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Research article

Observaciones fenológicas en clones de *Pinus patula* Schltdl. & Cham.

Phenological observations on *Pinus patula* Schltdl. & Cham. clones

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Abstract

The lack of floral synchronization in a seed orchard favors a decrease in the genetic diversity of the seed lot, increases the percentage of abortive ovules and empty seeds. Therefore, it is necessary to determine the phenological stages and the degree of synchronization between pollen dispersal and female receptivity. In a 1.5 generation *Pinus patula* clonal seed orchard, the start, end and duration dates of each phenological stage of the male and female reproductive structures were estimated by macro-SYNCHRO. The female receptivity period lasted 13 days average, and the pollen dispersal period, 27.5 days. Pollen dispersal and female receptivity occurred when 370.5 and 440 degree-days accumulated, respectively. The general synchronization index of the orchard is considered low (*PO*=0.24) so there is no total synchronization between clone pairs. A positive correlation was found between the onset and duration of both phenological events (*r*=0.41) with a synchrony of seven days; therefore, it is possible that pollination between clones in the orchard with moderate synchronization indexes (*PO* between 0.30 to 0.60) can take place, but it is necessary to determine the variability and genetic control of the clones in subsequent evaluations.

Key words: Pollen dispersal, degree-day, ramets, feminine receptiveness, seeds, phenological synchronization.

Resumen

La falta de sincronización floral en un huerto semillero propicia la disminución de la diversidad genética del lote de semillas, aumenta el porcentaje de óvulos abortivos y de semillas vacías. Por lo anterior, es necesario determinar las etapas fenológicas y el grado de sincronización entre la dispersión del polen y la receptividad femenina. En un huerto semillero asexual de *Pinus patula* de generación 1.5, se estimaron las fechas de inicio, fin y duración de cada etapa fenológica de las estructuras reproductivas masculinas y femeninas con el macro *SYNCHRO* de *SAS*®. El periodo de receptividad femenina duró 13 días en promedio y el de dispersión de polen 27.5 días. La dispersión de polen y receptividad femenina ocurrieron cuando se acumularon 370.5 y 440 grados-día, respectivamente. El Índice de sincronización general del huerto se considera bajo (*PO*=0.24), por lo que no existe una total sincronización entre los pares de clones. Se verificó correlación positiva entre el inicio y la duración de ambos eventos fenológicos (*r*=0.41) con sincronía de siete días; por tanto, es posible que se lleve a cabo la polinización entre los clones del huerto con índices de sincronización moderados (*PO* entre 0.30 a 0.60), pero se requiere determinar la variabilidad y control genético de los clones en evaluaciones subsecuentes.

Palabras clave: Dispersión de polen, grados-día, rametos, receptividad femenina, semillas, sincronización fenológica.

Introduction

Pinus patula Schltdl. & Cham. is one of the most widely used trees to establish commercial forest plantations outside its natural range. In tropical and subtropical regions of the world, plantations exist in Madagascar (Randriambanona *et al.*, 2019), Colombia, Brazil and South Africa (Dvorak *et al.*, 1995) due to its rapid growth, good crown conformation and natural pruning, straight stem and good quality wood (Nyoka, 2002). The area planted with *P. patula* worldwide is approximately one million hectares, of which 95 % correspond to plantations in Central, Eastern and Southern Africa (Tadesse and Fidalgo, 2022).

In Mexico, there are around 4 230 ha planted with this species (Conafor, 2011). However, to produce the plants required by plantation and reforestation programs, it is necessary to have an abundant supply of germplasm of high genetic quality, more productive plants and adapted to different environments (Di-Giovanni and Kevan, 1991). Based on this, sexual and asexual seed orchards aim to produce seeds of higher physiological quality, in sufficient amount, with high genetic efficiency and seeds adapted to specific environments (Wang *et al.*, 1991); however, the genetic and physiological quality of the seeds produced is affected by factors such as population size, foreign gene flow, inbreeding effects, reproductive success (referring to the contribution of gametes from the parents to the next generation) and the fertility of the offspring (Kang *et al.*, 2004).

