephyranthes leucantha T.M.Howard	Hidalgo	Bloom color: white / near white Bloom time: late summer / early fall; mid fall
Zephyranthes lindleyana Herb.	NE Mexico to C. America	Bloom color: magenta (pink-purple) Bloom time: late spring / early summer
Zephyranthes longifolia Hemsl.	SE. Arizona to W. Texas and Mexico	Bloom color: flowers erect to slightly inclined; pale yellow Bloom time: late summer / early fall; mid fall
Zephyranthes macrosiphon Baker	NE. Mexico	Bloom color: pink; rose / mauve Bloom time: mid fall
Zephyranthes minuta (Kunth) D.Dietr.	Mexico to Guatemala	Bloom color. pink, rose Big flowers
Zephyranthes miradorensis (Kraenzl.) Espejo & López-Ferr.	Veracruz	Bloom color: pink; white / near white Bloom time: late summer / early fall; mid fall
Zephyranthes moctezumae T.M.Howard	San Luis Potosi	Bloom color: pale pink especially on the outside of the petals Bloom time: late summer / early fall; mid fall
Zephyranthes morrisclintii Traub & T.M.Howard	Nuevo Leon	Bloom color: pale pink Bloom time: late spring / early summer
Zephyranthes nelsonii Greenm.	Estado de Mexico, Veracruz, Oaxaca, Chiapas	Bloom color: pale pink, sometimes with red stripes on the petals; white / near white Bloom time: late summer / early fall; mid fall
Zephyranthes nervosa Herb.	SE. Mexico	Bloom color: white / near white Bloom time: late summer / early fall; mid fall
Zephyranthes nymphaea T.M.Howard & S.Ogden	Tamaulipas, San Luis Potosi	Bloom color: chartreuse (yellow-green) Bloom time: late summer / early fall; mid fall
Zephyranthes orellanae Carnevali, Duno & J. L. Tapia	Yucatan	Flower erect, actinomorphic. Clear yellow, with or without pale reddish tinges toward the apices of the external faces of the external tepals. Species in critical condition.
Zephyranthes primulina T.M.Howard & S.Ogden	San Luis Potosi	Bloom color: pale or light yellow flowers backed pink-peach, most noticeable when in bud. Bloom time: late spring / early summer
Zephyranthes pulchella J.G.Sm.	Texas to NE. Mexico	Bloom color: flowers erect, bright yellow with orange or red tints on the petals Bloom time: late summer / early fall
Zephyranthes reginae T.M.Howard & S.Ogden	San Luis Potosi	Bloom color: pale yellow, coral / apricot Bloom time: mid summer. Rarely seen in cultivation.
Zephyranthes sessilis Herb.	State of Mexico and Distrito Federal	Bloom color: white, white with pink, white with reddish of the external faces of flower
Zephyranthes subflava L.B.Spencer	San Luis Potosi	Bloom color: white / near white; cream / tan Bloom time: mid summer; late summer / early fall
Zephyranthes traubii (W.Hayw.) Moldenke	SE. Texas to NE. Mexico	Bloom color: pale pink; white / near white Bloom time: late summer / early fall

niche they occupy, from xeric to temporarily flooded conditions, and have many coveted ornamental characteristics (Knox 2009).

Zephyranthes bulbs are rounded or ovoid, covered with a thin brown or black tunic. Depending on the species, the bulbs range in size from 2.5 cm to more than 5 cm in diameter (Knox 2005), the leaves are linear form bright grassy green to rather broad and glaucous, the size of the leaves varies from tiny in *Z. jonesii* (Cory) Traub to broad in *Z. lindleyana* Herb.; the scape is slender, hollow and leafless with one (rarely six) flower(s) at the apex. Rain lily flowers appear in spring, summer, or fall, depending on the species (Knox 2005). The flowers of *Zephyranthes* are funnel-shaped and have six petals; they are white, pink or yellow and crocus-like (Marta 2005). Flowers of novel hybrids occur in shades of pink, orange and red; some are multi-colored with striped or picotee patterns (Knox 2009). Some species have a sweet pleasant fragrance, which appears to be recessive; however, there are some species that carry the trait (*Z. drummondi* D.Don, *Z. morrisclintii* Traub & T.M.Howard, *Z. jonesii*) (Marta 2005; Roy Chowdhury 2006).

Zephyranthes propagation and culture

The flowers of *Zephyranthes* lasts just one or two days, depending on sunlight and temperature, however, new flowers continuously develop for several days, creating flushes of flowering. Rainfall triggers blooming (Knox *et al.* 2009). Most species under cultivation will bloom without the naturally imposed drought and wet that occurs in nature. When grown in greenhouses, rain lilies will bloom constantly; however, they have cycles of flowering. *Z. primulina* T.M.Howard & S.Ogden might be one of the longest blooming of all species (Marta 2005). Depending on the species, a cycle of dryness followed by watering encourages flowering.

Scagel (2003) planted bulbs of different *Zephyranthes* and *Habranthus* species (*Z. candida* (Lindl.) Herb., *Z. citrina* Baker, *H. robusta* Herb. ex Sweet) into cylindrical pots containing either a steam-pasteurized or a non-pasteurized 1:1 mixture of Willamette Valley alluvial silt loam and river sand (11 mg kg^{-1} available (Bray) phosphorus (P), pH of 6.3).

The pasteurized and non-pasteurized soil was inoculated with the vesicular-arbuscular mycorrhizal fungi (VAMF) (*Glomus intraradices* Schenck & Smith), at a rate of 1:166 (v/v), placing the inoculum at the base of each bulb at planting; as a control, sterilized inoculum was added at the base of the bulbs. The plants were maintained in glasshouses, fertilized and watered as needed. The results of Scagel (2003) showed that shoots of inoculated plants emerged 7-13 days before non-inoculated plants; in the case of *Z. candida* and *H. robusta* the emergence of flower bud was slightly delayed, and flower production was only increased when plants were grown in pasteurized soil; *Z. citrina* flowered 4-11 days earlier and the number of flowers was increased compared to non-inoculated plants; the leaf biomass was larger for *Z. citrina* but lower in *Z. candida* and *H. robusta* when the plants were inoculated. In a second growing cycle, the combined weight of bulbs and offsets was increased in *Z. candida* and *Z. citrina* by 50% to 150% at the end of the growing cycle.

