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Original article

Clonal variation and cone production stability in a 1.5 generation asexual seed orchard of Pinus patula

Variación clonal y estabilidad en la producción de conos en un huerto semillero asexual de ***Pinus patula*** *generación 1,5*

Variação clonal e estabilidade na produção de cones em um pomar de sementes assexuadas de ***Pinus patula*** *geração 1.5*

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ABSTRACT

The contribution of clones from a seed orchard to cone production determines the effective population size and is highly correlated with seed production. The objective was to determine clonal variation and stability in the productive capacity of female cones of *Pinus patula* clones established in a 1.5 generation asexual seed orchard . Mature cones

of all clones were collected and counted at the end of March in the years 2021, 2022, 2023 and 2024. Genetic variation between clones and years of production, broad heritability (H^2_c), Spearman's correlation coefficient of mean cone production per clone between years of evaluated were determined, phenotypic correlations of clone means (r_p) and genetic correlation type B (r_B) were estimated. Female cone production showed a wide variation between clones and years. Spearman's correlation coefficients between production and production years were high and positive from 0.80 to 0.88. The degree of variation in cone production was higher among clones (σ^2_c) than within clones (σ^2_e,), the r_B was 0.79 and H^2_c was 0.83 in the joint analysis of cone production over four years of evaluation, indicating high genetic control in cone production ability. Only 12 clones contributed between 80 and 85 % of the total female cone production. The HSA presents an imbalance in clonal contribution to cone production which negatively affects the effective population size.

Keywords: cone production, genetic correlation, genetic variation, heritability, phenotypic correlation, variation coefficient.

RESUMEN

La contribución de los clones de un huerto semillero a la producción de conos determina el tamaño efectivo de la población y está altamente correlacionada con la producción de semillas. El objetivo fue determinar la variación clonal y estabilidad en la capacidad productiva de conos femeninos de clones de *Pinus patula* establecidos en un huerto semillero asexual de generación 1,5. Se recolectaron y contaron los conos maduros de todos los clones a finales de marzo en los años 2021, 2022, 2023 y 2024. Se determinó la variación genética entre clones y años de producción, la heredabilidad en sentido amplio (H^2_c), el coeficiente de correlación de Spearman de la producción promedio de conos por clon entre años de evaluación, además se estimaron correlaciones fenotípicas de las medias de clones (r_p) y la correlación genética tipo B (r_B). La producción de conos femeninos mostró una amplia variación entre clones y entre años. Los coeficientes de correlación de Spearman entre los años de producción de conos fueron altos y positivos de 0,80 a 0,88. El grado de variación en la producción de conos fue mayor entre clones (σ^2_c) que dentro de clones (σ^2_c), la r_B fue de 0,79 y la H^2_c de 0,83 en el análisis conjunto de

la producción de conos en cuatro años de evaluación, lo que indica que existe un elevado control genético en la capacidad de producción de conos. Solo 12 clones aportaron entre el 80 y 85 % de la producción total de conos femeninos. El HSA presenta un desbalance en la contribución clonal en la producción de conos lo que afecta negativamente el tamaño efectivo de población.

Palabras clave: coeficiente de variación, correlación fenotípica, correlación genética, heredabilidad, producción de conos, variación genética.

RESUMO

A contribuição dos clones em um pomar de sementes para a produção de cones determina o tamanho efetivo da população e está altamente correlacionada com a produção de sementes. O objetivo foi determinar a variação clonal e a estabilidade na capacidade produtiva de cones femininos de clones de Pinus patula estabelecidos em um pomar de sementes assexuado de 1,5 geração. Cones maduros de todos os clones foram coletados e contados no final de março de 2021, 2022, 2023 e 2024. Foram estimadas a variação genética entre clones e anos de produção, a herdabilidade em sentido amplo (H_c^2), o coeficiente de correlação de Spearman da produção média de cones por clone entre os anos de avaliação, as correlações fenotípicas das médias dos clones (r_P) e a correlação genética do tipo B (r_B). A produção de cones femininos apresentou ampla variação entre clones e entre anos. Os coeficientes de correlação de Spearman entre os anos de produção de cones foram altos e positivos, variando de 0,80 a 0,88. O grau de variação na produção de cones foi maior entre clones (σ_c^2) do que dentro de cada clone (σ_c^2). O rB foi de 0,79 e o H_c^2 foi de 0,83 na análise combinada da produção de cones ao longo de quatro anos de avaliação, indicando forte controle genético da capacidade de produção de cones. Apenas 12 clones contribuíram com entre 80% e 85% da produção total de cones das fêmeas. A HSA exibe um desequilíbrio na contribuição clonal para a produção de cones, o que impacta negativamente o tamanho efetivo da população.

