Mexican Geophytes I. The Genus Polianthes

Rodrigo Barba-Gonzalez1 • José Manuel Rodríguez-Domínguez1 • Ma. Claudia Castañeda-Saucedo2 • Aaron Rodriguez3 • Jaap M. Van Tuy1 • Ernesto Tapia-Campos4*

1 Centro de Investigación y Asistencia en Tecnología y Diseño del Estado de Jalisco A.C. Biotecología Vegetal, Av. Normalistas #800. Colinas de la Normal, Guadalajara Jalisco, C.P. 44270, México
2 Centro Universitario del Sur, Universidad de Guadalajara, Av. Prolongación Colón S/N, Km 3 Carretera Cd. Guzmán, Ciudad Guzmán, Jalisco, C.P. 49000, México
3 Centro Universitario de Ciencias Biológicas y Agropecuarias, Instituto de Botánica y Zoología, Universidad de Guadalajara, Km. 15.5 Carretera a Nogales, Predio las Agujas, Zapopan, Jalisco México
4 Plant Breeding, Wageningen University and Research Center, Droevendaalsesteeg 1, 6708 PB, Wageningen, The Netherlands

* Corresponding author: etapia@ciatej.net.mx

ABSTRACT

Members of the genus Polianthes L. are bulbous ornamentals in the Agavaceae, includes 15 species three varieties and a two cultivars native to Mexico. Polianthes tuberosa L. (Tuberose) is the only species cultivated as an ornamental cut flower in tropical and subtropical areas. The cultivation of tuberose occupies a prime position in the floriculture industry in countries such as Mexico, China, India, New Zealand and Taiwan. The Flower colour of all known cultivars of P. tuberosa is white; however, attempts have been made to introduce colors from related species. Besides its use as an ornamental, it is cultivated for use in manufacturing: as a source of fragrant essences in perfumery, to extract polysaccharides and glycosides; in addition P. geminiflora (Llave & Lexarza) Rose is utilized as a source of saponins for soap. The main diseases in this crop are caused by virus and it is affected by a coleoptera (Scyphophorus acupunctatus) whose larva feeds on the bulbs. In this review we will cover the uses, distribution, species, of the genus and the current state of tuberose breeding as a further reference for tuberose breeding programmes.

Keywords: breeding, native, ornamental

CONTENTS

INTRODUCTION ........................................................................................................................................................................ 122
IMPORTANCE AND USES ........................................................................................................................................................ 122
ORIGIN ..................................................................................................................................................................................... 123
DISTRIBUTION ....................................................................................................................................................................... 123
PESTS AND DISEASES ........................................................................................................................................................... 125
BREEDING OF POLIANTHES .................................................................................................................................................. 126
CONCLUSION ........................................................................................................................................................................... 127
ACKNOWLEDGEMENTS ........................................................................................................................................................ 127
REFERENCES ......................................................................................................................................................................... 127

INTRODUCTION

Mexico is rich in biological diversity due to its geographical position and its range of different climates (Ramamoorthy et al. 1998; Toledo 1988). Globally it is considered among the nations with higher biological richness (Villaseñor 1991), with between 8 and 12% of species on the planet being found there (Challenger 1998). Its phanerogamic flora is estimated to be around 22,351 species and 56% of the species in the Mexican flora are endemic (Villaseñor 2003).

A variety of families, genera and species originating from the Mexican flora have contributed to world horticulture: Bromeliaceae, Cactaceae, Compositae, Crassulaceae, Euphorbiaceae, orchids and the genera Ageratum, Bouvardia, Dahlia (dahlia), Cosmos (mirlós), Euphorbia (nochebuena), and Tocotes (camposuchitl) (Moran 2004).

The genus Polianthes L. (Agavaceae) is endemic to Mexico, and includes 15 species three varieties and a few cultivars. Most species in this genus are used for ornamental and ceremonial purposes. The best known taxon is Polianthes tuberosa L. (Tuberose), which has been cultivated and used for medicinal and ceremonial practices since pre-hispanic times (Solano and Feria 2007; Solano and Ríos-Gómez 2011).