The viability of the seed is lost rapidly; germination occurs in two to six weeks; under ideal conditions, seedlings will flower in 8 to 12 months (Knox 2009), but 2 years from seed to flower are reported (Smith *et al.* 1999). For this reason, rain lilies are traditionally propagated by bulb division or seeds; however, this conventional propagation is slow, seasonal and inconsistent. Additionally, hybrids may vary in the numbers of offsets they produce (Smith *et al*. 1999; Knox 2009; Gongopadhyay *et al*. 2010).

To achieve massive production of bulbs, a viable alternative to conventional propagation is micropropagation. Disinfestation is a crucial step for *in vitro* cultures, and on many occasions a considerable amount of plant tissue is needed because in every disinfestation process, some tissue must be discarded. The bulbs of some *Zephyranthes* species are small, and surface-disinfestation is difficult due to contamination, therefore, different tissue sources should be utilized. With this aim, Smith *et al.* (1999) established *in vitro* culture from seeds of different *Zephyranthes* species; the seeds were surface-sterilized for 2 min. in 95% alcohol, followed by 20% bleach for 15 min. and rinsed three times with sterile water. The seeds were germinated in a media containing MS inorganic salts and 30 g/l sucrose. The bulbs, twin scales and cross sections of the leaves, as well as the leaves from the aseptically germinated plants, served as explants for multiplication and adventitious regeneration. Bulbs were produced from the twin scale explants and embryogenic callus was obtained.

Aware of the contamination problems for micropropagation in the genus *Zephyranthes*, Gongopadhyay *et al*. (2010) collected bulbs of *Z. grandiflora* Lindl. (= *Z. minuta* D. Dietr.) and washed them thoroughly under running tap water, removed the outermost scale and immersed them in *Teepol* for 2-5 min. with continuous shaking, then rinsed them in distilled water. Later the bulbs where surface-sterilized with 0.1% $HgCl_2$ for 2 s, washed 3-4 times in sterile water, cut in segments and placed in MS media supplemented with 3% sucrose and 1 mg/l 6-benzylaminopurine (BA). The decontamination protocol was unsuccessful and had to be discarded due to microbial contamination. In a later attempt to decontaminate the *Z. candida* bulbs, Gongopadhyay *et al*. (2010) repeated the decontamination protocol, nevertheless, this time they treated the bulbs with 0.2 % *Bavistin*® and 0.1% *Pantomycin* for 2, 3, 4, and 5 h under continuous shaking before surface sterilization with $HgCl_2$. The antibiotic addition proved to be efficient and they obtained a 67% (4-h treatment) of non-contaminated explants. The *in vitro*-established bulbs were utilized for further micropropagation experiments and two types of explants were used: i) segmented bulbs and ii) bulb scales from the inner 2-3 layers. The explants were transferred to MS media supplemented with 3% sucrose and 2 mg/l BA. From the basal half of the bulb scales 11 shoots in average were regenerated and more shoots emerged on a basal achlorophyllous bulbous part. The shoots were transferred to MS media augmented with 2 mg/l BA and 1 mg/l gibberellic acid (GA_3) for enhancement. Stout roots were developed in the presence of 1 mg/l indole-3-butyric acid (IBA) and the plants were successfully transferred to the greenhouse.

Zephyranthes reproduction

Different chromosome numbers have been reported for different species of *Zephyranthes*, which varies even among the same species (**Table 3**). The different chromosome numbers range from 2n = 18 to 96 (Raina and Khoshoo 1971b) and shows an interesting aneuploid-polyploid chromosomal polymorphism. Not only different chromosome numbers but even different cytotypes have been reported for different *Zephyranthes* species in a detailed study of chromosome sets accomplished by Coe (1954). He found different chromosome numbers and cytotypes among plants of *Z. chlorosolen* D. Dietr.; in a couple of plants he found 58 and 59 chromosomes, while in others the chromosome number was 48; interestingly, the chromosomes from the plants with 58 and 59 chromosomes were smaller than those with 48 chromosomes and the total length of the chromosomes in a cell of the 59-chromosome plant was not greater than those in a cell of a 48-chromosome plant. Furthermore, the chromosome set in a 48-chromosome plant was not represented by 24 pairs of homologous chromosomes but by 23 homologous pairs and 2 chromosomes without morphological homologues. Similarly, *Z. drummondii* D. Don presented chromosome numbers of 24 and 48 in the same plant; different chromosome sets of 48-chromosome plants were constituted by 23 and 22 homologous chromosomes and 2 and 4 chromosomes without mor-

Table 3 Chromosome numbers (2n) reported for *Zephyranthes* species.

Species	Synonym	2n Chromosome numbers	Reference
Z. atamasco		24	Radford *et al.* 1968
Z. candida		19, 32, 38, 40	Tohibi Devi and Borua 1997
		38	Yokouchi 1965
		38, 40, 41	Raina and Khoshoo 1972a
Z. chlosolen	*Z. brazosensis*	48, 55, 56, 58, 59	Coe 1954
Z. citrina	*Z. sulphurea*	48	Raina and Khoshoo 1972c
Z. drummondii	*Z. pedunculata*	24, 48	Coe 1954
Z. longifolia		24, 44, 45, 46, 48, 49, 50	Coe 1954
Z. aff. mesochloa		12	Daviña and Fernandez 1989
Z. minuta	*Z. grandiflora*	24	Tohibi Devi and Borua 1997
		24	Kaboor and Tandom 1963
		24	Raina and Khoshoo 1972a
		48	Coe 1954
Z. puertoricensis	*Z. tubispatha*	24	Raina and Khoshoo 1972a
		25	Raina and Khoshoo 1971
Z. rosea		24	Raina and Khoshoo 1972a
Z. aff stellaris		20	Daviña and Fernandez 1989
Z. taubii		24	Coe 1954

phological homologues, respectively.

The most probable basic number of the genus is $x = 6$. (Flory 1968; Raina and Khoshoo 1971; Flory 1977; Meerow *et al.* 1999) although $x = 5$ has also been proposed (Daviña and Fernandez 1989). To determine whether 6 or 5 is the basic chromosome number of the genus, meiotic studies had to be performed, though meiotic analyses are scarce due to the difficulty of obtaining meiotic cells as the flowers develop inside the bulbs and the bulb has to be destroyed to obtain the flower buds and it is not possible to know in advance the meiotic stage of the cells.