Palavras-chave: coeficiente de variação, correlação fenotípica, correlação genética, herdabilidade, produção de cones, variação genética.

INTRODUCTION

Pinus patula Schiede ex Schltdl . et Cham has been very successful in commercial forest plantations in Mexico and other parts of the world, and has even been the subject of improvement abroad, in countries such as Colombia, Brazil, and South Africa (Dvorak *et al*., 1995). In Mexico, progress has already been made in genetic improvement programs for the production of high-quality timber and to supply seedlings for reforestation programs. These programs allow for the production of germplasm in sufficient quantity and with the appropriate genetic quality adapted to different planting sites. As proof of this, in the Aquixtla region of Puebla, in 2003, a first-generation asexual seed orchard (ASO) was established with seedlings generated by grafting 94 clones in a completely randomized design, on land belonging to the "El Manantial" Multifunctional Forest Reserve. In 2005 and 2007, progeny trials were established using seeds from the selection population to determine the best parents (Salaya-Domínguez *et al*., 2012). The 11 best clones were selected based on their growth and wood density (Escobar-Sandoval *et al*., 2018); controlled crosses were performed, from which rootstock plants were produced and grafted, again with scions from the first-generation orchard (Velasco-Hernández and Muñoz-Gutiérrez, 2024). In August 2016, the 1.5 generation HSA was established with 31 different clones on the Chichicaxtla property (19°45´14¨N, 97°58´20¨W; altitude 2,679 m) (Velasco-Hernández and Muñoz-Gutiérrez, 2024).

In many countries, seed orchards constitute the largest source of seeds. In Slovakia, 40% of the plants used for reforestation come from seed orchards (Gömöry *et al*., 2003), in Finland 60% (Jansson *et al*., 2016), and in Sweden over 90% (Haapanen *et al*., 2015). Therefore, it is necessary to determine the quantity of seed produced and understand the contribution of clones to the seed harvest. This latter factor is crucial for determining the genetic value of the seed produced in the orchard and thus ensuring the required quality and genetic diversity (Park *et al*., 2023).

Cone production has been shown to be highly correlated with seed production in a seed orchard (El- Kassaby *et al*., 1989), in conifers a significant variation between clones and years has been observed in the production of female cones, as in HSA of *Pseudotsuga menziesii* (Mirb.) Franco (El- Kassaby *et al*., 1989), *Pinus thunbergii* Parl. (Kang *et al*., 2004),

P. sylvestris L. (Bilir *et al*., 2008), *P. tabuliformis* Carriere (Yuan *et al*., 2014), *P. nigra* subsp . *pallasiana* (Lamb.) (Uysal, 2015), *Abies alba* Mill. (Teodosiu *et al*., 2023), among others.

In this regard, Kang (2001) indicates that in a reproductive cycle in seed orchards, not all clones produce the same number or at the same time. Therefore, the seed lot harvested in a year does not represent the total genetic pool of the orchard clones, since a small portion of the clones may contribute the majority to the orchard's seed production, increasing the genetic relatedness in the progeny produced and causing a reduction in genetic diversity (Reynolds and El- Kassaby, 1990; Kang *et al*., 2001). Based on the above, the objective was to determine the clonal variation and stability in the productive capacity of female cones from *Pinus clones. patula* established in an asexual seed orchard of generation 1.5.

MATERIALS AND METHODS

Study area

The study was carried out in a clonal seed orchard of *P. patula* of generation 1.5, established in the Multifunctional Forest Reserve "El Manantial", Chichicaxtla property, Aquixtla, Puebla, Mexico (19°45'14'' N, 97°58'20'' W; altitude of 2,679 m), has 31 clones and different number of ramets per clone (8-14 ramets), in a completely randomized design with a spacing of 3.0 x 3.0 m (Velasco-Hernández and Muñoz-Gutiérrez, 2024).