The development of reproductive structures and their periods of receptivity and pollen dispersal in particular may vary depending on the origin of the parents, the age of the trees, orchard management and environmental factors (Chaisurisri and El-Kassaby, 1993; Burczyk and Chalupka, 1997). Phenological synchrony is one of the main requirements for random crossing (panmixia) and reproductive success between pairs of clones established in orchards (El-Kassaby *et al.*, 1984; Matziris, 1994). Variations in the phenology of the parents lead to a reduction in the possible crossing combinations; assortative (selective) crossings may occur between some clones, that is, preferential crossing between individuals with similar phenotypes, which implies imbalance in reproductive success, non-random crossings and an increase in the proportion of empty seeds (Codesido *et al.*, 2005).

Reproductive phenology in seed orchards was determined in several conifers; the lack of phenological synchrony is common in *Pseudotsuga menziesii* (Mirb.) Franco (El-Kassaby *et al.*, 1984; Copes and Sniezko, 1991), *Picea sitchensis* (Bong.) Carrière (El-Kassaby and Reynolds, 1990), *Pinus radiata* D. Don (Griffin, 1984), *Pinus taeda* L. (Askew, 1986) and *Pinus thunbergii* Parl. (Chaix *et al.*, 2007); on the opposite, in seed orchards of *Pinus sylvestris* L. (Jonsson *et al.*, 1976), *Picea mariana* (Mill.) Britton, Sterns & Poggenb. (O´Reilly *et al.*, 1982) and *Picea abies* (L.) H. Karst. (Nikkanen, 2001) synchrony was high.

In order to achieve maximum genetic efficiency in an open-pollinated seed orchard, certain conditions must be met, including that the receptivity of the female ovules must be synchronized with pollen dispersion in all clones (Eriksson and Adams*,* 1989), since differences in reproductive phenology between clones reduce the effective size of the orchard, promote self-fertilization and increase the risk of contamination by external pollen (Burczyk and Chalupka, 1997). Therefore, it is important to define the start, end and duration periods of each stage of development of the female and male reproductive structures, since it has been observed that the start of female receptivity has a stronger genetic control than its male counterpart (Griffin, 1984; Nikkanen, 2001); while the duration of pollen dispersal is completely determined by environmental factors such as temperature and precipitation (Matziris, 1994).

Based on the above, the objectives of this work were to determine the phenological stages, the degree of synchronization between pollen dispersal and female receptivity and the accumulation of degree-days, in an asexual seed orchard of generation 1.5 of *P. patula*. The hypothesis states that the differences between clones with respect to their phenological stages are a function of the accumulated amount of temperature (degree-days) during the differentiation process and subsequent development of the reproductive structures.

Materials and Methods

Study area

A forest genetic improvement program in the *Aquixtla* region, *Puebla* state, began with the selection of 94 phenotypes in natural stands of *P. patula* in the *El Manantial* Multifunctional Forest Reserve. An asexual seed orchard, with plants generated by grafting, was established in 2003; later in 2005 and 2007, progeny trials were established with seeds from the selection population to determine the best parents (Salaya-Domínguez *et al.*, 2012; Escobar-Sandoval *et al.*, 2018). The 11 best clones were selected based on growth and wood density (Escobar-Sandoval *et al.*, 2018). Controlled crosses were performed, from which a rootstock plant was produced and grafted again with scions from the first generation orchard. Thus, in August 2016, the 1.5 generation asexual seed orchard (ASO) was established on the *Chichicaxtla* property, *Aquixtla*, *Puebla*, Mexico (19°45’14’’ N, 97°58’20’’ W; 2 679 m altitude); a completely randomized design was followed with a spacing of 3×3 m with different number of ramets per clone which belonged to 31 different clones.

Evaluation of the phenology of reproductive structures

The phenology of reproductive structures was recorded in a sample of 25 clones with three ramets per clone, which were selected for their history of cone production in two consecutive years. During February and April 2022, observations were made on the phenological progress, with a frequency of 4 to 5 days; three branches from the middle to the top of the crown were marked for female strobili and three branches from the middle to the bottom of the crown for male strobili. To define the phenological stages of both types of reproductive structures, the methodology of Hernández *et al.* (2016) and Muñoz-Gutiérrez *et al.* (2019) was used.