In a cytological study of reproduction in *Z. drummondii* (Coe 1953) the microsporogenesis analyses revealed several abnormalities such as precocious chromosomes, bridges and fragments, non-disjunctions and chromosome eliminations; despite all the irregularities observed, the pollen fertility was about 91%. The more interesting abnormality was the clumpling of multivalent formations, containing more than 20 chromosomes in some cases. Tohibi Devi and Borua (1997) reported trivalent, quadrivalent and pentavalent associations in microsporogenesis analyses of *Z. minuta* D. Dietr. and *Z. candida* and low fertility in pollen germination. It seems that such abnormalities are common in *Zephyranthes* species; in a study of the pollen grain mitosis in *Z. puertoricensis*, Traub the chromosome numbers ranged from n = 1–16 (Raina and Khoshoo 1971), where those with less than 6 chromosomes might not be fertile, but those with 6 or more might be able to generate odd chromosome numbers. In the genus *Lilium* (2n = *2x* = 24), triploid hybrids (2n = *3x* = 36) were able to produce progeny, however, the chromosome numbers of the progeny was, in some cases, aneuploid, due to the production of pollen with odd chromosome numbers (Barba-Gonzalez *et al.* 2006). Despite all the abnormalities in meiosis, the pollen fertility does not seem to be affected. In a pollen fertility screening of different cytotypes of *Zephyranthes* whose chromosome numbers ranged from 24 to 73, all of them were fertile to some degree, from a maximum of 95% in those cytotypes with 48 chromosomes to 30% in those with 24 (Raina and Khoshoo 1972a). Kapoor and Tandon (1963) analyzed the endosperm formation in *Z .minuta* (2n = 24) (= *Z. grandiflora*; World Check List of Selected Plant Families) which had an endosperm of 3n = 36.

Cytological studies performed in *Z. drummondii* D.Don (= *Cooperia pedunculata* Herb.); World Check List of Selected Species) showed that it is a pseudogamous apomictic and that the occurrence of semigamy is frequent. Pollination is a pre-requisite for the setting of seed (Coe 1953).

In addition to the apomictic condition of some *Zephyranthes* it seem that species with styles longer than the filaments are self-incompatible, those with styles shorter than the filaments are self-compatible and those with styles more or less equal to the length of the filaments are self-incompatible (Raina and Khoshoo 1972c). However, this seems not to be the rule as in the case of *Z. atamasco*, a long-styled species is reported to be fully self-compatible (Broyles and Wyatt 1991).

One of the closest relatives of *Zephyranthes* is the genus *Habranthus* (Meerow *et al.* 1999) where chromosomal numbers of 12 and 18 are found (Felix *et al.* 2008). Considering these numbers, the aneusomaty (Coe 1954), the multivalent formation and all the abnormalities during meiosis (Coe 1953; Tohibi Devi and Borua 1997) present in different species of the genus *Zephyranthes*, it is clear that the genus has polyploidy, ranging from $2x$ to $16x$ with a basic number of $x = 6$ (Raina and Khoshoo 1972a). All this, coupled with self-compatibility / incompatibility and sexual apomictic reproduction, together with hybridization and polyploidy, the production of sex cells with a wide range of numbers, tolerated due to the inherent polyploidy constitution, has lead to a cycle of aneuploid variability, with a genetic system in the genus with the potential to conserve and preserve all heterozygosity through agamospermy and in particular through vegetative multiplication (Raina and Khoshoo 1972c).

Zephyranthes breeding

There are many traits that are pursued in *Zephyranthes* breeding, these include ruffled petals, bronze foliage, fragrance, colors of varying intensity (ranging from apricot to salmon, orange, cherry red and purple), stripes, picotees, bicolours as well as flowers that remain open for as long as 3 days (RoyChowdhury and Hubstenberger 2006)

Many *Zephyranthes* species are apomictic [*Z. primulina*, *katheriniae* L.B. Spencer, *macrosiphon* Baker, *citrina*, *longifolia* Hemsl., *pulchella* J.G. Sm. are apomictic (Roy Chowdhury and Hubstenberger 2006)]. This trait is inheritable (RoyChowdhury and Hubstenberger 2006), and is seen as a desirable character in breeding programs, because once a cultivar is established it will produce many seeds and the progeny will be genetically identical to the mother plant. On the other hand, when breeding for new traits, the apomictic species have a drawback when used as female parents because the crosses will always be successful, but never produce hybrid seed (RoyChowdhury and Hubstenberger 2006). For this reason, identified apomictic species are utilized as male parents.

There are many *Zephyranthes* intra- and interspecific hybrids. Perhaps the most well known hybrid is 'Ajax', which is a cross between *Z. candida x Z. citrina* (Knox 2009), but is not an 'easy to find' hybrid these days. After 'Ajax' another popular hybrid is the trihybrid 'Grandjax' from the cross between *Z. grandiflora x* Z. 'Ajax'. Like these hybrids, many others have been produced, but in most of them the lineages are not clear. There are a few hybridization programs that can be mentioned, among them are the hybrids developed by RoyChowdhury and Hubstenberger (2006), who utilized 44 different female parents, including botanical species and hybrid (some of them interspecific) and trihybrid cultivars such as [(*Z. candida x Z. citrina*) *x Z. macrosiphon*). The 44 female parents were crossed with 46 male parents, in total 215 crosses were performed of which 41% (87) were successful. Within these crosses 34 out of the 44 female parents made at least one fertile cross. Chu (2009) produced a series of interesting hybrids, where different color combinations were obtained in which selfing of different species was proven in the production of these hybrids; *Z. citrina* yielded seeds in 100% of the self-pollinations, while *Z. rosea*, *Z. candida* and *Z. grandiflora* (= *Z. minuta*; World Checklist of Selected Families) produced seeds in 22.6, 5.3 and 1.1% of the crosses, respectively. Successful interspecific crosses included *Z. candida* x *Z. citrina*; *Z. citrina* x *Z. candida*, *Z. minuta* and *Z. rosea*. Selfing of the F1 generation were performed with success. BC1 crosses were performed as follows: *Z. candida* x (*Z. candida* x *Z. citrina*); (*Z. citrina* x *Z. minuta*) x *Z. candida* and (*Z. citrina* x *Z. minuta*) x *Z. citrina*. However, it is noticeable that in most of the crosses involving *Z. citrina* as maternal parent, the progeny resembled the maternal phenotype, suggesting that these plants might not true hybrids, but a product of the apomictic nature of *Z. citrina.*

Fig. 3 ***Sprekelia formossisima.*** Photo: A. Rodriguez.