IMPORTANCE AND USES

The genus Polianthes is most widely used as an ornamental in horticulture, principally represented by Polianthes tuberosa, which was grown as an ornamental and medicinal plant by the Aztecs more than 400 year ago. It is also one of the most important cut flowers in tropical and subtropical areas (Benschop 1993). The flower remains fresh for a very long time and stands long distances transportation. P. tuberosa is grown commercially for its fragrant cut flowers in India, New Zealand, Japan and Mexico. It is also cultivated for the perfume industry in India and France.

The natural oil of Tuberose remains one of the most expensive raw materials. The most common constituents of Tuberose concrete are geranial, nerol, benzyl alcohol methyl benzoate, methyl silicate, ethanol, benzyl benzoate...
and methyl anthranilate (Sheela 2008). The fragrant oil, almost all of which comes from India, is one of the most expensive of the fragrant oils used in perfumes, valued more than $2,000.00 per pound (Hodges 2010). Some of the components present in oil of tuberose (mainly geraniol, indole and methyl anthranilate) are known to have antifungal activity (Nidrty and Babu 2005).

Due to the high concentration of sapogenin in their rhizomes and tuberous roots, many species have been used as substitutes of soap, including: P. geminiflora, P. graminifolia Rose and P. tuberosa. For this use, these species are known by the Nahuaht name ‘amole’ which signifies soap, and are also called omoloxochitl or omiloxochitl (‘soap flower’ in Nahauatl) (Rose 1903; Trueblood 1973). However, this property is more evident in Manfreda Salisb. and Prochnyanthes S. Watson (closely related to Polianthes), than Polianthes with its smaller rhizomes.

A more recent development in the genus is using wild Polianthes species, mainly those with novel colours, to introduce this feature in tuberose varieties through a breeding programme. Some of these wild species have yellow, pink, orange, red and purple colored flowers, and apparently there are not serious barriers in crossing these with white tuberose (Shen et al. 1997).

**ORIGIN**

The genus Polianthes is native to México; and P. tuberosa was spread to different parts of the world during the 16th century. It belongs to the Agavaceae as originally proposed by Hutchinson (1959) and Traub (1953) rather than the Amaryllidaceae, and this is supported by cytogenetic studies. These studies showed that species in the genus have 5 large L-shaped and 25 small haploid chromosomes, indicating a close relationship with the Agavaceae family (Trueblood 1973).

The genus Agave L. with c. 166 species is the largest genus in the family Agavaceae, a family that contains 9 genera and c. 293 species (Eguiarte et al. 2000). The genus Agave is paraphyletic to the genera Manfreda Salisb., Polianthes L. and Prochnyanthes S. Watson, and the entire clade comprising the 208 species that belong in the four genera has been termed Agave sensu lato (Eguiarte et al. 2000). The genus Agave sensu stricto is predominantly monocarpic and harbors the most dry-adapted (and succulent) members of the family Agavaceae (Good-Avila et al. 2006). It is divided into two subgenera, Liattacea (53 species) and Agave (113 species) based on the inflorescence (Gentry 1982). The three genera that are additionally included in Agave sensu lato, Manfreda, Polianthes and Prochnyanthes are predominantly polycarpic, herbaceous, and inhabit a more temperate environment. They are mainly found in Mega-México 3 (México and contiguous parts of southwestern U.S. and Central America that share a similar flora) (Eguiarte et al. 2000).

Even though there is a controversy regarding the inclusion of these herbaceous genera in the family Agavaceae (Trueblood 1973; Verhoek 1975) and McVaugh (1899), reject the family due mainly to inclusion of these genera; both molecular (Eguiarte et al. 2000; Good-Avila et al. 2006) and morphological (Hernandez 1995) evidence are consistent with their inclusion in this family. The recent molecular analysis indicates an estimated age of the family between 20 and 26 million years and an age of Agave sensu lato of ≤ 10 million years (Good-Avila et al. 2006). The lineage of the herbaceous Agavaceae (Poliannates, Manfreda and Prochnyanthes) has its origin 3 million years ago (Eguiarte et al. 2000).

Verhoek-Williams (1975) divided the genus Polianthes into two subgenera: Polianthes and Bravoa. These subgenera were separated based on the position of the flowers, colour, size, orientation and position of the lobes of the perianth and insertion of the stamens. Although this proposal has not been published formally (Solano and Rios-Gomez 2011).