Four stages were defined for female strobili. E1: The vegetative bud is cylindrical in shape and increases in size, at the base the reproductive buds covered by cataphylls appear; E2: The apical part of the bud begins to open, the strobilus emerges, the ovules are not receptive but the pollen grains can remain between the scales, and if they survive until the next stage, they can fertilize, therefore, it was considered 20 % receptivity; E3: The scales gradually separate until they form a right angle with the axis of the strobilus, pollen grains can easily penetrate between the scales and reach the ovules, and corresponds to the stage of maximum receptivity (100 %); and E4: The scales increase in size and thickness, so that pollen can no longer pollinate, and receptivity ceases (Figure 1).

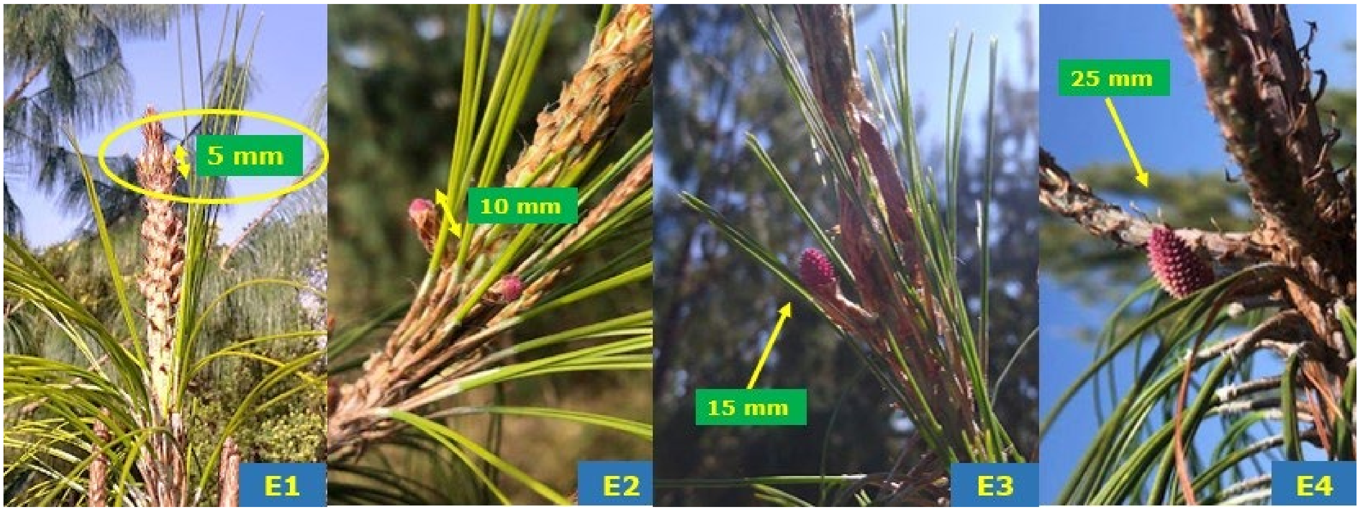


Figure 1. Phenological stages of female strobili of *Pinus patula* Schltdl. & Cham.

Four stages were also defined for male strobili. E1: Male strobili are visible at the base of the vegetative bud with the pollen sacs covered by cataphylls; E2: Elongation of the strobili occurs and the cataphylls are exposed; E3: The strobili continue to elongate until they acquire a yellow color, and maximum pollen dispersal occurs; E4: Pollen emission ends completely, the pollen sacs wither and the strobili fall off (Figure 2).

Figure 2. Phenological stages of male strobili of *Pinus patula* Schltdl. & Cham.

Data analysis

For each ramet and clone, the start, end and duration dates of each of the phenological stages were determined with the macro-SYNCHRO (Zas *et al.*, 2003) of version 9.4 SAS® (SAS, 2013); previously the dates on which the observations were made were converted to Julian days (number of days from January 1st). With these data, the Phenological Synchronization Index (*PO*) was calculated between pairs of clones according to the procedure proposed by Askew and Blush (1990), which is a quantitative measure that allows knowing the symmetrical proportion of the male and female phenograms generated by the SYNCHRO program; and the Pearson correlation coefficient (r_P) was calculated between the respective values of the indexes obtained for each clone in the evaluated reproductive cycle.

