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Flowering in *Hylocereus* spp.: comparative analysis and self-incompatibility

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ABSTRACT

Objective: To know the variables of the reproductive component of materials for manual cross-pollination purposes, for which the search for sexual synchrony is emphasized.

Design/methodology/approach: Four materials were analyzed, two with white pulp and two with red pulp, about which it is unknown if they present sexual self-incompatibility, and the synchrony in flowering is also unknown. The flowering phase and the variables that can shed light on its reproductive behavior were analyzed

Results: It was found that the red materials present strong hercogamy, they cannot self-fertilize. There is also no floral synchrony, but there is closeness between the date of anthesis in a pitahaya with white pulp and a red one, which would allow promoting cross-pollination.

Study limitations/implications: *Hylocereus* spp. is consumed in a large part of the world and has acquired a very strong importance since the industrial demand is increasing; however, several of the genotypes used in commercial production in Mexico show low fruit set compared to high floral emission, which is considered self-incompatibility.

Findings/conclusions: The presence of hercogamy, stronger in the red-fleshed materials, indicates the existence of sexual self-incompatibility, explaining the fact that the materials emit a large number of flowers, but do not achieve fruit setting.

Keywords: Cactaceae, pollination, fruit trees.

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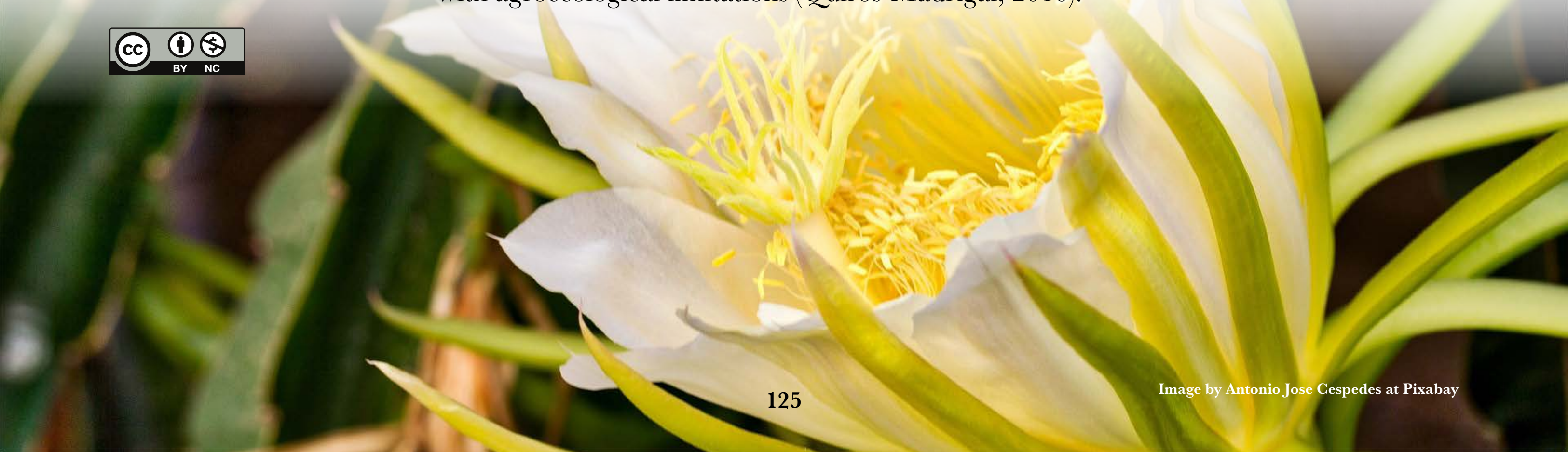
INTRODUCTION

Pitahaya (*Hylocereus* spp.) is a fruit tree with potential for the national and international market due to its demand for fresh consumption and industrial use, since it favors economic profitability (Centurión-Yah *et al.*, 2008), and can be a strategy to increase the contribution of the sector and to make more dynamic rural development processes, particularly in areas with agroecological limitations (Quirós-Madrigal, 2010).



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The origin of pitahaya is attributed to the forested regions of the tropics and subtropics of Mexico, Central and South America; its cultivation is distributed throughout the world, especially because it can grow in soils with low organic matter content and nutrient deficiencies (de Oliveira *et al.*, 2020). It has climbing habits and requires a tutor, since its stems climb trees and rocks. It uses the crassulacean acid metabolism (CAM) pathway (Osuna-Enciso *et al.*, 2016), so greater water use efficiency is expected and it is exceptionally tolerant to long periods of drought so it can be cultivated in arid and semi-arid areas (Tel-Zur *et al.*, 2011).

