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Variation in strobilus and cone production in clonal seed orchards of Anatolian black pine*

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Abstract Anatolian black pine [*Pinus nigra* Arnold subsp. *pallasiana* (Lamb.) Holmboe] is an economically and ecologically important forest tree species with a natural distribution of 4.2 million ha, 32% of which is unproductive due to forest fire and other damages in Turkish forestry. The species is widely used in afforestation and conversion of unproductive forests by deploying genetically improved seed from seed orchards because of high adaptation capability to various environmental conditions, and a target species of national tree breeding programme of Anatolian black pine. Estimated variation in reproductive characters can be used as an important guide for managing of seed orchards. The number of cones, female and male strobili were studied in three seed orchards established in 1991, 1993 and 1985 composed of 30, 30 and 34 clones each. Five grafts of each clone were evaluated from each seed orchard for three consecutive years (2022-2024). This study estimated the variation of broad-sense heritability (H^2) and the correlation among cone and strobili production at the graft and clone level. Positive and significant ($p<0.05$) relations were calculated between female and male strobili within year in all orchards both ramet and clone levels, together with significant ($p<0.05$) relations among years for cone productions in the orchards. Significant ($p<0.05$) differences were found for the characters among clones and among years within orchard. Year x clone and clone x ramet interactions were generally significant ($p<0.05$) for the characters. Female strobili seemed a good predictor for cone production. However, the heritability in broad sense was mostly on average below 0.5 for the characters in each seed orchard except of female strobili in an orchard in year-24. It indicated that the reproductive characters under environmental control, and they could give to reflect to management practices.

Keywords: clone, genetic variation, heritability, reproductive characters, seed orchards.

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Introduction

Black pine (*Pinus nigra* Arnold.) is native to Euro-Asia and extends from Spain and Morocco to eastern Turkey, south to Cyprus, and north to northeastern Austria and Crimea, Ukraine. It is also widely planted in United States, New England, the Great lakes, and in the Northwest (Van Haverbeke 1990). Anatolian black pine [*Pinus nigra* Arnold. subsp. *pallasiana* (Lamb.) Holmboe] is one of the five subspecies of Black pine (Gaussen et al. 1964). It grows up to 40 m height and more than 1 m diameter (Saatçioğlu 1976). Female and male flowers appear in May at 15-20 years, and then conelets develop to mature cones of about 5-12 cm length, in 20-24 months after flowering in monoecious Anatolian black pine. Good seed years occur in intervals of 2-3 years in the species depending on elevation (Saatçioğlu 1976).

Türkiye has about 23.4 million ha under forests of which 9.6 million ha is unproductive, while Anatolian black pine has a natural distribution of 4.2 million ha of which 32% is unproductive according to the latest forestry inventory (OGM 2024). The species is one of the most economically and ecologically important forest tree species because of its valuable wood, large distribution and drought tolerance, and also adaptability to different environmental conditions (Atalay & Efe 2012). Anatolian black pine is also one of the main species included in the "National Tree Breeding and Seed Production Programme" (Koski & Antola 1993). Estimation of genetic variation is a main stage of the tree breeding and seed production programme, and a guide for establishment and management of seed sources for successful afforestation. The species is used widely in afforestation practices of Türkiye (Ayan et al. 2017) because of these advantages. Seed orchards established with superior genotypes play an important role in production of improved seed for enhancing the productivity of productive forests. Anatolian black pine has 71 selected seed stands of 9029.4 ha, and 54 seed orchards established in 483.7 ha (ORTOHUM 2024) to produce abundant seed of high genetic quality for reforestation practices (Zobel et al. 1958). The parent trees were selected based on phenotypic traits such as height, diameter, stem straightness and wood quality (Zobel & Talbert 2003). The growth and reproductive characteristics can be combined when genetic information (e.g., heritability, variation, correlation) of reproductive traits is known. However, limited studies included the genetic information were carried out in seed orchards of Anatolian black pine (i.e., Bilir 2002).

The objectives of this study are (1) to investigate genetic variation in cone and strobilus productions in three Anatolian black pine seed orchards; (2) to estimate variance components and heritability; (3) to evaluate the correlations among the characters; 4) to discuss establishment and management practices of seed orchards of the species based on three consecutive years.