To determine the amount of accumulated temperature (degree-days) on the start and end dates of female receptivity and pollen dispersal, the maximum and minimum temperatures recorded on the AccuWeather (2022) website for *Aquixtla* municipality, *Puebla*, during the study period were used to calculate the accumulated degree-days (*GD*) from the first day of January until the end of the receptivity and dispersal period. The equation used to calculate the *GD* was as follows (Lozada and Angelocci, 1997):

$$GD = \left[\frac{T^\circ\, max + T^\circ\, min}{2}\right] - T^\circ\, threshold$$

Where:

GD = Degree-days

T° max = Daily maximum temperature (°C)

T° min = Daily minimum temperature (°C)

T° threshold = Lower threshold temperature of the species (°C) =6 °C (Muñoz-Gutiérrez *et al.*, 2017).

Results

Phenology of reproductive structures

The evaluated clones behaved as late and early; for example, the start and end of the periods of receptivity and pollen dispersal in clones considered as early occurred with a difference of 7.5 days (d) (Table 1). While receptivity was shorter than that of dispersal with a difference of 14.5 d.

Table 1. Average values of the start, end and duration dates of female receptivity and pollen dispersal in *Pinus patula* Schltdl. & Cham.

Phenological event	Precocious clones			Late clones		
	Start	End	Duration (days)	Start	End	Duration (days)
Female receptivity	49.5	62.5	13.0	76.5	86.0	9.5
Pollen dispersal	42.0	69.5	27.5	76.5	86.0	9.5

On the other hand, there were clones that started their phenological events late, up to 76.5 d and lasted only 9.5 d (Table 1).

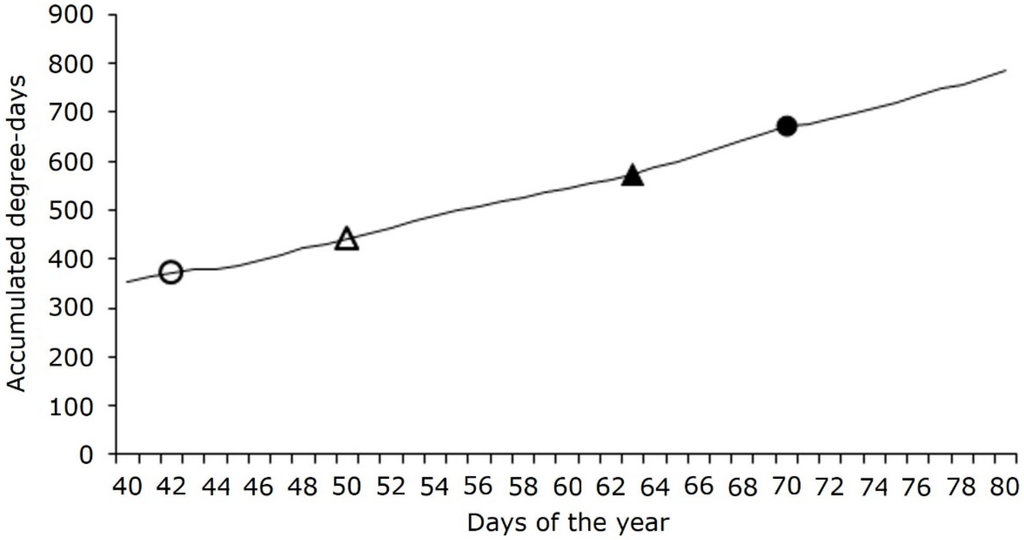
The correlation coefficients were moderate to low and not significant, except for the onset of receptivity with the duration of pollen dispersal (*r*=-0.474; *p*=0.034) and between the duration of both events *r*=0.419 (*p*=0.065) (Table 2).

Table 2. Correlation coefficient (r_P) (*p* values) between female receptivity and pollen dispersal of *Pinus patula* Schltdl. & Cham.

		Pollen dispersal		
		Start	End	Duration
Female receptivity	Start	0.410 (0.071)	0.322 (0.165)	-0.474 (0.034)
	End	0.064 (0.788)	0.317 (0.172)	-0.004 (0.983)
	Duration	-0.289 (0.216)	-0.087 (0.714)	0.419 (0.065)

Reproductive phenology and degree-day accumulation

The onset of both phenological events occurred when 370.5 *GD* for pollen dispersal and 440 *GD* for female receptivity were accumulated, while the end of the stages occurred when 572.5 *GD* for female strobili and 672 *GD* for male structures were accumulated (Figure 3).