Hylocereus spp. is found in the wild in Mexico and its seeds are disseminated by birds. It has a wide diversity and variability of materials, which generate fruits with different characteristics and qualities that can be directed to different demands of the agrifood chain. The main consumption of *Hylocereus* is as fresh fruit, but the flowers and tender shoots are also consumed as fresh vegetables and its potential for cultivation is expanding due to strong demand in the industrial, food technology and pharmaceutical areas. Within the industrial market, various authors (Esquivel & Araya, 2012; Woo *et al.*, 2011; Wong & Siow, 2015), pointed out the importance of pitahayas for their betalains, especially betanins as a natural food colorant, and pectin as a good quality thickener, as well as a colorant in the cosmetology industry (Le Bellec, 2004; Retana-Sanchez *et al.*, 2019). Al-Alwani *et al.*, 2017, replaced the use of silicon with pitahaya dye to fabricate solar cells and to generate a low-cost and environmentally-friendly sensitizer.

The demand for pitahaya has favored its commercial development in Asian countries that take advantage of windows of opportunity in the European market throughout the year, such as Vietnam and Thailand, which have hybrids, as well as Israel; the cultivation techniques are in pots in protected environments, with fertigation and cross-pollination. In Mexico, it is grown commercially in Puebla, Oaxaca, Yucatán, Campeche, Quintana Roo, Chiapas, Tabasco, Sinaloa and Veracruz with variable average yields ranging from 3.5 to 16.0 ton/ha (Martínez-Ruiz *et al.*, 2017; Osuna-Enciso *et al.*, 2016). The fruit that reaches Mexico's markets comes from small commercial plantations and orchards that use materials of wild origin or selected by the producers. One of the most important problems is the low proportion of fruits developed in relation to the flowers produced, mainly in red-fleshed pitahaya, which is associated with sexual self-incompatibility; various reports point out that some genotypes are self-incompatible, that is, incapable of self-pollinating and fertilizing with their own pollen, even though the pollen itself is viable (Cohen & Tel-Zur, 2012; Lichtenzveig *et al.*, 2000). Self-incompatibility is due to some species-specific mechanisms such as hercogamy and gynoheterostyly, which affect pollination (Márquez-Guzmán *et al.*, 2005; Weiss *et al.*, 1994). As a result, growers harvest fruit of different sizes, many of the fruits are not marketable and yields are low. To solve this problem, it is necessary to carry out manual cross-pollination, when the materials have a certain level of self-incompatibility. Strong self-incompatibility has been reported in red-fleshed genotypes, which should be pollinated with pollen from white materials.

Therefore, the flowering stage of *Hylocereus* spp. and some floral biology variables of four materials are analyzed: two of red pulp, Rojo Ch and Rojo P, from Chiapas and Puebla, which are cultivated commercially; the other two are of white pulp and were selected by INIFAP, Andrea of pink peel and Tanith of yellow peel, with high potential for commercial cultivation, about which it is unknown whether or not they have traits of self-incompatibility. The final objective of the analysis is to determine variables of the reproductive component of the materials for the purpose of manual cross-pollination, for which the search for sexual synchrony is emphasized.

MATERIALS AND METHODS

The study was carried out at two sites, first an orchard at the Cotaxtla Experimental Field in Veracruz (INIFAP) where the white materials were established, and second a farm in Suchiapa Chiapas where the red genotypes are grown. The Cotaxtla Experimental Field is located in the municipality of Medellín, Veracruz, Mexico (18° 56' 1.8" N, 96° 11' 35.5" W), with an altitude of 10 m. The average rainfall is 1336 mm, where the rainiest months are July and September and the average annual temperature is 26 °C [12]. Suchiapa is located at 16° 37' 30" latitude North and 93° 6' 0" longitude West and an altitude of 530 m. The climate is warm sub-humid with periodic rains, the average annual temperature is 28 °C, with an average rainfall of 956 mm (H. Ayuntamiento Municipal de Suchiapa, 2019).