Materials and Methods

Seed orchards and data collection

The study was carried out in three clonal seed orchards denoted SO_1, SO_2 and SO_3 of Anatolian black pine (Table 1, Figure 1). The number of cones (CN_{22}, CN_{23} & CN_{24}), female ($N_{♀22}$, $N_{♀23}$ & $N_{♀24}$) and male ($N_{♂22}$, $N_{♂23}$ & $N_{♂24}$) strobili were counted on five grafts, chosen randomly, from each clone in each seed orchard in the spring for strobili production, and autumn for cone production in three consecutive years (2022-2024).

Table 1 Studied seed orchards and their origins.

Seed orchard	SO_1	SO_2	SO_3
Orchard latitude (N)	37°57′58″	38°04′19″	37°09′28″
Orchard longitude (E)	30°34′25″	30°05′46″	29°40′19″
Orchard altitude (m)	1050	970	1035
Establishment year	1994	1991	1985
Clones	30	30	34
Number of grafts	2800	2000	1248
Establishment area (ha)	17.6	13.8	9.4
Spacing at planting (m)	8*8	8*8	8*8
Origin latitude (N)	37°32′	37°34′	37°02′
Origin longitude (E)	31°08′	31°22′	29°27′
Origin altitude (m)	1650	1350	1150

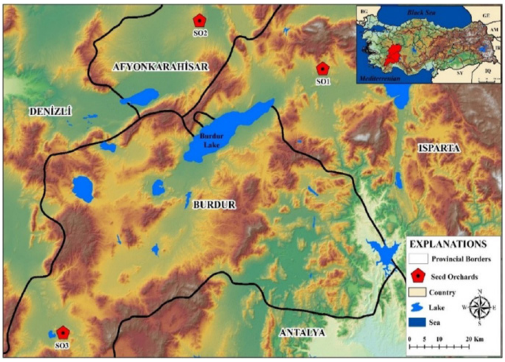

Figure 1 Location of the seed orchards.

Data analysis

The following GLM of ANOVA was used to analyze the difference in cone and strobili production among clones and among years within orchard (SAS 2004):

$$Y_{ijk}=\mu+Y_{1}+C_{j(i)}+C(R)_{j(k)}+e_{ijk} \quad (1)$$

where Y_{ijk} is the observation from the i^{th} graft of the j^{th} clone in the k^{th} year, μ is the overall mean of the character, Y_i is the effect of i^{th} year, C_{ij} is the effect of the j^{th} clone in the i^{th} year, $YC_{(ij)}$ is the effect of interaction between year and clone, $C(R)_{j(k)}$ is the effect of interaction between clone and ramet, and e_{ijk} is the random error.

Broad-sense heritability (clonal repeatability, the fraction of the variance which is genetic among clones, H^2) was estimated (SAS 2004) as:

$$H^2=\frac{\sigma_C^2}{\sigma_C^2+\sigma_e^2} \quad (2)$$

where σ^2_C is the variance among clones, σ^2_e is the variance within clone.

Variance components, expressed as coefficient of variation among clones (CV_C) and within clone (CV_e), were estimated as:

$$CV_C=\frac{100\sigma_C}{\bar{x}};\ CV_E=\frac{100\sigma_e}{\bar{x}} \quad (3\,a\,\&\,b)$$

Where $\bar{x}$ is overall mean of the character, σ^2_C and σ^2_e are the variance among clones, and the variance within clone, respectively.

Correlation among characters were calculated for the individual graft and clonal mean value (Bilir et al. 2006). Pearson' correlations (r_p) among the traits were estimated as (Rohlf and Sokal 1995):

$$r_p=\frac{\sum xy}{\sqrt{\sum x^2 \sum y^2}} \quad (4)$$

where $\sum xy$ is the sum of the factors of the traits x and y, $\sum x^2$ and $\sum y^2$ are phenotypic variances of the traits x and y.

Results

Strobili and cone productions

Strobili and cone productions varied among orchards, among clones within orchard, and among years within the orchard (Table 2, Figures 2-4), while the second seed orchard (SO_2) had higher values for all traits in years-22 and 23 opposite to the highest productivity of year-24 in first seed orchard (SO_1) (Table 2). The range of values was a higher among grafts than among clones for all characters. The number of cones differed by 4x among grafts of a clone of seed orchards (SO_1 & SO_2) and by 3*x* in SO_3 across three years. The female and male strobilus ($N_♀$ & $N_♂$) production was the highest in year-22 but the cone production (CN) was the highest in year-24 in the orchards (Table 2).