Subgenus Polianthes is characterized by the distal portion of the tube in a horizontal position or close to this position, the flowers are white to light pink and the perianth lobes are erect or revolute reflexed. Members of the subgenus Bravoa have pendant flowers, reddish pink, red or coral coloured flowers with short, erect lobes (Verhoek-Williams 1975; Solano 2000).

While, the morphological and molecular evidence suggests that Manfreda, Polianthes and Prochnyanthes are closely related genera, and sometimes difficult to distinguish, there are some morphological traits that can be used to identify and separate them. Species of Manfreda and Prochnyanthes are relatively small in comparison with those of Agave, but most are larger than any Polianthes.

In general, Manfreda is characterized by spikes of solitary yellow-green flowers that are sometimes streaked or tipped with maroon, exerted stamens and styles, herbaceous leaves and thick, upright, rhizomes. The genus Prochnyanthes differs from Manfreda in having paired flowers (similar to Polianthes) at the nodes and included styles and stamens. Like Manfreda, and unlike Agave, the leaves of Prochnyanthes are not woody, and there is also a thick, tuberous rhizome (Verhoek 1978).

The genus Polianthes is more herbaceous than Manfreda, with more delicate leaves and inflorescences. Most species have whitish flowers, but P. geminiflora (Lex.) Rose, has reddish-orange flowers, and P. densiflora (B.L.Rob & Fernald) Shinners, yellow ones. Hawkmoth pollination has been suggested for most species except for P. geminiflora, which has been considered to be pollinated by hummingbirds (Rocha et al. 2006).

Prochnyanthes is very closely related to Polianthes and possibly belongs to that genus. The primary difference between the two genera is that the flowers of Prochnyanthes have a very distinct structure with a narrow tubular corolla that widens markedly in the middle. The flowers are whitish or pale green (Rocha et al. 2006).

**DISTRIBUTION**

*Polianthes tuberosa* is native to Mexico and was spread around the world during the 16th century, and is known worldwide as an ornamental and multipurpose species. The wild species of this genus are only found in Mexico and the highest number of species occurs in the state of Jalisco (Fig. 1).

Species of *Polianthes* have been recorded in 18 Mexican states, where most occur in pine forest, oak forest, or pine-oak forest, some in grasslands, and a few in tropical dry or semi-deciduous forests. The genus *Polianthes* has the highest concentration of species in the southern Sierra Madre Occidental and the northwest side of the Trans-Mexican Volcanic Belt (Solano and Feria 2007). In particular, the Transvolcanic Belt is considered very important as a
biographic barrier for Polianthes species dispersal, and may be the explanation for only two species (*P. bicolore* and *P. oaxacana* García-Mend. & E.Solano) occurring in Oaxaca (Solano 2000).

*Polianthes geminiflora* (Fig. 2A, 2B, 2C, 2D, 2O) is the species with the broadest geographical and ecological distribution (Solano 2000); while five species, *P. densiflora*, *P. howardi* Verh.-Will. (Fig. 2G), *P. longiflora* Rose (Fig. 2H), *P. palustris* Rose (Fig. 2K, 2Q), and *P. platyphylla* Rose (Fig. 2L) are listed as rare and are considered to be in the category of special protection according to Mexican law (DOF 2002). Habitat destruction is one of the main factors affecting populations of *Polianthes* species (Solano and Feria 2007). More recently Feria-Arrollo *et al.* (2010), re-evaluating the extinction risk of these five species, determined that *P. howardi* is in danger of extinction, *P. longiflora* and *P. platyphylla* are endangered and *P. palustris* is probably extinct. However, a wild population of *P. palustris* has been found recently 40 km north of Acaponeta, in Nayarit (Fig. 2K, 2Q), and this discovery can be a great opportunity to gather more morphological data for this species and provide us with new information about its distribution (Perez *et al.* 2010). Recently, Solano and Ríos-Gómez (2011) described *P. zapopanensis* like a new species in Jalisco, México.