Female receptivity: Start (Δ) and end (▲); Pollen dispersal: Start (○) and end (●).

Figure 3. Accumulated degree-days in cycle 2022 (solid line).

Phenological Synchronization Index (*PO*)

In the middle of the period of phenological events, only 22 % of the clones coincided in pollen receptivity and dispersal; then a second dispersal peak was verified in which approximately 30 % of the clones were involved, while only 8 % were receptive; finally, in a third phase, the clones continued to disperse pollen and the participation was greater, approximately 68 %, but only 18 % of the females were receptive (Figure 4). Between 20 and 70 % of the clones had maximum pollen dispersal for 22.5 days on average; during this period, between 10 and 15 % of the female structures were receptive (Figure 4).

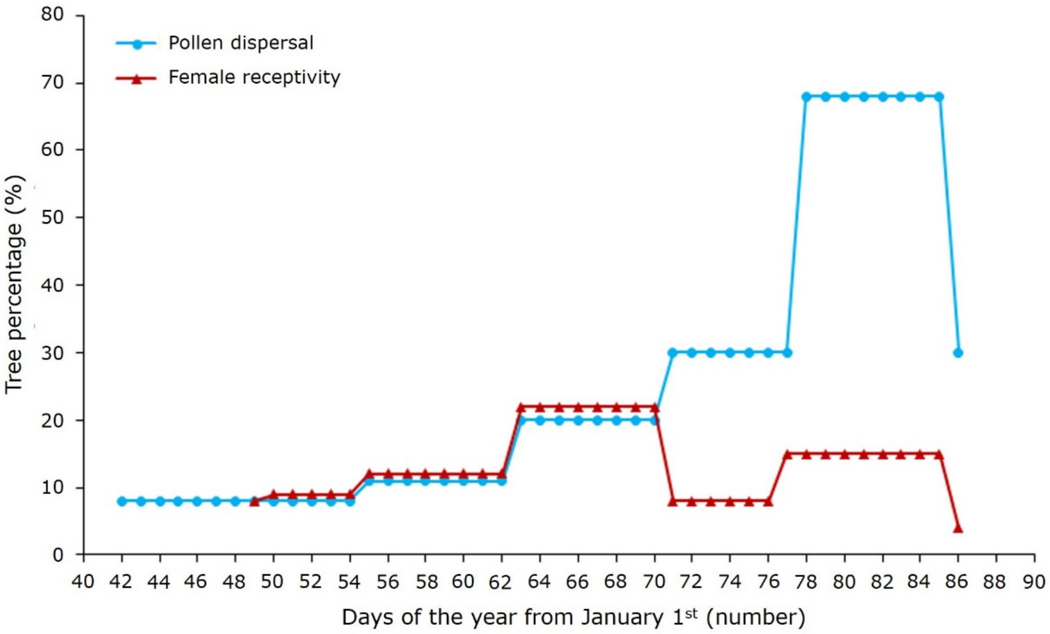


Figure 4. Phenological synchronization of female receptivity and pollen dispersal.

The average Phenological Synchronization Index (*PO*) was 0.24 between the periods of female receptivity and pollen dispersal. Synchronization indices between clones for female receptivity ranged between 0.03 and 0.54; while those for pollen dispersal were between 0.11 and 0.42, except for two clones with extreme values of *PO*=0 (clone 36S) and *PO*=1 (clone 37R), indicating that clone 36S did not participate as a pollinator; instead, clone 37R had the highest participation (Table 3).

Table 3. Phenological Synchronization Index (*PO*) between female receptivity and pollen dispersal among *Pinus patula* Schltdl. & Cham. clones.