Harvesting mature cones

For each production cycle, all mature cones present in the crown of these 31 clones with five ramets per clone (155 trees) were collected and counted at the end of March in the years 2021, 2022, 2023 and 2024, which correspond to the reproductive cycles that began in spring of 2019, 2020, 2021 and 2022, respectively.

Data analysis

An analysis of variance was performed using the number of cones collected each year (2021, 2022, 2023, and 2024) to estimate the genetic variation among clones and years in the productive capacity of female cones during the evaluation years, using the Mixed

procedure of the SAS statistical analysis program (SAS, 2023). Prior to the analysis, the original cone number data (x) were transformed using the √x function to homogenize the variance among years and among clones (Steel and Torrie, 1980). The broad-sense heritability (H^2_c) of cone production capacity of the clone means (clonal repeatability) was calculated using the formula (Falconer and Mackay, 1996):

$$H_c^2 = \frac{\sigma_c^2}{\sigma_c^2 + \left(\frac{\sigma_{ac}^2}{a}\right) + \left(\frac{\sigma_e^2}{ra}\right)}$$

Where: σ_c^2 is the variance between clones; σ_{ac}^2 is the variance due to the interaction of years by clones; σ_e^2 is the variance due to error; a is the number of years and r is the number of ramets per clone. In addition, to evaluate the degree of genetic stability in the contribution of clones to the total cone production between years, the type B genetic correlation (r_B) was calculated with the formula $r_B = (\sigma_c^2)/(\sigma_c^2 + \sigma_{ac}^2)$ (Falconer and Mackay, 1996); Spearman's correlation coefficient of average cone production per clone was estimated between the different evaluation years, and phenotypic correlations were estimated using Pearson's correlation coefficient and genotypic correlations through clone variances and covariances (σ_c^2) obtained from the analysis of variance.

RESULTS

Variation in cone production

Analysis of variance indicated that there are highly significant differences ($p \leq 0.0001$) between years in cone production, between clones and of the clones × years interaction on the variation in cone production capacity in the HSA of *P. patula* generation 1.5 (Table 1).

Table 1. *- Statistical significance of the factor's year, clone and the interaction between both on the productive capacity of cones in clones of the seed orchard of P. patula*

Factor	Degrees of freedom	Value of F	P > F
Year	3	37.39	<0.0001
Clone	30	21.65	<0.0001
Year x Clone	90	2.31	<0.0001

Cone production from the orchard clones showed wide variation across the four years of evaluation. In 2021, the average production per tree was 2.8 ± 5.4 with a high coefficient of variation (CV) of 193.7, while in the other three years of evaluation, the average cone production per tree increased as the orchard age increased, and the coefficients of variation ranged from 166.5 to 202.5 (Table 2).

Table 2. *- Average annual values per clone and indicators of variation in the number of cones in a seed orchard of P. patula*

Year	N	Average	Minimum	Maximum	Standard deviation	Coefficient of variation (%)
2021	31	2.8	0	41	5.4	193.7
2022	31	10.3	0	157	19.4	187.7
2023	31	13.2	0	174	26.8	202.5
2024	31	18.3	0	164	30.4	166.5

Correlation in cone production between clones and years

Spearman's correlation coefficients between production cycles were high and positive from 0.80 to 0.88 ($p \leq 0.0001$) in the years of good production corresponding to the 2021-2022, 2021-2024, 2022-2024 and 2023-2024 cycles, and moderate at 0.76 ($p \leq 0.001$) in the 2021-2023 and 2022-2023 cycles (Table 3).

Table 3. *- Spearman correlation coefficient values for average cone production per clone between different evaluation years in a P. patula seed orchard.*

Year	2021	2022	2023	2024
2021	-	0.87<0.0001	0.76<0.0001	0.81<0.0001
2022		-	0.77 <0.0001	0.82<0.0001
2023			-	0.88<0.0001
2024				-

The degree of variation in cone production was greater among clones (σ_c^2) than within clones (σ_e^2, environmental effect), except for the 2023-2024 cycle. The type B genetic correlation (r_B) was 0.79 in the complete analysis, with values from 0.62 to 0.95 among the different pairs of years, while the phenotypic correlations (r_p) between years were *positive, high,* and significant ($r_p \geq 0.81$) in the last three production cycles. The overall broad-sense heritability of clone means (clonal repeatability) was 0.83, although the estimated values fluctuated from 0.67 to 0.87, indicating high genetic control of cone production capacity (Table 4).