SPREKELIA

Biology and morphology

Sprekelia Heist. (2n = 60, 120) is an herbaceous monocotyledonous genus of perennial bulbs of the Amaryllidaceae commonly known as 'Aztec lily' and 'Jacobean lily'. The genus comprises two recognized species (World Checklist of Selected Species 2011) viz. *Sprekelia formosissima* (L.) Herb. and *Sprekelia howardii* Lehmiller; nevertheless other species are mentioned in literature, however it may be a monotypic genus and the mentioned species are variants of *S. formosissima* (**Fig. 3**) (Rodriguez-Contreras A, Instituto de Botanica y Zoologia, Universidad de Guadalajara, Mexico, pers. comm.). It is cultured worldwide as a pot plant. Its introduction to Europe can be traced back to the end of the 16th century, when it was known as '*Narcissus Indicus Jacobeus*' (Ramon-Laca Menendez de Luarca 1997).

It has a zygomorphic perianth adapted for hummingbird pollination (Meerow *et al.* 2000). The flower stems are 40-70 cm high, sometimes reaching 90 cm; they are orchid-shaped and occur in various shades of red (Howard 2001), often with a white line in the center of the tepals and sometimes with white borders on tepals 1, 3 and 5. Two groups have been described, the first with wide perennial leaves and the second with thin deciduous leaves (Borys *et al.* 2005b). The leaves are sometimes glaucous.

It is distributed from the North of Mexico from Chihuahua to the south in the state of Oaxaca (Howard 2001).

It belongs to the Zephyranthinae subtribe of the Hippeastrae tribe, of the American clade. It is a sister genus to *Zephyranthes* to which it is closely related (Meerow *et al.* 1999).

Sprekelia propagation and culture

Plants of *Sprekelia* grow in a wide variety of soils, from deep to shallow, clayish, sandy or rocky, and from temperate to dry and hot climates (Borys *et al.* 2005b). Naturally it grows among xeric bushes, among rocks in oak forests and disturbed places, from 750 to 2700 m (Ortiz-Medina 1996). Flowering of *Sprekelia* is reported to occur from April to July, however, under irrigation it can be extended to August, (Borys and Leszczynska-Borys 1999). The bulbs have a dormancy period in winter and spring, which can be overcome by dry storage for a few weeks after flowering (Lozano 1992).

The traditional propagation of *Sprekelia* is through bulb division and occasionally by seeds; bulb division is preferred because bulb maturity takes up to four years when grown from seed. An average of 85% germination of *S. formosissima* seeds was reported in temperatures ranging from 10-35°C, it took four days at temperatures ranging from 20-25°C, however, at extreme temperatures (10-15°C and 30-35°C) the germination percentage decreased slightly and the days to germinate increased (Borys *et al.* 2005c).

Besides traditional propagation, micropropagation of *Sprekelia* has been achieved with 83% survival utilizing small bulbs established *in vitro,* cultured in media containing MS inorganic salts, supplemented with 100 mg L^{-1} *myo*-inositol, 0.4 mg L^{-1} thiamine, 1.0 mg L^{-1} pyridoxine, 1.0 mg L^{-1} niacin, 0.4 mg L^{-1} glycine, 80 mg L^{-1} adenine sulphate, 20 µm 6-benzyladenine (BA) and 3% sucrose. The bulblet growth was promoted by subculturing the bulblets in the same media without the adenine sulphate and the BA, with a sucrose concentration of 5%. The bulbs were rooted in a medium containing MS inorganic salts, supplemented with 100 mg L^{-1} *myo*-inositol, 0.4 mg L^{-1} thiamine, 1.0 mg L^{-1} pyridoxine, 1.0 mg L^{-1} niacin, 0.4 mg L^{-1} glycine, 0.2 mg L^{-1} IBA and 3% sucrose (Cazarez-Prado *et al.* 2010).

Sprekelia breeding

Several *Sprekelia* cultivars have been released to the market, 'Orient Red' is considered to be one of the best cultivars, which flowers with the first rains and is able to flower again in the fall (Howard 2001). Besides the intra-specific hybrids, perhaps one of the most interesting features of *Sprekelia* is the relative ease that it is hybridized with other genera. Several intergeneric hybrids have been reported, such as i) *Hippeastrum* x *Sprekelia* = *x Hippeastrelia*, whose chromosome number has been doubled *in vitro* to restore fertility (Van Tuyl pers. comm.); among this group there are complicated crosses such as (*H. papilio* (Ravenna) Van Scheepen x *H. fragrantissimum* (Cárdenas) Meerow) x *Sprekelia formosissima* (Fellers 1998); 'Mystique' is a remarkable hybrid because the plant sets fertile seeds (Howard 2001) and *Sprekelia* x *Habranthus* = x *Sprekanthus* Traub. Recently, another intergeneric hybrid has been reported as x *Sprekelianthes* Lehmiller, this is the result of a cross of *Sprekelia formosissima* x *Zephyranthes traubii*; the bigene-

Table 4 Alkaloids present in different species of the genus *Hymenocallis.*

Alkaloids	***Hymenocallis* species**									
	H. bolivariana	***H. harrisiana***	***H. littoralis***	***H. latifolia***	***H. lobata***	***H. rotata***	***H. sonorensis***	***H. speciosa***	***H. tubiflora***	***H. venezuelensis***
(+)-8-*O*-demethylmaritidine			+[9]							
1-*O*-acetylpseudolycorine									+[8]	
4,5-dehydro-anhydrolycorine									+[8]	+[8]
4,5-dehydro-anhydro-pseudolycorine									+[8]	+[8]
7-deoxynarciclasine			+[5,7]							
7-deoxy-*trans*-dihydronarciclasine			+[5,7]	+[5]						
11-Hydroxyvittatine			+[9]							
N-demethylgalanthamine									+[8]	
Anhydrolycorine					+[8]				+[8]	+[8]
Anhydro-pseudolycorine					+[8]				+[8]	
Caranine		+[2]								
Galanthamine isomer	+[8]				+[8]					+[8]
Galanthine		+[2]								
Haemanthidine		+[2]		+[4]						
Haemanthamine		+[2]				+[1]		+[1]		
Hippeasterine			+[9]	+[4]		+[1]		+[1]		
Lycoramine	+[8]				+[8]					+[8]
Lycorine		+[2]	+[9]			+[1]		+[1]	+[8]	+[8]
Narciclasine			+[5,7]	+[6]				+[6]		
Narcissidine		+[2]								
Nerinine								+[1]		
Pancratistatin			+[3,5,7]	+[6]			+[6]	+[6]		
Pseudolycorine		+[2]			+[8]				+[8]	+[8]
Tazettine		+[2]		+[4]		+[1]		+[1]		