This study analyzes the flowering stage and certain aspects of floral biology of four materials, two of red pulp (Rojo Ch and Rojo P, from Chiapas and Puebla, *H. purpusii* and *H. ocamponis*, respectively), grown commercially in Chiapas due to their high productive potential. The other two are white-fleshed and were selected by INIFAP (Andrea, of pink peel and Tanith of yellow peel, both *H. undatus*) because of their great potential for commercial cultivation. Therefore, since the interest is focused on the flowering stage, nine variables were considered: flower length, ovary length and diameter, style length and diameter, number of stigma lobes, locule length and diameter, and hercogamy distance.

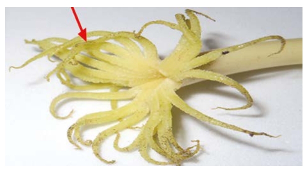
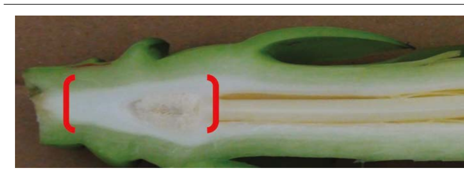
The four materials are rainfed and only manual auxiliary irrigation is used during the installation stage of the orchard in the field. Producers consider the included materials to be of great importance, to offer in the international market. Fifteen flowers of each material were used, which were sectioned to collect the data of the variables included in the analysis. Most of them come from the most abundant floral flushes, the second from the white-fleshed pitahayas, and the second and third from the red-fleshed pitahayas. Table 1 shows the variables of interest.

To help determine the sexual synchrony of the materials, four phases of the flowering stage were considered: emergence of the flower bud (when the areola begins to swell), anthesis (flower opening), fruit setting, and arrival at fruit maturity (as the end of the stage). The sequence was followed from the first flush of flower buds and during the total flushes of each material, since those with white pulp only yielded four, while those with red pulp managed to emit five.

RESULTS AND DISCUSSION

Pitahaya is a perennial plant that grows wild in southeastern Mexico and Central America. Its metabolism is crassulacean acid (CAM), which uses PEP carboxylase (an enzyme that binds CO_2 to phosphoenolpyruvate) in the fixation of atmospheric CO_2.

Table 1. Flower characteristics of the materials analyzed.

Internal characters of the flower	**Data**		
Style (cm)	**Selection**	**Longitude**	**Width**
	Tanith	25.2	0.48
	Andrea	25	0.44
	Roja Ch	23.04	0.52
	Roja P	22.95	0.50
Stigma lobe (cm)		**Longitude**	**Width**
	Tanith	2.3	26.8
	Andrea	1.8	25.8
	Roja Ch	2.3	19.6
	Roja P	2.3	25.0
Herkogamy (cm)		**Distance**	
	Tanith	1.1	
	Andrea	1.3	
	Roja Ch	2.1	
	Roja P	2.9	
Ovary region (cm)		**Longitude**	**Width**
	Tanith	6.2	3.7
	Andrea	5.3	3.8
	Roja Ch	5.6	
	Roja P	6.50	3.2
Loculus		**Longitude**	**Width**
	Tanith	1.6	1.0
	Andrea	1.5	0.9
	Roja Ch	2.1	2.6
	Roja P	1.6	1.4
Flower (cm)		**Longitude**	**Color**
	Tanith	39	White
	Andrea	38	White
	Roja Ch	34	White
	Roja P	33	White

This type of plant keeps stomata closed during the hot and dry hours of the day and opens them at night, with less loss of water vapor (Méndez *et al.*, 2009). Its nocturnal flowering and anthesis mechanism occurs only one night; the first flower flush happens from the end of April to September, but some materials offer early flower flushes from the end of March. The flowers are hermaphrodite, some white to cream colored, and in some red-fleshed materials some reddish coloration is observed in the external sepals. They open around 18:00 h and close between 10:00 and 11:00 AM; anthesis in the flower occurs from 15 to 17 hours (Valiente-Banuet *et al*., 2007).

Therefore, pitahaya for its natural pollination requires nocturnal pollinators such as bats, which are the most efficient, and nocturnal moths and beetles are also very important although they are less efficient (Valiente-Banuet *et al*., 2007). On the other hand, various authors point out the existence of self-incompatibility in several genotypes of *Hylocereus*, which constitutes a genetic barrier in the progamic phase that happens between the pollen and the stigma or during the development of the pollen tubes in the style, which occurs mainly in clones of *H. costaricensis* and *H. polyrhizus* (Weiss *et al*., 1994). The same authors point out the inability of these genotypes to form fruits after self-pollination, while in *H. undatus* they found 50% of self-incompatibility.