ID clone	*PO average female*	*PO average male*
01Z	0.05	0.42
02R	0.37	0.18
02Z	0.03	0.30
03Z	0.18	0.39
04Z	0.54	0.20
05Z	0.16	0.21
10R	0.35	0.14
10S	0.39	0.18
113C	0.20	0.15
117C	0.16	0.16
12C	0.11	0.14
15R	0.23	0.19
17R	0.17	0.16
17S	0.12	0.21
23S	0.38	0.13
25R	0.15	0.22
34S	0.40	0.11
36C	0.14	0.15
36S	0.36	0.00
37R	0.26	1.00
58C	0.44	0.42
64R	0.10	0.25
72R	0.21	0.41
83S	0.22	0.16
91C	0.25	0.19

General	0.24	0.24

Discussion

According to the results, the duration of female receptivity was shorter than that reported in a first-generation orchard of *P. patula* in consecutive years (2012: 25 d, 2013: 18 d, 2014: 29.8 d, 2015: 32.2 d) (Hernández *et al.*, 2016; Muñoz-Gutiérrez *et al.*, 2019). For P. *radiata*, receptivity was 35 d (Matziris, 1994; Codesido *et al.*, 2005) and for *P. sylvestris*, 31 d (Jonsson *et al.*, 1976).

On the other hand, in the evaluated clones, pollen dispersal lasted longer than strobili receptivity. Therefore, the differences in these events between clones have a great impact on the genetic variability of the seed produced in the orchard, since there will be clones that do not participate in seed production just because of the difference of 7.5 days in which the pollen begins to disperse and there are no receptive female structures, and, therefore, pollination does not take place. However, the overlap between both events is wide, but with low participation of clones, barely 20 %.

It was expected to achieve greater genetic efficiency in the 1.5 generation orchard, in which all trees should contribute equally to seed production, and higher synchronization rates between clones, because they are better adapted to the environment (Jaquish, 2004); however, phenological variables are phenotypic observation factors that change with temperature and humidity (Webber, 1995), in addition to the influence of the age of the trees, the conditions of the planting site, the location of the clones within the orchard (Muñoz-Gutiérrez *et al.*, 2019), the exposure, the slope, and the space between individuals (Nikkanen, 2001).

The existence of early and late clones indicated that there were possibly variations in temperature and relative humidity (Muñoz-Gutiérrez *et al.*, 2019); the late ones would have a greater probability of being pollinated by those clones that also behaved in the same way in pollen dispersal.

However, the fact that there are early clones in receptivity and late in dispersal increases the probability of obtaining greater production of empty seeds (Burczyk and Chalupka, 1997). This same behavior was observed in the first generation orchard, from which the material with which the ASO of generation 1.5 was established comes (Hernández *et al.*, 2016; Muñoz-Gutiérrez *et al.*, 2019); since they are the same clones that continue to behave as early or late, which is partly due to the fact that some of the components of the reproductive phenology have a strong genetic control (Matziris, 1994), since the parents selected from the populations of origin are expected to conserve their phenological characteristics, regardless of the *ex situ* conditions in which the first and 1.5 generation orchards were established (Funda and El-Kassaby, 2012).

Female reproductive phenology and the onset of receptivity in particular present a strong genetic control as has been observed in *Pinus radiata* (Codesido *et al.,* 2005), *P. nigra* J. F. Arnold (Matziris, 1994) and *Picea abies* (Nikkanen, 2001). While environmental factors such as accumulated temperature (*GD*) and precipitation influence the seasonal pattern days before and during pollen dispersal in *Pinus thunbergii* (Matziris, 1994), *Pseudotsuga menziesii* (Erickson and Adams, 1989), *Pinus radiata* (Codesido *et al.*, 2005), and in first generation orchard clones of *Pinus patula*; although in the latter, the pollen dispersal period showed greater genetic control (r=0.76) than the female receptivity period, in particular, the start date and duration of dispersal (Muñoz-Gutiérrez *et al.*, 2017).

On the contrary, in *P. sylvestris* pollen dispersal exhibits lower heritability (0.21) (Rodríguez, 2001); it has been determined that dispersion is mostly conditioned by climatic factors such as the amount of solar radiation or high temperatures

(Nikkanen, 2001), in addition to the particular conditions of the microsite that nourish the particular tree (Nikkanen and Ruotsalainen, 2000).