*Polianthes tuberosa* has white flowers that are sweetly scented. It usually flowers during summer and early autumn, after planting in spring. There are up to 20-30 flowers in one inflorescence and the length of rachis varies between 14 and 28 cm, depending upon size of bulb planted. As well as a source of essential oils for the perfume industry, it is commonly used in bouquets and in vases for interior decoration. Tuberose has two flower types, single and double. The single type is often called ‘Mexican tuberose’ or ‘Single’ while the double-flowered type is sold as ‘The Pearl’ or ‘Double’. Worldwide, the double forms are more popular for cut flowers while the single forms are used mainly in the essences industry. Although the flowers are pure white, the
The wild species of *Polianthes* are considered perennial, their foliage remains only one growth season and they are dormant in winter. Consequently this species can be propagated vegetatively by using the bulbs or sexual by seeds.

The main disadvantage of seed propagation is the time required for the plants to reach maturity, however, this can be an important mean to maintain the genetic diversity and propagate the endangered species of *Polianthes*. The seeds of some wild *Polianthes* were studied by Serrano-Casas et al. (2000), and determined that three species (*P. geminiflora* var. *geminiflora*, *P. sp. and P. longiflora*) have epigeal germination, and their cotyledon develop a haustorium. None of these three species exhibited seed dormancy. In general, the seeds of these species remain in the soil for a long time, and are dispersed in the autumn, remaining dormant in the dry winter period and ready to germinate in the summer rainfall period. Therefore these seeds have a long period of viability and are considered ‘orthodox’ seeds.

Tuberose is propagated by bulbs, bulblets and seeds. Similar to wild *Polianthes*, the plants raised from seed take longer time to flower than those raised from bulbs. Seed production is poor in the single-flowered types, and germination rates are very low (Sheela 2008; Hodges 2010). Thus, vegetative propagation from bulbs is the most economical method of propagation, and seed is only used breeding programmes.

Tissue culture is used to obtain virus-free plants or for bulk uping, and has been successfully developed for use in research and breeding programmes. The main objective in tuberose micropropagation has been to obtain many plants in a short time (Table 2). Scientific reports about in *vitro* culture of wild *Polianthes* are not known.

### PESTS AND DISEASES

There is not much information about pests or diseases in the wild species of *Polianthes*. In the case of *P. tuberosa*, while it is considered relatively free of pests and easy to grow and propagate, there are some common pests which affect its culture. The main insect pests are thrips and red spider mites, which can be controlled using common insecticides.
The greasy streak nematode (Aphelancoides besseyis) and root-knot nematode (Meloidogyne incognita) may cause damage (Sheela 2008).

In recent years, producers in Mexico have noticed severe damage caused by an insect that they call black weevil, which was identified as Synophorus acuminatus Gyllenhal (Coleoptera: Curculionidae) (Camino et al. 2002). Most damage is caused by the weevil larvae boring into the bulb. In Mexico it has been reported attacking several economically important plants in the Agavaceae, such as Agave tequilana (Leiva-Vazquez et al. 2001) and A. fourcroydes (Valdes et al. 2004) and Yucca valida Brandegge (Servin et al. 2006) and some wild genera from the same family. In Mexico this insect is considered the most important pest affecting tuberose cultivation, because, if this is not controlled in time, it can devastate plantations. In fact, the high cost to control this insect in a badly infested field is the main reason that in Morelos, México, some plantations are discarded. In the municipalities of Tepalcingo and Coatlán del Río, Morelos, cultivation of A. tequilana F.A.C. Weber began some years ago, whereas in Emiliano Zapata there are wild agaves, predominantly A. angustifolia Haw., in the hills near cultivated P. tuberosa. These two agaves may serve as a refuge for S. acpunctatus during chemical applications or when tuberose is not in the field, complicating its control (Camino et al. 2002).