Sexual incompatibility is the inability of a fertile hermaphrodite plant to produce zygotes after self-pollination (Nobel & De la Barrera, 2002). It is a genetic-biochemical mechanism, where the pistil rejects its own pollen, but accepts pollen from genetically different plants; it occurs to avoid inbreeding and favors cross-pollination. It should be added that, on the other hand, the distance between the stigma and the anthers, that is, hercogamy, can also decrease the probability of autogamy (Valiente-Banuet *et al*., 2007).

Table 2 shows the description of the floral structure in the four materials considered important in the pollination phase.

Table 2 shows that there is a very strong statistical difference in eight of the variables included that differentiate the floral structure of the materials. The data of flower length indicate that due to the average size of the flower in white-fleshed materials, they are larger and have longer style length, more stigma lobes, smaller locule diameter, and lower hercogamy.

Figure 1A presents the explanatory variables on the factorial axes; it is observed that ovary diameter, flower length and style length are of greater importance in defining the white-fleshed materials (Andrea and Tanith), while number of stigma lobes and ovary length, although important, show a secondary weight that differentiates them from the

Table 2. Flower characteristics of *Hylocereus* spp. for four materials.

Changeful	Andrea	Tanith	Roja P	Roja Ch	p (0.05)
Flower length	38.0 a	39.1 a	32.8 b	34.4 ab	$<$0.0001
Ovary length	5.3 a	6.2 ab	6.5 b	4.4 a	$<$0.0001
Ovary diameter	3.8 ab	3.7 b	3.2 a	3.5 ab	0.0097
Style length	25 b	25 b	23 a	23.0 ab	$<$0.0001
Style diameter	0.4 a	0.5 a	0.5 a	0.5 a	0.4405
Number of lobes	25.8 b	26.8 b	25 ab	19.6 a	0.0007
Loculu length	1.5 a	1.6 ab	1.7 ab	2.1 b	0.0125
Locule diameter	0.9 a	1.1 ab	1.4 b	1.2 ab	0.0062
Herkogamy	1.3 a	1.1 a	2.9 b	2.1 ab	$<$0.0001

Kruskal-Wallis, 0.05. Means with different letters are statistically different.

red-fleshed pitahayas. Figure 1A also shows how the variables hercogamy, locule diameter, locule length and style diameter define a difference between Rojo P and Rojo Ch, with Andrea and Tanith. Figure 1B shows that considering the explanatory variables used, there is a very marked difference between the materials, and manages to include 98.4% of the variability. This allowed representing in different quadrants the materials, and pointing out that the white-fleshed materials are located in an opposite dimension from the red-fleshed, where Tanith and Andrea are located in the same plane and are close to each other; with certain similarities, since an area of conflict is observed where they are intertwined, that is to say, some of their explanatory variables are similar. The red-fleshed materials, in diametrically opposite planes, are not observed as close and in a way it is because they are different materials, *H. purpusii* and *H. ocamponis*.

The variables that in some way determine the strongest differences in the floral structure of the white materials are ovary diameter, flower length and style length. The Rojo P material shows as distinctive feature a very strong hercogamy (Table 1A).

Flowering phases

Figure 2 shows the phenological development of the materials during the four phases (emergence, anthesis, fruit setting and fruit maturity) and in the floral flushes of each material. The Tanith and Andrea materials only reached four flushes, the second being the one with the highest flower emission; in the case of the red pulp materials, they reached five flushes, but only the second and third emitted the highest number of flowers; however, fewer flowers took. It was also observed that new flushes appear before maturity of the previous flush.

Figure 2 shows that the two red-fleshed cultivars emitted their first flower emissions earlier than the white-fleshed pitahayas, at the end of March and beginning of April. In white-fleshed pitahayas, the Tanith cultivar emitted its first flower flush (emergence) in early May, and Andrea at the end of May. Four productive floral flushes were observed in