The superscript refers to the bibliographic source as follows: 1 Boit 1958; 2 Boit 1960; 3 Backhaus *et al.* 1992; 4 Antoun 1993; 5 Petit *et al.* 1993; 6 Petiti *et al.* 1995; 7 Idso *et al.* 2000; 8 Rivero *et al.* 2004; 9 Abou-Donia 2008.

ric hybrid resembles *Sprekelia*, it displays the same characteristics, but its dimension is about half the size of *Sprekelia* (Lehmiller 2003-2004). It is argued that the relative ease of *Sprekelia* hybridization with the above-mentioned genera is due to its taxonomic proximity. Meerow *et al.* (1999) groups the genus *Sprekelia* in the Hippeastrae tribe, together with *Habranthus*, *Zephyranthes*, *Hippeastrum*, *Rhodophiala* and *Traubia.*

ALKALOIDS OF *HYMENOCALLIS*, *SPREKELIA* AND *ZEPHYRANTHES*

Besides the ornamental importance of the genera, several genera of the Amaryllidaceae are of pharmaceutical importance due to their alkaloid content. Alkaloids are groups of complex heterocyclic nitrogen compounds, which have strong physiological activity, are often toxic, and retain their own basic chemical properties' (Aniszewski 2007).

The alkaloids of the Amaryllidaceae are a group of isoquinoline alkaloids, produced almost solely by members of this family. These alkaloids have attracted considerable amount of interest due to some important pharmacological activities they have been shown to possess (Unver 2007).

There are many different L-tyrosine-derived alkaloids present in the genus *Hymenocallis* where at least 24 alkaloids have been reported (**Table 4**) (Boit and Döpke 1958, 1960; Backhaus 1992; Antoun *et al.* 1993; Pettit *et al.* 1993, 1995; Idso *et al.* 2000; Rivero *et al.* 2004; Abou-Donia *et al.* 2008); in the genus *Zephyranthes* there are 18 reported alkaloids and 7 for *Sprekelia formosissima* (**Table 5**) (Pettit 1984; Pettit *et al.* 1990; Gabrielsen *et al.* 1992; Hohmann 2002; Mutsuga 2002; Kaur *et al.* 2007; Unver 2007; Wu *et al*. 2009a, 2009b, 2010).

These alkaloids have a wide range of biological activities, they are known to have analgesic, cytotoxic activity against various human tumoral cell lines, and anti-malarial, antineoplastic and display effects on the central nervous system (Aniszewski 2007). Among the different alkaloids present in the genera *Hymenocallis*, *Zephyranthes* and *Sprekelia* the lycorine-type alkaloids are particularly important for Alzheimer's disease. Other alkaloids present in the different genera have been useful in the treatment of tumors, breast cancer, diabetes mellitus and human epidermoid carcinoma as well as other anti-cancer activities (Pettit 1984; Kaur *et al.* 2007). Alkaloids from *Z. carinata* Herb. induced apoptosis in tumor cells by blocking the progression of the cell cycle at G_0/G_1 and S phases; and *Z. candida* was found to contain *trans*-dihydronarciclasine, a cytostatic constituent utilized for leukemia treatment (Pettit *et al*. 1990).

Also, the alkaloids in these genera present antiviral activity and *in vitro* inhibition of poxvirus (Gabrielsen *et al.* 1992; Mutsuga 2002).

In addition to the alkaloids and other substances obtained from bulbs and seeds of the genus *Zephyranthes*, six ceramides have recently been identified in *Z. candida*: candidamide A and B, zephyrantnamide A, B, C and D. These are the first reported for the Amaryllidaceae. The importance of ceramides lies in its role as signalling molecules involved, among other functions, in programmed cell death and apoptosis. Candidamide A and B displayed moderate activities against bacteria *Staphylococcus aureus* and *Escherichia coli*, and fungi *Aspergillus niger*, *Candida albicans* and *Trichophyton rubrum* (Wu *et al*. 2009a, 2009b, 2010).

CONCLUSIONS

The genera *Hymenocallis*, *Sprekelia* and *Zephyranthes* offer great potential as ornamental plants and many cultivars and hybrids are already present in the market. However, the addition of Mexican species for breeding programmes would provide genetic variability resulting in novel cultivars with interesting ornamental traits of importance. These three genera are related and interspecific hybridization as well as intergeneric hybridization is possible. The inclusion of other related genera, such as *Habranthus* could speed up the breeding process. The development of micropropagation

Table 5 Alkaloids present in different *Zephyranthes* and *Sprekelia* species.

Alkaloids	**Species**						
	Z. candida	***Z. carinata***	***Z. citrina***	***Z. minuta***	***Z. rosea***	**'Ajax' (*Z. candida* x *Z. Citrina*)**	***Sprekelia formossisima***
1-*O*-(3-hydroxybutyryl)pancratistatin		+[5]					
1-*O*-(3-*O*-β-*O*-glucopyranosylbutyryl)pancratistatin		+[5]					
3-epimacrinine							+[6]
7-deoxynarciclasine				+[4]			
8-*O*-demethylmaritidine							+[6]
Crinamine					+[2]		
Crinidine						+[1]	
Epimaritidine					+[2]		
Galanthine			+[7]				
Haemanthamine	+[8]		+[7]		+[2]	+[1]	+[6]
Haemanthidine	+[3,8]						+[6]
Ismine							+[6]
Lycorenine	+[3]		+[7]				
Lycorine	+[8]		+[7]			+[1]	
Maritidine			+[7]		+[2]		
Narcissidine						+[1]	
Nerinine	+[3]					+[1]	
Oxomaritidine			+[7]				
Pancracine			+[7]				
Pancratistatin	+[8]			+[4]			
Pretazettine							+[6]
Tazettine	+[3]					+[1]	+[6]
trans-dihydronarciclasine	+[4]						
Vittatine			+[7]				

The superscript refers to the bibliographic source as follows: 1 Boit and Döpke 1961; 2 Ghosal and Razdan 1985; 3 Petit et al 1990; 4 Gabrielsen et al 1992; 5 Kojima et al 1998; 6 Hohmann *et al* . 2002; 7 Aniszewski 2007; 8 Wu et al 2009

techniques in the different genera should speed the development of new varieties. Basic, as well as applied research must be performed in order to understand the complicated chromosomal segregation, especially in the genus *Zephyranthes*. This research might help to unravel the mystery of the family origin in the Americas. There are many species of the different genera that must be domesticated to become part of breeding programmes; research has been conducted regarding the phenology of several species, however future research must be conducted to determine the phenology of species that are not commercially known.