Tuberoses have been affected by many fungal and viral diseases. Among the fungal diseases, bulb rot caused by Fusarium oxysporum is a serious disease. It causes severe yield loss (Muthukumar et al. 2006). Another fungal disease in the flowers is Botrytis cinerea which occurs under cool temperatures. In Asia, mainly in Taiwan, there is a viral disease which causes severe damage in tuberose plantations, the Tuberose Mild Mosaic Virus (TMMV), a newly recognized potyvirus, distinguished from other known potyviruses based on its serological and biological characteristics, recorded in 1998 (Chen and Chang 1998). TMMV was found in nearly every tuberose plant examined in Taiwan but did not cause evident damage on cut flower production during the summer season. However, during other growing seasons when the temperature is below 25°C, infected tuberoses tend to express pronounced foliar symptoms and usually their growth vigor is significantly reduced (Chen and Chang 1998; Chen et al. 2002), reducing the quality of flowers and bulbs, which leads to decreased profits to growers and propagators. Such symptoms on tuberose, which had not been described in a few countries like New Zealand (Pearson and Horner 1986), Taiwan (Chen and Chang 1998) and China (Lin et al. 2004). In India, tuberose plantations were heavily infected, indicating its widespread nature (Kulshreshta et al. 2005). The causal agent could only be transmitted mechanically to tuberose, indicating a narrow host range. Further, the virus could be transmitted by aphis vectors in a non-persistent manner (Chen and Chang 1998; Kulshreshta et al. 2005). Scientific reports about TMMV in Tuberose from America are not known.

### BREEDING OF POLIANTHES

Although *P. tuberosa* is an ornamental species of economic importance worldwide, the development of new cultivars has not been very successful; only two major varieties (single and double) are cultivated, both of them have white flowers. The single tuberose (Mexican single) has one row of corolla segments; the semi-double have two or three rows of corolla segments and the double-flowered plants has three rows of corolla segments (Sheela 2008). Although very few cultivars are available in the U.S., internationally several dozen cultivars are reported (Hodges 2010).

Howard (2001) described three interspecific hybrids with novel variants in flower colour: *P. x blissii* (*P. geminiflora* x *P. tuberosa*) with orange-red flowers; *P. x bundrantii* ‘Mexican fireracker’ like a modern hybrid between *P. howardii* and *P. tuberosa* with flowers marked internally in shades of white or purple and externally in red or pink and green and the hybrid *P. Sunset.* *P. sp. #2* x *P. tuberosa*, with pinkish or reddish exteriors and yellow interiors.

Single-tepalled cultivars are more suitable for bouquets and essential oils, while double-tepalled cultivars are only used in the first one purpose. For pot culture, dwarf cultivars with variegated leaves are the better choice (Sheela 2008).

Mutation breeding has been used to improve tuberose (Younis and Borham 1975; Abraham and Desai 1976). In the National Botanical Research Institute, in India, bulbs of the cultivars ‘Mexican simple’ and ‘Double Pearl’ were irradiated from which two new cultivars were developed and released in 1974: ‘RajatRekha’ and ‘SwarmaRekha’, both cultivars have white flowers (Sheela 2008).

There is some interspecific and intergeneric breeding research being conducted in Japan, Taiwan, India, and the U.S. to develop orange-, yellow-, pink-, and lavender-flowered tuberose for the cut flower market as well as dwarf types for garden use. At present, the colour and colour intensity of these hybrids are not consistent and are affected by environmental conditions. Tuberoses with coloured flowers are not yet commercially available in the U.S. Most of the Polianthes species and related genera with coloured flowers are not fragrant (Hodges 2010).

Shen et al. (1987) report reciprocal crosses between single and double varieties of tuberose in Taiwan, producing many single and few double plants in the progenies. On the other hand, Sheela (2008) mentioned the commercial use of tuberose hybrids in India, some of which were developed using single and double cultivars like: ‘Shingar’ and ‘Suvasini’.

The use of wild Polianthes species in tuberose breeding programmes has previously been reported in the works published by Shen (Shen et al. 1997, 2003), who made interspecific crosses mainly using single and double cultivars of *P. tuberosa* and *P. howardii* (reddish-purple flowers) in order to bring the flower colour of *P. howardii* into *P. tuberosa*, and several hybrids have been reported showing...
pink, reddish-purple, purple, orange and yellow suitable only for cut flowers.

Huang et al. (2001), analyzed the pigments in the hybrids obtained by Shen, and reported the presence of either carotenoids or anthocyanins in the tepals of some hybrids and both pigments in others. They concluded that the use of P. howardii in tuberose breeding can contribute to the extension of the diversity of flower colors.