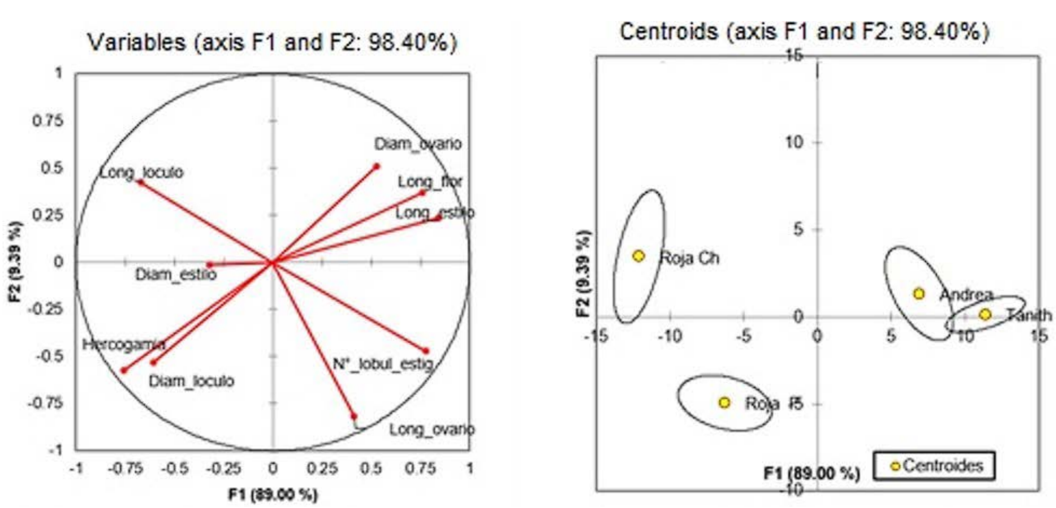


Figure 1. A: Explanatory variables and importance in the materials (p<0.0001, 0.05). B: Position of red and white materials analyzed.

Tanith and Andrea cultivars, and five in red-fleshed pitahayas. A new flush was found to emerge before fruit maturity from the previous flushes in all four cultivars.

Because the synchrony of anthesis is important for those who wish to carry out manual cross-pollination, and because the literature reports that this type of pollination improves production, since it generates larger fruits and the size of the fruit to be sent to market can be controlled. On the other hand, the literature also reports that red-fleshed materials have sexual self-incompatibility and although they offer more flower flushes than white-fleshed cultivars, self-incompatibility decreases production; on the other hand, white-fleshed materials may have partial but not total self-incompatibility. For all these reasons, it is important to know the synchrony of the materials for pollination.

Anthesis is the floral opening that occurs on a single night and is the process of growth and separation of the sepals and petals of the flowers, exposing stigmas and stamens.

The red-fleshed materials had 20-21 days from emergence to anthesis, while the white-fleshed materials had 16-17 days, an interval very close to that reported by Le Bellec (2004), of 20-21 days, and less than that found by Centurión-Yah *et al.* (2008) in Mexico of 25 to 31 days.

Figure 2 shows that no synchrony was found in the anthesis of the four materials, but there is proximity between them as in the case of Tanith and Rojo Ch during the second floral flush. Anthesis of Tanith happened on May 19 and Rojo Ch until May 21, but it is possible to refrigerate Tanith pollen at 10 °C. Another point of anthesis proximity was also between the same materials during anthesis of the third flush of Tanith on 22 July and the fourth of Rojo Ch on 21 July. Finally, the fourth flush of Tanith, on August 21, showed close proximity with the fifth flush of Rojo Ch on August 23. Flower drop was observed after self-pollination (free pollination) in red-fleshed pitahaya plants, which affected yield; on the other hand, the quality (appearance and size) is low because the fruits are of different sizes with a tendency to very low weight.