Table 4. *- Variance components, broad sense heritability (H^2_c) and type B genetic correlations (r_B) for the productive capacity of cones in the seed orchard of P. patula*

Parameter	Productive capacity of female cones						
	Joint analysis	2021-2022	2021-2023	2021-2024	2022-2023	2022-2024	2023-2024
σ_c^2	2.70	1.65	1.69	2.08	2.40	3.63	4.77
σ_c^2	0.73	0.22	1.05	1.14	1.25	0.49	0.23
σ_c^2	2.79	2.02	1.79	2.59	3.00	3.79	3.57
$\sigma_{ac}^2 / \sigma_c^2$	0.27	0.13	0.62	0.55	0.52	0.13	0.05
H_c^2	0.83	0.79	0.67	0.68	0.68	0.81	0.87
r_B	0.79	0.88	0.62	0.65	0.66	0.88	0.95
r_p		0.79	0.68	0.47	0.91*	0.81*	0.95*

**Significant differences with P <0.001. σ_c^2: variance between clones; σ_{ac}^2: variance due to the interaction of years per clone; σ_e^2: variance due to error; H_c^2: broad-sense heritability of clone means; r_B: type B genetic correlations; r_p: phenotypic correlations of clone means*

Contribution of clones to cone production

It was determined that the number of cones produced per clone each year is variable, indicating that they do not contribute equally to the seed harvest. This condition is more evident in first-generation and 1.5-generation orchards; not all clones participate in cone production annually. In this case, the same clones participated consistently during the four years of evaluation; only seven clones were the most productive (17S, 117C, 58C, 36C, 91C, 04Z, and 83S). Additionally, clones 12C, 72R, 36S, 10R, and 10S also participated in cone production in at least two years (2021 and 2023). Together, these 12 clones contributed between 80 and 85% of the total female cone production (Figure 1).

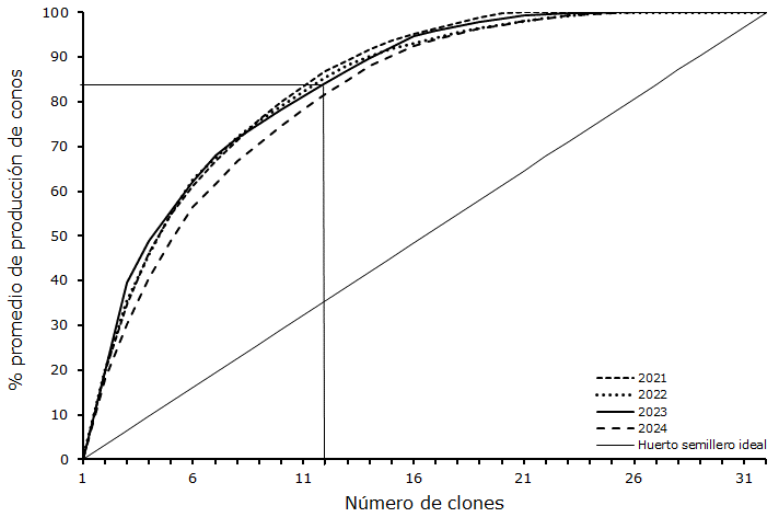


Figure 1. - *Cumulative contribution curve of cone production from P. patula seed orchard clones*

DISCUSSION

Seed orchards are designed to produce high-quality seed and genetic diversity, which implies that all individuals must contribute equally to gamete production and random crosses, without external gene flow (pollen) or other factors affecting variation in genetic diversity (Funda *et al., 2012).* In this case, strong interactions occurred between clones and environmental factors that must be taken into account in analyses of genetic variation in cone production (Table 1), similar to that reported in a *Pinus* seed orchard. first generation *patula (Muñoz Gutiérrez et al*., 2020). In this work, it was demonstrated

that there is variation in the fertility of the clones and ramets, therefore, the effective population size varied annually in cone production, which affects genetic improvement and genetic diversity (Nikkanen and Ruotsalainen, 2000), similar to what was reported in the first-generation HSA of *P. patula*.