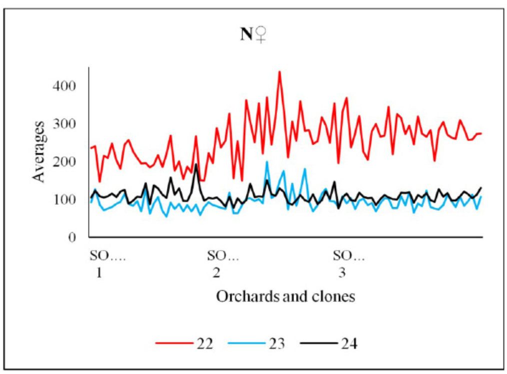

Figure 2 Clonal female strobili productions in the orchards for the years.

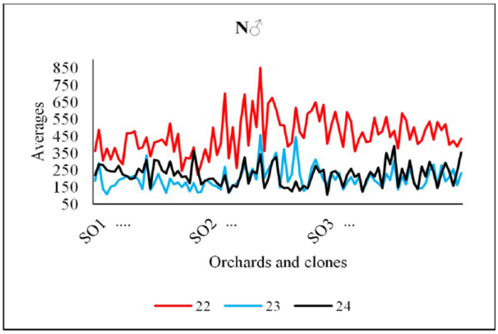

Figure 3 Clonal male strobili productions in the orchards for the years.

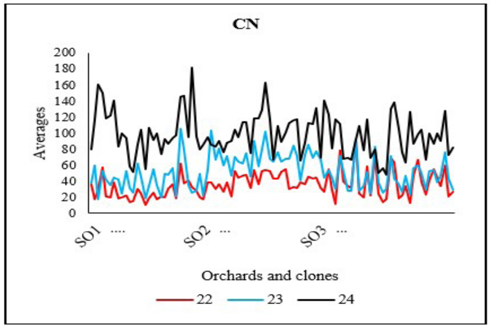

Figure 4 Clonal cone productions in the orchards for the years.

Table 2 Average ($\overline{x}$), standard deviation and ranges for strobili and cone productions in the orchards.

	SO_1			SO_2			SO_3		
	$\overline{x}$ *	clone range	graft range	$\overline{x}$	clone range	graft range	$\overline{x}$	clone range	graft range
N♀$_{22}$	205^c (75.7)**	147-267	48-480	283^b (103.1)	150-437	56-880	278^c (81.4)	202-368	90-528
N♀$_{23}$	86^a (29.7)	55-128	16-169	105^a (49.4)	64-199	18-275	92^a (30.7)	66-123	30-195
N♀$_{24}$	116^b (41.1)	88-193	60-270	106^a (33.7)	76-151	12-240	107^b (18.9)	85-131	60-164
N♂$_{22}$	375^c (137.8)	223-524	122-768	525^c (219.9)	261-850	117-1365	474^c (141.0)	361-594	156-945
N♂$_{23}$	179^a (76.5)	108-337	32-440	232^b (125.1)	116-456	40-650	198^a (78.6)	127-306	66-420
N♂$_{24}$	241^b (95.9)	142-363	24-560	199^a (97.2)	106-344	28-240	229^b (106.3)	122-394	80-520
CN_{22}	27^a (19.2)	11-62	7-96	41^a (15.7)	21-55	12-82	39^a (28.7)	12-96	8-128
CN_{23}	42^b (32.8)	17-106	10-204	70^b (31.4)	41-103	18-156	45^b (28.1)	24-92	8-148
CN_{24}	103^c (46.5)	51-181	20-140	101^c (33.2)	65-162	36-210	92^c (40.3)	48-141	24-280

Note: *Values followed by the same letters are not significantly different (*p<0.05*).
**Standard deviation of means in the parenthesis.