Pollen dispersal started when 370.5 *GD* were accumulated since January 1st, 2022, more than 100 heat units recorded for the same species and region in 2014 (255 *GD*) and 2015 (260 *GD*) (Muñoz-Gutiérrez *et al.*, 2017). In addition to the increase in temperature for the evaluation periods, there was no frost in 2022, the minimum temperature recorded was 3 °C (AccuWeather, 2022), which was contrary to the years 2013 and 2014 when minimum temperatures of up to -7.1 °C were recorded (Hernández *et al.*, 2016). In different studies it has been shown that the beginning of pollen dispersal is correlated with temperature and degree-day accumulation (Luomajoki, 1993), that is, a higher temperature indicated an earlier start date (Torimaru *et al.*, 2013); in the present work, pollen dispersion started at day 42 of the year (February 11th) and with a temperature accumulation of 370.5 *GD*; while in the years 2014 and 2015 the dispersion started until day 60 (March 1st) and 72 (March 13), respectively (Muñoz-Gutiérrez *et al.*, 2017); which supposes that the increase in temperature combined with the absence of precipitation accelerated the differentiation processes of the reproductive structures.

Synchronization indexes and overlap in dispersal periods are due to changes in temperatures that influence the development of reproductive structures. In the present work, up to three phases were visualized, in which there is no total synchronization between all clone pairs, so the synchronization indices were low. This behavior is very unusual, since in previous years in the first generation orchard, the periods coincided within a period of seven to 10 days (Hernández *et al.*, 2016; Muñoz-Gutiérrez *et al.*, 2019).

Higher values of the synchronization index were recorded in other conifers, such as *Pinus greggii* Engelm. *ex* Parl. (*PO*=0.38 and 0.31; Ruíz-Farfán *et al.*, 2015), *P. sylvestris* (*PO*=0.41; Burczyk and Chalupka, 1997) and *P. radiata* (*PO*=0.42 and 0.48; Zas *et al.*, 2003; Codesido *et al.*, 2005).

Moderate to low and non-significant correlations between the dates of onset of female receptivity and pollen dispersal indicated that when the majority of female strobili in stage three (of maximum receptivity) begin, it does not necessarily coincide with the peaks of maximum pollen dispersal, but they do contribute minimal amounts.

On the other hand, the positive correlation between the duration of both events explained the overlap that was verified at different times, even though not all clones participated as dispersers or receivers. Possibly the differences in reproductive phenology between orchard parents lead to the reduction of possible crossing combinations and cause positive assortative mating between them (*i. e.*, preferential crossing between similar phenotypes), but reduces the clonal contribution to the seed harvest (Funda and El-Kassaby, 2012). Variation in synchrony has been observed in species of the *Pinus* L. genus and other conifers regularly at early ages, and in seed orchards (Matziris, 1994); in these cases, the use of growth regulators and controlled crosses are alternatives to maximize the participation of all clones in the orchard (Ruiz-Farfán *et al.*, 2015; Muñoz-Gutiérrez *et al.*, 2019).

Conclusions

The results show that phenological events do not start at the same time, since the accumulation of heat to start their differentiation processes is different, since the dispersion of pollen in the orchard begins before the female receptivity and with less accumulation of degree-days. The differentiation of male strobili occurs earlier, they mature faster, their pollen dispersion begins earlier and with a longer duration. Therefore, with a wide dispersal period, it would be expected that the seed produced is actually the product of the cross between pairs of clones in the orchard, since it covers the receptivity periods. From the speed and short time of the receptivity period of the female strobili, it is not guaranteed that the pollination of all of them takes place entirely since there are differences in the participation of some clones; the low Phenological Synchronization Index indicates that not all of them participate at the same time as females or pollinators.

It is necessary to continue the assessments in subsequent years in order to determine the interaction of the clones and the climatic conditions of the year at the beginning, end and duration of flowering, as well as the behavior of the clones based on these factors. Likewise, to define the level of genetic control in the stages of maximum female receptivity and maximum period of pollen dispersal.

It is advisable to implement some pollen management strategies, such as controlling pollination between pairs of clones and, on a large scale, to improve the quality of the seeds produced, as well as promoting flowering in those individuals that are not yet flowering to increase the clonal contribution to the seed harvest.

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Conflicts of interest

The authors declare that there are no conflicts of interest. Liliana Muñoz Gutiérrez declares that she has not participated in any of the stages of the editorial process of this article.

Contribution by author

Sara Irene Velasco Hernández: data collection in the field, statistical analysis, interpretation of results and writing of the manuscript; Liliana Muñoz Gutiérrez: execution and supervision of the research, statistical analysis, interpretation of results and correction of the manuscript.

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