In the case of interspecific crosses, Verhoek-Williams (1975) made an extensive number of crosses between Manfreda and Polianthes. In the other hand the University of Arkansas began a breeding programme between Polianthes and Manfreda in 2003 in order to obtain cultivars more tolerant for hot and dry conditions, and reported that the flower colour of Polianthes is dominant over that of Manfreda virginica (L.). Salisb. and M. maculosa (Hooker) Rose and these hybrids showed hybrid vigor characterized by larger plant size and extended blooming time. Some hybrids of this project were successfully over-wintered suggesting that M. virginica may confer additional cold-hardiness (Lindstrom 2006).

Sterility in tuberose has been reported mainly in the double cultivar (Verhoek-Williams 1975; Shen et al. 1987) that cannot be used as a pollen parents. The double cultivar has been subjected to artificial selection for a long time and currently is not known to exist in the wild, the pistil and stamens have become petaloid segments or staminoid. Vegetative propagation has favored this transformation and most individuals in cultivation are sterile (Solano 2000). Shen et al. (1987) found that the double cultivar is fertile in early flowering stage, when the female parent is 2-3 days after anthesis and can be used as both pollen and seed parents. It is also reported that P. tuberosa is self-incompatible and reported no seed production in both selfed single varieties and selfed double varieties due to self-incompatibility (Shen et al. 1987); however, Huang et al. (2001) found that selfed progenies could be produced. On the other hand Verhoek (1975) demonstrated that P. geminiflora is self-compatible.

In our experience, doing some interspecific and intergeneric crosses with Polianthes in the Plant Biotechnology Unit of CIATEJ, Jalisco, México in 2010, we found that P. geminiflora var. clivicola McVaugh was successful both as a receiver of pollen as well a donor, with different Prochnyanthes var. clivicola McVaugh was successful both as a receiver of pollen as well a donor, with different

Table 3 Parents, crosses, number of fruits and number of seeds in some Polianthes interspecific and intergeneric crosses made in 2010 in CIATEJ.

<table>
<thead>
<tr>
<th>Female parent</th>
<th>Male parent</th>
<th>No. of crosses</th>
<th>No. of fertilized fruits</th>
<th>Seeds/capsule</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. geminiflora var. clivicola</td>
<td>Prochnyanthes</td>
<td>151</td>
<td>13</td>
<td>15.4</td>
</tr>
<tr>
<td>P. geminiflora var. clivicola</td>
<td>P. howardii</td>
<td>30</td>
<td>4</td>
<td>14.27</td>
</tr>
<tr>
<td>Prochnyanthes</td>
<td>P. geminiflora var. clivicola</td>
<td>26</td>
<td>2</td>
<td>28.5</td>
</tr>
<tr>
<td>Manfreda elongata</td>
<td>P. geminiflora var. clivicola</td>
<td>11</td>
<td>1</td>
<td>10</td>
</tr>
<tr>
<td>P. montana</td>
<td>P. howardii</td>
<td>2</td>
<td>1</td>
<td>13</td>
</tr>
<tr>
<td>P. platyphylla</td>
<td>P. howardii</td>
<td>6</td>
<td>2</td>
<td>34</td>
</tr>
<tr>
<td>P. tuberosa</td>
<td>P. howardii</td>
<td>153</td>
<td>4</td>
<td>20.5</td>
</tr>
<tr>
<td>P. platyphylla</td>
<td>P. montana</td>
<td>4</td>
<td>2</td>
<td>10.5</td>
</tr>
<tr>
<td>P. tuberosa (var. Mexican Double)</td>
<td>Manfreda elongata</td>
<td>162</td>
<td>2</td>
<td>21</td>
</tr>
</tbody>
</table>

Total | 445 | 27 |

CONCLUSION

The genus Polianthes is represented by a group of species with a high ornamental potential worldwide. Internationally, the only reported ornamental species from this genus is P. tuberosa, however due to the international demand for novel ornamental varieties; wild species of this genus can be useful source of genes to generate new flower colours, shapes, and more pest resistant varieties. At the same time, some of these wild species are currently used as ornamentals locally in Mexico, thus domestication and selection of these species can easily be achieved in the near future. Nevertheless, the endangered status of many of these species, coupled with the loss of their natural habitat, has made necessary to develop a management and conservation programme for them in their natural habitats and in both working collections and germplasm banks.

ACKNOWLEDGEMENTS

The authors want to express their gratitude to the CONACYT Mexico (Reg. 84167) for the funding provided for this work.

REFERENCES