The analysis of variance showed significant (*p<0.05*) difference for most characters among clones within orchard, and among years, and also year x clone, and clone x ramet interactions were generally significant (*p<0.05*) for the characters (Table 3). The number of mature cones per hectare ranged from 4219 (SO_1) to 6406 (SO_2) in year 22, and 6563 (SO_1) to 10938 (SO_2) in year 23, and 14375 (SO_3) to 16094 (SO_1) in year 24. The ratios between male and female strobili production in the orchards was similar (1.79 in year 22, 2.15 in year 23, and 2.03 in year 24) in the years.

Heritability and correlations

Coefficient of variation among individual grafts within clones (CV_e) expressed as the genetic variation was higher than coefficient of variation among clones (CV_C) except of female strobili in third seed orchard (SO_3) in year-24 (Table 4). As seen in Table 4, variation among and within clones was mostly higher in cone production than strobili production in years 22 and 23, while it changed in orchards for year 24. The broad sense heritability was mostly on average below 0.5 for the characters in an

Table 3 Results of analysis of variance for clonal and annual comparison of the traits.

	SO_1			SO_2			SO_3		
Source	N♀	N♂	CN	N♀	N♂	CN	N♀	N♂	CN
Year (Y)	**	**	**	**	**	**	**	**	**
Clone (C)	**	**	**	**	**	**	*	**	**
Y x C	NS	**	**	*	*	NS	NS	NS	**
Clone x Ramet	**	**	**	*	**	NS	NS	*	*

Note: * and ** indicate statistically significant at the probability levels of 0,05 and 0.01. NS indicates non-significant.

individual seed orchard except of $N_♀$ in SO_3 in year-24, while it changed with the orchard, character and year of observation (Table 4). The result showed that the reproductive traits are under environmental control as evidenced by the coefficient of variation. Male strobili had mostly higher variation among and within clones than the female strobili in the orchards across the years. It could be said that $N_♂$ had higher heritability than $N_♀$ (Table 4). It was evident that cone production had the highest heritability in years 22 and 23 (0.47 & 0.33) in SO_3, while it was 0.31 in year 24 of SO_1. There was no observed high clonal variation for cone production in SO_2, (heritability was close to 0 in year 23) (Table 4). However, maturation of strobilus to cones took 20-24 months in the species.

There was a significant ($p<0.05$) positive correlation between $N_♀$ and $N_♂$ within years, as well as among CNs across years in individual grafts and clones, while the correlation between other traits varied across orchards and year (Table 5). However, $N_♀$ seemed a reasonable predictor for cone production based on the correlation value.

Table 4 Coefficient of variation among (CV_C%) and within clones (CV_e%); and broad sense heritability (H^2) for strobili (N♀& N♂) and cone productions (CN) for the years in the orchards.

	SO_1			SO_2			SO_3		
	CV_C	CV_e	H_2	CV_C	CV_e	H_2	CV_C	CV_e	H_2
$N_{♀22}$	1.85	36.88	0.03	18.14	31.8	0.25	6.85	28.43	0.06
$N_{♀23}$	14.87	31.39	0.18	27.55	38.44	0.34	10.82	31.14	0.11
$N_{♀24}$	11.11	33.77	0.01	11.62	29.66	0.13	9.61	8.77	0.55
$N_{♂22}$	12.87	34.51	0.12	19.71	37.16	0.22	6.96	29.41	0.05
$N_{♂23}$	22.29	36.66	0.27	32.96	43.07	0.37	19.91	33.92	0.26
$N_{♂24}$	10.74	38.38	0.07	27.85	40.45	0.32	25.19	35.78	0.33
CN_{22}	35.23	62.79	0.24	15.66	35.08	0.17	51.88	54.99	0.47
CN_{23}	33.36	71.44	0.18	3.57	44.74	0.06	35.09	49.80	0.33
CN_{24}	25.16	37.81	0.31	17.51	27.84	0.28	24.66	37.37	0.30

Table 5 Correlations between grafts (below diagonal) and clones (above diagonal) in the orchards.