ACKNOWLEDGEMENTS

The authors would like to express their gratitude to Dr. Aaron Rodriguez-Contreras, of the Instituto de Botanica y Zoologia, Universidad de Guadalajara, Mexico for pictures for this work.

REFERENCES

Abou-Donia AH, Toaima SM, Hammoda HM, Shawky E, Kinoshita E, Takayama H (2008) Phytochemical and biological investigation of *Hymenocallis littoralis* Salisb. *Chemistry and Biodiversity* **5**, 332-340

Aniszewski T (2007) *Alkaloids – Secrets of life. Alkaloid Chemistry, Biological Significance, Applications and Ecological Role* (1st Edn), Elsevier, Amsterdam, NL, 316 pp

Antoun MD, Mendoza NT, Rios YR, Proctor GR, Mahinda-Wickramaratne DB, Pezzuto JM, Douglas-Kinghorn A (1993) Cytotoxicity of *Hymenocallis expansa* alkaloids. *Journal of Natural Products* **56**, 1423-1425

Axelrod DI (1973) History of the Mediterranean ecosystem in California. In: di Castri F, Mooney HA (Eds) *Mediterranean Type Ecosystems: Origin and Structure* (1st Edn, Ecological Studies Vol 7) Springer-Verlag, Berlin, New York, pp 225-227

Axelrod DI (1975) Evolution and biogeography of Madrean-Thethyan sclerophyll vegetation. *Annals of the Missouri Botanical Garden* **62**, 280-334

Backhaus RA, Pettit III GR, Huang D-S, Pettit GR, Groszek G, Odgers JC, Ho J, Meerow A (1992) Biosynthesis of the antineoplastic pancratistatin following tissue culture of *Hymenocallis littoralis* (Amaryllidaceae). *Acta Horticulturae* **306**, 364-366

Barba-Gonzalez R, Van Silfhout AA, Visser RGF, Ramanna MS, Van Tuyl JM (2006) Progenies of allotriploids of Oriental x Asiatic lilies (*Lilium*) examined by GISH analysis. *Euphytica* **151**, 243-250

Bauml JA (1979) A study of the genus *Hymenocallis* (Amaryllidaceae) in Mexico. MSc thesis, Cornell University, 189 pp

Boit H-G, Döpke W (1958) Alkaloide aus Hymenocallis-Arten. *Die Naturwissenschaften* **45**, 315

Boit H-G, Döpke W, Stender W (1958) Alkaloide aus *Hippeastrum rutilum*, *Lycoris albiflora*, *Zephyranthes andersoniana* und *Sternbergia fischeriana*. *Die Naturwissenschaften* **45**, 390

Boit H-G, Döpke W (1961) Alkaloide aus *Haemanthus*-, *Zephyranthes*-, *Galanthus*-und *Crinum*-Arten. *Die Naturwissenschaften* **48**, 406-407

Borys MW, Leszczynska-Borys H, Galvan JL (1999) Observations on flowering in *Sprekelia formossisima* (L.) Herbert. *Revista Chapingo Serie Horticultura* **5**, 153-158

Borys MW, Leszczynska-Borys H, Galvan JL (2005a) *Hymenocallis* Salisb. germination variants and seedling yield. *Acta Horticulturae* **673**, 191-198

Borys MW, Leszczynska-Borys H, Galvan JL (2005b) Variants in *Sprekelia formossisima* (L.) Heber. In: *51st Annual Meeting – Interamerican Society for Tropical Horticulture.* 10-14 October, Boca Chica, Republica Dominicana (Abstract)

Borys MW, Leszczynska-Borys H, Galvan JL (2005c) Seeds germination of ornamental related to constant temperature. In: *51st Annual Meeting – Interamerican Society for Tropical Horticulture.* 10-14 October, Boca Chica, Republica Dominicana (Abstract)

Borys MW, Leszczynska-Borys H, Galvan JL (2008) Variants in *Hymenocallis* Salisb. *Acta Horticulturae* **766**, 391-398

Borys MW, Leszczynska-Borys H, Galvan JL (2009) *Hymenocallis* Salisb. – Bulbs reactions to applied temperatures. *Acta Horticulturae* **813**, 631-636

Broyles SB, Wyatt R (1991) The breeding system of *Zephyranthes atamasco* (Amaryllidaceae). *Bulletin of the Torrey Botanical Club* **118**, 137-140

Castillo-Campos G, Medina-Abreo ME, Davila-Aranda PD, Zavala-Hurtado JA (2005) Contribución al conocimiento del endemismo de la flora vascular en Veracruz, México. *Acta Botanica Mexicana* **73**, 19-57

Cazarez-Prado M, Andrade-Rodriguez M, Villegas-Monter A, Alia-Tejacal I, Villegas-Torres OG, Lopez-Martinez V (2010) *In vitro* propagation of *Sprekelia formossisima* Herbert., a wild plant with ornamental potential. *Revista Fitotecnia Mexicana* **33**, 197-203

Chu C-Y (2009) Interspecific hybridization of *Zephyranthes*. MSc thesis. National Chung Husing University. Taiwan. (Abstract)

Coe GE (1953) Cytology of reproduction in *Cooperia pedunculata*. *American Journal of Botany* **40**, 335-343

Coe GE (1954) Chromosome numbers and morphology in *Habranthus* and *Zephyranthes. Bulletin of the Torrey Botanical Club* **81**, 141-148

Daviña JR, Fernandez A (1989) Karyotype and meiotic behavior in *Zephyranthes* (Amaryllidaceae) from South America. *Cytologia* **54**, 269-274

De Hertogh AA, Le Nard M (1993) *The Physiology of Flower Bulbs* (1st Edn), Elsevier, Amsterdam, NL, 812 pp