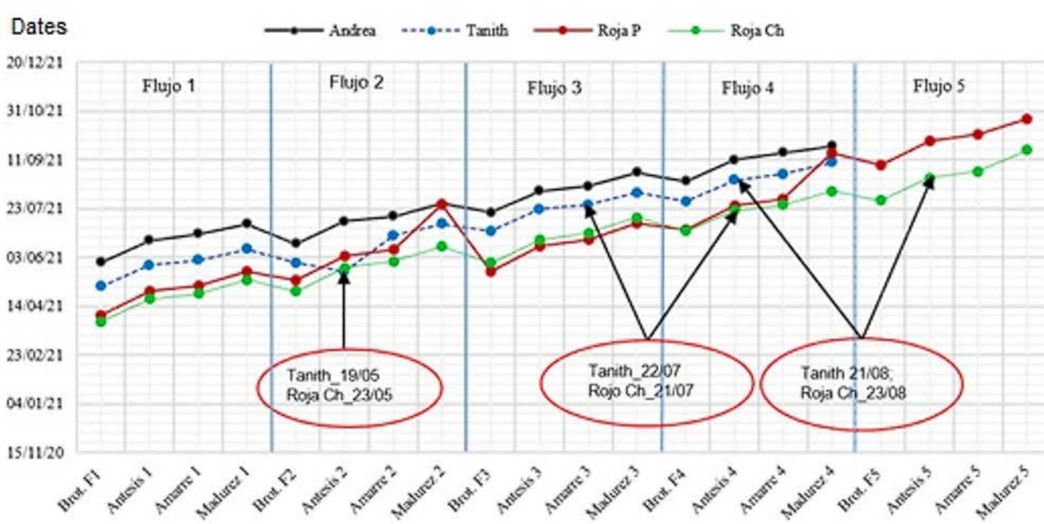


Figure 2. Phases of the flowering stage in the materials analyzed.

The other materials did not show proximity in the occurrence of anthesis, which is very important for those who wish to increase fruit setting by cross-pollination of materials. The data suggest the importance of working with more materials to ensure cross-pollination between those of white and red flesh. All pitahayas, both white and red-fleshed, reached anthesis and fruit setting at the flush rates presented, with adequate average night, minimum and maximum temperatures. The days from emergence to anthesis during the first floral flush in the white-fleshed materials was 22 days, while in Rojo Ch it was 23 days and in Rojo P 20 days, and for the white-fleshed pitahayas (*Hylocereus undatus*) it was 22 days (Figure 3). This interval was greater than that reported by Osuna *et al*. (2016) who found that on the Pacific coast, the flowers of *H. undatus* reached anthesis in 2 weeks and in autumn in three weeks. In this case, the first floral flush of the red-fleshed genotypes (*Hylocereus* spp.) was early, and emergence began at the end of March and beginning of April with minimum night temperatures of 12 °C for Rojo P and 21 °C for Rojo Ch, and 23.5 °C for white-fleshed pitahayas. On the other hand, the same authors point out that flowering is associated with an increase in temperature and relative humidity, and according to (Ortiz, 1995), for *Hylocereus* to flower it requires 10 to 12 hours of light per day and temperatures of 21 to 35 °C. Figure 3 shows the average, minimum and maximum night temperatures during floral emission during each of the flushes. Only the Rojo P genotype developed at very low temperatures, but which exceeded the survival limit of the plants.

The temperature favored the materials in some way, since above 44 °C, pitahaya plants suffer physiological stress, while the base temperature for plant survival is 7 °C. It can be said that during the productive phase they had a favorable condition to assimilate CO_2, since according to Nobel and de la Barrera, (2002), for the case of *H. undatus* a maximum net total CO_2 uptake is achieved at night temperatures averaging 20 °C, since the highest absorption happens at that time.

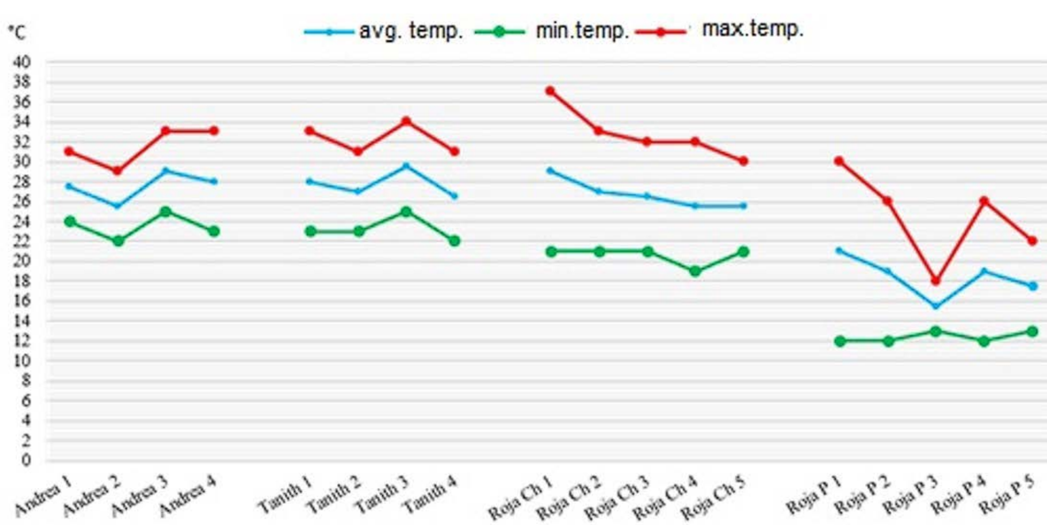


Figure 3. Nighttime temperatures of the pitahaya materials analyzed.