	r	$N♀_{22}$	$N♂_{22}$	CN_{22}	$N♀_{23}$	$N♂_{23}$	CN_{23}	$N♀_{24}$	$N♂_{24}$	CN_{24}
$N♀_{22}$	SO_1	-	.719**	-.091^{NS}	.382*	.393*	.105^{NS}	.375**	.319^{NS}	-.319^{NS}
	SO_2	-	.726**	.745**	.624**	.573**	.560**	.637**	.624**	.677**
	SO_3	-	.618**	.437**	.164 ^{NS}	.108^{NS}	.369*	.281^{NS}	.139^{NS}	.234^{NS}
$N♂_{22}$	SO_1	.710**	-	-.212^{NS}	.497**	.554**	.173^{NS}	.325^{NS}	.326^{NS}	-.359^{NS}
	SO_2	.682**	-	.508**	.643**	.684**	.385*	.655**	.780**	.400*
	SO_3	.617**	-	.348*	.245^{NS}	.132^{NS}	.258^{NS}	.222^{NS}	.199^{NS}	.183^{NS}
CN_{22}	SO_1	.199*	.154^{NS}	-	-.133^{NS}	-.261^{NS}	.603**	.093^{NS}	.133^{NS}	.582**
	SO_2	.386**	.409**	-	.448*	.402*	.399*	.538**	.510**	.480**
	SO_3	.198**	.087^{NS}	-	-.200^{NS}	-.258^{NS}	.887**	-.156^{NS}	-.362*	.371*
$N♀_{23}$	SO_1	.431**	.393**	.091^{NS}	-	.893**	.165^{NS}	.339^{NS}	.405*	-.104^{NS}
	SO_2	.374**	.417**	.353**	-	.952**	.370*	.489**	.599**	.535**
	SO_3	-.022^{NS}	.067^{NS}	.014^{NS}	-	.894**	-.204^{NS}	.456**	.603**	-.146^{NS}
$N♂_{23}$	SO_1	.445**	.442**	.007^{NS}	.828**	-	.174^{NS}	.295^{NS}	.374*	-.227^{NS}
	SO_2	.332**	.440**	.267**	.875**	-	.383*	.461*	.594**	.507**
	SO_3	.025^{NS}	.104^{NS}	-.087^{NS}	.806**	-	-.277^{NS}	.372*	.621**	-.260^{NS}
CN_{23}	SO_1	.302**	.339**	.590**	.275**	.237**	-	.039^{NS}	.010^{NS}	.286^{NS}
	SO_2	.327**	.322**	.285**	.216**	.213**	-	.364*	.361*	.522**
	SO_3	.259**	.094^{NS}	.619**	.044^{NS}	-.071^{NS}	-	-.234^{NS}	-.454**	.312^{NS}
$N♀_{24}$	SO_1	.325**	.290**	.184*	.214**	.253**	.045^{NS}	-	.790**	.093^{NS}
	SO_2	.384**	.340**	.292**	.276**	.293**	.389**	-	.797**	.620**
	SO_3	-.022^{NS}	.003^{NS}	-.028^{NS}	.299**	.320**	-.160*	-	.823**	-.217^{NS}
$N♂_{24}$	SO_1	.287**	.288**	.193*	.227**	.306**	.073^{NS}	.813**	-	.217^{NS}
	SO_2	.480**	.547**	.365**	.422**	.450**	.297**	.693**	-	.481*
	SO_3	.041^{NS}	.107^{NS}	-.238**	.247**	.367**	-.306**	.738**	-	-.464**
CN_{24}	SO_1	.039^{NS}	-.059^{NS}	.274**	.083^{NS}	.053^{NS}	.246**	.116^{NS}	.257**	-
	SO_2	.405**	.257**	.203**	.306**	.231**	.177*	.207*	.170*	-
	SO_3	-.014^{NS}	-.036^{NS}	.226**	.142^{NS}	.038^{NS}	.195*	.037^{NS}	-.083^{NS}	-

Note: * and ** are the statistically significant at *0.05* and *0.01* probability levels. ^{NS} is the non-significant statistically.