The coefficients of variation were very high between years of cone production, indicating that not all clones participate and those that produce are not stable each year despite the fact that a tendency to increase production according to the age of the orchard was observed (Table 1), the above is attributed to changes in temperature and humidity patterns, reproductive phenology (Velasco-Hernández and Muñoz-Gutiérrez, 2024), pollen dispersal, pollen quality, self-incompatibility and reproductive success (El-Kassaby and Ritland, 1992).

In orchards of advanced generations, it is necessary to identify clones that not only produce cones and seeds but also exhibit low variability, that is, a lower coefficient of variation (CV) in production across different years and environments (Table 2). The elimination or retention of clones with high cone production depends on the specific situation, since highly productive clones can continue to be selected for advanced generations of breeding, as the number of years in which these clones adapt better to environmental conditions is greater, and some have stable production.

The correlation coefficients fluctuated between production cycles, and this can be explained by several factors: clones have different growth rates in relation to cone production, which is determined by genetic factors; flowering and fruiting rates vary from one clone to another; changes in environmental factors influence flowering processes to varying degrees (Yuan *et al*., 2014); and in this 1.5 generation orchard, some clones are not the same age, due to planting failures, they have been replanted in later years, therefore they are not yet in production.

Genetic correlation coefficients differed between years, and phenotypic correlation coefficients were higher in at least two production cycles (Table 4), indicating that in some cases, cone production is under strong genetic control, while in other years environmental factors such as temperature, wind, and humidity have a greater influence. Furthermore, the differences in heritability among clones reflect changes in

cone production between years, possibly due to changes in early or late flowering events in response to environmental factors. Moderate heritability values of 0.67 and 0.68 in three production cycles likely indicate variation in ramets within clones, and this variation decreases with increasing orchard age.

Compared to the work of Muñoz Gutiérrez *et al*., (2020) in a first-generation orchard of the same species, it is observed that the production of cones is more stable and constant as the age of the trees increases; however, it differs from the ideal contribution line of a seed orchard, where 100% of the clones participate equally in the production of cones.

On the other hand, the cumulative contribution curves for cone production (Figure 1) showed a lower clonal contribution than expected compared to the ideal orchard. In seed orchards, the greatest genetic diversity is only achieved when all parents contribute equally to the gamete gene pool (e.g., Hardy-Weinberg equilibrium) (Teodosiu *et al*., 2023). The imbalance in the contribution of clones to the female cone yield reduces the effective population size in the orchard and the genetic diversity of the progeny (Reynolds and El- Kassaby, 1990). In the case of *P. patula,* the level of clonal participation was high, since between 20 and 22 clones out of 31 are producing female cones, although only 12 of them contribute between 80 and 85% of the total production and seven consistently in the four years of evaluation similar to that found by Muñoz Gutiérrez *et al*. (2020).

Seed orchards of later generations typically have fewer clones than those of the first generation; therefore, it is important to evaluate and select clones effectively. Ideal clones should have the genetic potential for superior performance at different sites with contrasting environmental conditions and should also produce seed adapted to less favorable environments. Clones with low cone production should be eliminated, in accordance with the conclusions of Kang and Lindgren (1998). Selection should focus on clones with moderate to high cone production, under the assumption that these clones exhibit less clonal variation and interaction with environmental factors, are better adapted to environmental conditions, have a stable production of female structures, and as the trees age, their production is expected to stabilize and they are likely to pass these characteristics on to their offspring.

CONCLUSIONS

There is a wide variation in cone production between clones, and this stabilizes as the orchard ages, indicating a high degree of genetic control over cone production capacity.

Moderate heritability values (0.67 and 0.68) show variation between ramets within clones.

The contribution of clones to cone production is relatively stable in 12 clones (17S, 117C, 58C, 36C, 91C, 04Z, 83S, 12C, 72R, 36S, 10R and 10S) which together contribute 80 to 85% of the total female cone production.

The imbalance in the contribution of these clones to the cone harvest negatively affects the effective population size consistently across the four years of evaluation.

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The authors have participated in the writing of the work and analysis of the documents.

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