Production achieved by open pollination

The pitahaya production system in Mexico has evolved from backyard to traditional and semi-technified commercial production, although rainfed planting with auxiliary irrigation is predominant. For producers, obtaining the fruit is the most important objective, since their survival depends not only on the harvest but also on the continuity of the crop, whatever it may be. Among the problems encountered in the cultivation of pitahaya, particularly the red-fleshed genotypes, is the fall of flowers and small fruit. Red genotypes emit abundant flowers, but flower setting differs in each material (Figure 4).

Figure 4 shows the average number of flowers emitted per plant in the cycle, as well as the percentage of setting; less setting is observed in the red-fleshed materials, despite the fact that they emit more flowers than the white-fleshed ones; the latter achieved 94% setting, while the red ones achieved less than 45%. There is a need to increase the percentage of setting of red-fleshed genotypes due to their high industrial demand. In general, the average number of fruits in *Hylocereus* spp. was 45 fruits per plant.

The average weight showed significant statistical difference, considering for marketing purposes, but the cultivars Tanith and Andrea stand out, since the cultivars Rojo Ch and Rojo P achieved a lower average weight, although it is possible to improve the fruit size with manual pollination. The ° Brix variable is lower in white-fleshed pitahayas, with the Tanith cultivar standing out with the lowest level and Rojo P with the highest °Brix.

Table 3. Characteristics of fruits of the materials analyzed.

Genotype	Average weight (g)	° Brix
Roja P	322.4 a	14.4 b
Andrea	366.6 ab	12.4 ab
Roja Ch	360.8 ab	13.1 ab
Tanith	413 b	11.2 a
P (0.05)	0.0244	0.0003

Kruskal-Wallis, 0.05. Means with different letters are statistically different.

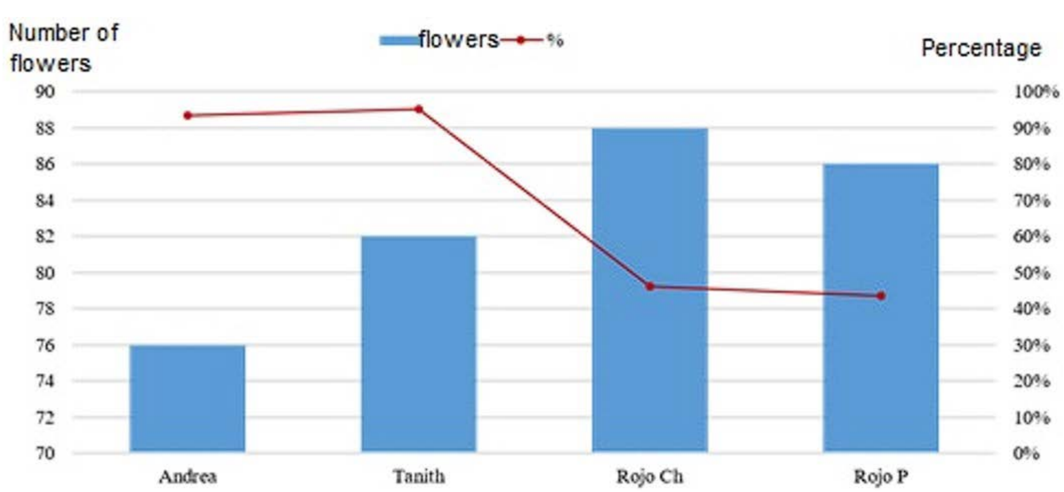


Figure 4. Flower emission and percentage of setting in each of the materials analyzed.

CONCLUSIONS

The analysis of the flowering phase of the materials shows that the variables used allow differentiating the materials, so the absence of synchrony indicates that these materials should not be planted together in an orchard when cross-pollination is sought. Only some proximity was observed in the anthesis of Tanith and Rojo Ch, so if there is the intention of planting these materials it is convenient to collect the pollen from Tanith and store it at 4 °C to pollinate Rojo Ch.

The presence of hercogamy, stronger in the red-fleshed materials, indicates the existence of sexual self-incompatibility, explaining the fact that the materials emit a large number of flowers, but do not achieve fruit setting. White pulp materials have weak self-incompatibility.

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