Felix WJP, Dutilh JHA, De Melo NF, Fernandez AA, Felix LP (2008) Intrapopulational chromosome number variation in *Zephyranthes sylvatica* Baker (Amaryllidaceae: Hippeastrae) from Northeast Brazil. *Revista Brasileira de Botânica* **31**, 371-375

Fellers JD (1998) Progeny of *Hippeastrum papilio. Herbertia* **53**, 129-144

Flory WS (1968) Chromosome diversity in species, and in hybrids of tribe Zephyrantheae. *Nucleus* **11**, 79-95

Flory WS (1977) Overview of chromosomal evolution in the Amaryllidaceae. *Nucleus* **20**, 70-88

Gabrielsen B, Monath TP, Huggins JW, Kefauver D (1992) Antiviral (RNA) activity of selected Amaryllidaceae isoquinoline constituents and synthesis of related substances. *Journal of Natural Products* **55**, 1569-1581

Ghosal S, Ashutosh, Razdan S (1985) (+)-Epimaritidine, an alkaloid from *Zephyranthes rosea*. *Phytochemistry* **24**, 635-637

Ghosal S, Singh SK, Unnikrishnan SG (1986) Phosphatidylpyrrolophenanthridine alkaloids from *Zephyranthes flava*. *Phytochemistry* **26**, 823-828

Gongopadhyay M, Chakrabotry D, Dewanje S, Bhattacharya S (2010) Clonal propagation of *Zephyranthes* using bulbs as explants. *Biologia Plantarum* **54**, 793-797

Greathouse GA, Rigler NE (1941) Alkaloids from *Zephyranthes texana, Cooperia pedunculata* and other Amaryllidaceae and their toxicity to *Phymatotrichum omnivorum*. *American Journal of Botany* **28**, 702-704

Grossi A (2007) *Hymenocallis* and other spider lilies. *The Plantsman* **6**, 222-226

Hanks GR, Jones SK (1987) The growth and flowering of *Hymenocallis x festalis. Scientia Horticulturae* **30**, 301-313

Herrera MR, Machocho AK, Brun R, Viladomat F, Codina C, Bastida J (2001) Crinane and lycorane-type alkaloids from *Zephyranthes citrine. Planta Medica* **67**, 191-193

Hohmann J, Forgo P, Molnar J, Wolfard K, Molnar A, Thalhammer T, Mathe I, Sharples D (2002) Alkaloids isolated from the bulbs of *Sprekelia formosissima* and *Hymenocallis* x *festalis*. *Planta Medica* **68**, 454-457

Howard TM (1978) New *Hymenocallis* species from Mexico. *Plant Life* **34**, 60-68

Howard TM (2001) *Bulbs for Warm Climates* (1st Edn), University of Texas Press, Texas, USA, 288 pp

Huber H (1969) Die sammenmerkmale und verwandtschafts verhaltnisse der Liliiflorae. *Mitteilungen der Botanischen Staatssammlung München* **30**, 479-484

Idso SB, Kimball BA, Pettit III GR, Garner LC, Pettit GR, Backhaus RA (2000) Effects of atmospheric CO_2 enrichment on the growth and development of *Hymenocallis littoralis* (Amaryllidaceae) and the concentration of several antineoplastic and antiviral constituents of its bulbs. *American Journal of Botany* **87**, 769-773

Kapoor BM, Tandon SL (1963) Contributions to the cytology of endosperm in some angiosperms IV. *Zephyranthes grandiflora* Lindl. *Genetica* **34**, 102-112

Kaur A, Kamboj SS, Singh J, Singh R, Abrahams M, Kotwal GJ, Saxena AK (2007) Purification of 3 monomeric monocot man-nose-binding lectins and their evaluation for antipoxviral activity: Potential applications in multiple viral diseases caused by enveloped viruses. *Biochemistry and Cell Biology* **85**, 88-95

Knox GW (2009) Rainlily, *Zephyranthes* and *Habranthus* spp.: Low maintenance flowering bulbs for Florida gardens. Environmental Horticulture Department, Florida Cooperative Extension Service, Institute of Food and Agricultural Sciences, University of Florida, Florida USA, 12 pp

Kojima K, Mutsuga M, Inoue M, Ogihara Y (1998) Two alkaloids from *Zephyranthes carinata*. *Phytochemistry* **48**, 1199-1202

Köhler E, Brückner P (1989) The genus *Buxus* (Buxaceae): Aspects of its differentatiation in space and time. *Plant Systematics and Evolution* **162**, 267-283

Kornienko A, Evidente A (2008) Chemistry, biology and medicinal potential of narciclasine and its congeners. *Chemical Reviews* **108**, 1982-2014

Lehmiller DJ (2003-2004) A new nothogeneric taxon: x *Sprekelianthes* (Amaryllidaceae). *Herbertia* **58**, 123-126

Leszczynska-Borys H, Borys MW, Galvan JL (2005) Cloning of the *Hymenocallis* Salisb. *Acta Horticulturae* **673**, 691-697

Little EL, Critchfield WB (1969) Subdivisions of the genus *Pinus* (Pinus). *United States Department of Agriculture Forest Service*, Miscellaneous Publication 1144

Liston A, Reiseberg LH, Hanson MA (1992) Geographic partitioning of chloroplast SNA variation in the genus *Datisca* (Datiscaceae). *Plant Systematics and Evolution* **181**, 121-132

Lozano PA (1992) Relación entre el tamaño de bulbo y la floración de *Sprekelia formossisima* (L.) Herbert. Thesis. Universidad Popular Autonoma de Puebla, 60 pp

Marta F (2005) Breeding of rainlilies. *Bulbs* **7**, 25-32

Meerow AW (1987) Biosystematics of tetraploid *Ecorsia* (Amaryllidaceae). *Annals of the Missouri Botanical Garden* **74**, 291-309

Meerow AW (1989) A monograph of the Amazon lilies, *Eucharis* and *Caliphruria* (Amaryllidaceae). *Annals of the Missouri Botanical Garden* **76**, 136-220

Meerow AW, Dehgan B (1995) Towards a phylogeny of the Amaryllidaceae. In: Rudall PJ, Cribb PJ, Cutler DF, Humphries CJ (Eds) *Monocotyledons: Systematics and Evolution* (1st Edn), Kew Publishing, UK, pp 169-179

Meerow AW, Fay MF, Guy CL, Li Q-B, Zaman FQ, Chase MW (1999) Systematics of Amaryllidaceae based on cladistic analysis of plastid *rcbL* and *trnL-F* sequence data. *American Journal of Botany* **86**, 1325-1345

Merrow AW, Guy CL, Li Q-B, Yang S-L (2000) Phylogeny of the American Amaryllidaceae based on nrDNA ITS sequences. *Systematic Botany* **25**, 708-726

Meerow AW, Guy CL, Li Q-B, Clayton JR (2002) Phylogeny of the tribe Hymenocallidae (Amaryllidaceae) based on morphology and molecular characters. *Annals of the Missouri Botanical Garden* **89**, 400-413

Mori G, Imanishi H, Sakanshi Y (1991) Effect of temperature on flowering of *Hymenocallis speciosa* Salisb. *Journal of the Japanese Society for Horticultural Sciences* **60**, 387-393

Murashige T, Skoog F (1962) A revised medium for rapid growth and bioassay with tobacco tissue culture. *Physiologia Plantarum* **15**, 473-497

Mutsuga M, Kojima K, Yamashita M, Ohno T, Ogihara Y, Inoue M (2002) Inhibition of cell cycle progression through specific phase by pancrastatin derivatives. *Biological and Pharmaceutical Bulletin* **25**, 223-228

Ogden S (2007) *Garden Bulbs for the South* (2nd Edn), Timber Press, Portland, Oregon, USA, 396 pp

Ortiz-Medina E (1996) Juvenilidad e inducción a floración en *Sprekelia formosissima* Hebert. MSc thesis, Colegio de Postgraduados, 115 pp

Pettit GR, Gaddamidi V, Cragg GM (1984) Antineoplastic agents, 105. *Zephyranthes grandiflora*[1]. *Journal of Natural Products* **47**, 1018-1020

Pettit GR, Cragg GM, Singh SB, Duke JA, Doubek D (1990) Antineoplastic agents, 162. *Zephyranthes candida. Journal of Natural Products* **53**, 176-178

Pettit GR, Pettit III GR, Backhaus RA, Boyd MR, Merrow A (1993) Antineoplastic agents, 256. Cell growth inhibitory isocarbostyrils from *Hymenocallis*. *Journal of Natural Products* **56**, 1682-1687

Preuss KD (2002) Spider lilies for the South. *Bulbs* **4**, 27-31

Radford AE, Ahles HE, Bell CR (1968) *Manual of the Vascular Flora of the Carolinas* (1st Edn), University of North Carolina Press, Chapel Hill, North Carolina, USA, 1183 pp

Raina SN, Khoshoo TN (1972a) Cytogenetics of tropical bulbous ornamentals VII. Male meiosis in some cultivated taxa of *Zephyranthes*. *Cytologia* **37**, 217-224

Raina SN, Khoshoo TN (1972b) Cytogenetics of tropical bulbous ornamentals VI. Chromosomal polymorphism in cultivated *Zephyranthes*. *Caryologia* **24**, 217-227

Raina SN, Khoshoo TN (1972c) Cytogenetics of tropical bulbous ornamentals. IX Breeding systems in *Zephyranthes*. *Euphytica* **21**, 317-323

Ramon-Laca Menendez de Luarca L (1997) Las plantas vasculares de la Península Iberica en la obra de Clusio: Envíos de semillas de Sevilla a Leiden. *Anales del Jardin Botanico de Madrid* **55**, 419-427

Raven PH, Axelrod DI (1974) Angiosperm biogeography and past continental movements. *Annals of the Missouri Botanical Garden* **61**, 539-673

Ray MF (1994) Biogeography and systematic of Lavatera and Malva species. In: *American Journal of Botany. Annual Meeting of the Botanical Society of America with Other Affiliated Societies University of Tennessee/Knoxville,* 7-11 August, 1994, Tennessee, United States p 199 (Abstract)

Rivero N, Gomez M, Medina JD (2004) Search for bioactive alkaloids in *Hymenocallis* species. *Pharmaceutical Biology* **42**, 280-285

RoyChowdhury M, Hubstenberger J (2006) Evaluation of cross pollination of *Zephyranthes* and *Habranthus* species and hybrids. *Journal of the Arkansas Academy of Sciences* **60**, 113-118

Scagel CF (2003) Soil pasteurization and incubation with *Glomus intraradices* alters flower production and bulb composition of *Zephyranthes* spp. *Journal of Horticultural Science and Biotechnology* **78**, 798-812

Smith GL, Flory WS (1990) Studies on *Hymenocallis henryae* (Amaryllidaceae). *Brittonia* **42**, 212-220

Smith GL, Flory WS (2001) *Hymenocallis* (Amaryllidaceae) in Texas, with a new varietal combination. *Novon* **11**, 229-232

Smith GL, Anderson LC, Flory WS (2001) A new species of *Hymenocallis* (Amaryllidaceae) in the lower central Florida Panhandle. *Novon* **11**, 233-240

Smith RH, Burrows J, Kurten K (1999) Challenges associated with micropropagation of *Zephyranthes* and *Hippeastrum* sp. (Amaryllidaceae). *In Vitro Cellular and Developmental Biology – Plant* **35**, 281-282

Tohibi Devi T, Borua PK (1997) Meiotic behavior and pollen fertility in three species of *Zephyranthes* (Amaryllidaceae). *Biologia Plantarum* **39**, 355-360

Traub HP (1962) Key to the subgenera, alliances and species of *Hymenocallis*. *Plant Life* **18**, 55-72

Unver N (2007) New skeletons and new concepts in Amaryllidaceae alkaloids. *Phytochemistry Reviews* **6**, 125-135

World Checklist of Selected Plant Families (2011) The Board of Trustees of the Royal Botanic Gardens, Kew. Available online: http://www.kew.org/wcsp/

Wu Z, Chen Y, Xia B, Wang M, Dong Y-F, Feng X (2009a) Two novel ceramides with a phytosphingolipid and a tertiary amide structure from *Zephyranthes candida*. *Lipids* **44**, 63-70

Wu Z, Chen Y, Feng X, Xia B, Wang M, Dong Y (2009b) Two new ceramides from *Zephyranthes candida. Chemistry of Natural Compounds* **45**, 829-833

Wu Z, Chen Y, Feng X, Xia B, Wang M, Dong Y (2010) Another two novel ceramides from *Zephyranthes candida. Chemistry of Natural Compounds* **46**, 187-191

Yokouchi Y (1965) Chromosome studies on *Zephyranthes*. III Chromosome ring of *Z. candida. La Kromosoma* **61**, 1989-1990