Discussion

Strobili and cone production were variable among orchards, among clones and among years (Table 2, Figures 2-4). For instance, all orchards had over two times higher strobili production in year 22 than year 23, an opposite trend was however seen in cone production, while the cone productions were the highest for the orchards in year 24 (Table 2). The results were well accordance with intervals of good seed year of the species (Saatçioğlu 1976). Similar trends were reported in clonal seed orchards of Scots pine (e.g., Bilir et al. 2006 & 2008), Black pine (e.g., Matziris 1993), and other forest tree species (e.g., Bilir 2002, Matziris 1997 & 1998, Varghese et al. 2006). The results emphasize the importance of selecting a population and fixing the age for seed collection since fertility was low in in the youngest seed orchard, SO_1 (Table 2). It is reported that seed orchard cannot give reasonable reproductive data in young ages (Kang 2001). Year x clone, and clone x ramet interactions were generally significant ($p<0.05$), while they changed for the characters and orchards (Table 3). Many biotic and abiotic factors could influence the gamete contribution of clones (Eriksson et al. 1973, Hedegart 1976, Zobel & Talbert 2003, Kang & Bilir 2021). For instance, altitude influenced strobili production in natural stands of Brutian pine (Bilir et al. 2005), and seed collection during good seed years was important in Anatolian black pine (Saatçioğlu 1976).

The quotients of male and female strobilus production varied from 1.79 in year 22 to 2.15 in year 23. Similar variation across years was reported in a clonal seed orchard of Anatolian black pine by Ertekin (2010), and a quotient of 2.4 was reported in clonal seed orchards of Scots pine (Bilir et al. 2002 & 2006). The quotient indicates the pollination success that can play an important role in conversion of female strobilus to cone and seed maturations, and productivity of seed crop (i.e., number of filled seeds).

Variation in cone production among clones (CV_C) was lower than that among individual grafts within clones (CV_e) (Table 4). It may also be due to graft establishment error such as position and direction from where the scion was collected in the crown. Variation in cone production was unexpectedly higher than strobili production (Table 4) which may be due the greater impact of biotic and abiotic factors like rain, wind and insect damage on cones than strobili, as they are retained longer in the tree from pollination to maturation. Gene diversity of orchard crop will be lower in actual situation where unequal fertility contribution occurs among orchard parents (Kang & Bilir 2021) compared to the ideal situation of non-relatedness and equal contribution among parents.

Broad sense heritability was mostly below 0.5, but varied with orchard and production year (Table 4) indicating the environmental control on reproductive characters. Male strobili showed higher variation among and within clones than the female strobili. It could be said that N♂ was more heritable than N♀ (Table 4) opposite to Korean pine (Kim et al. 2024), while heritability of cone production in SO_3 was the highest in years 22 and 23 (0.47 & 0.33), and 0.31 in SO_1 of year 24. Higher heritability in N♂ than N♀ was reported in clonal seed orchards of other tree species (i.e., Hannerz et al. 2001, Bilir et al. 2006). Low heritability for strobili production is reported in different forest tree species (i.e., Nikkanen & Ruotsalainen 2000, Kang 2000, Bilir 2002, Jeon et al. 2022) contrary to the report of Schmidtling (1983) who reported H_2 values of 0.64 and 0.39 for N♂, 0.42 and 0.13 for N♀ in Lodgepole pine (Hannerz et al. 2001), and generally in Korean pine for years (Kim et al. 2024). However, no high clonal variation was observed for cone production in SO_2 meant heritability close to 0 in year 23 (Table 4). Broad-sense heritability values derived for cone-set varied from 0.29 to 0.57 in Norway spruce (Almqvist et al. 2001), 0.4 in Aleppo pine (Matziris 1997) and 0.32 in Scots pine orchards (Bilir et al. 2008), while high heritability (>0.8) was reported in a seed orchard of Black pine (Matziris 1993). These results emphasize the importance of practices such as pruning, soil treatment, fertilization, and hormone application in seed orchard management.

There was a significant (*p<0.05*) positive correlation between N♀ and N♂ within the year in individual grafts and the clone average values. Positive and significant correlation between N♂ and N♀ are in accordance with the results reported in a clonal seed orchard of Anatolian black pine (Bilir et al. 2002), and populations of other forest tree species (Schmidtling 1983, Kjaer 1996, Bilir et al. 2002, 2005 & 2006). A contrary to negative trend was also reported in other forest tree species (Schultz 1971, Savolainen et al. 1993, Hannerz et al. 2001). CNs showed positive and significant (*p<0.05*) correlation among years for the individual graft and clone level in the orchards. However, other correlations among the characters changed across years and orchards (Table 5). Based on correlation analysis, N♀ was identified to be a reasonable predictor for cone production. These trends could be used for management practices (e.g., hormone application) of seed orchards in the species.

Conclusion

There were positive and significant (*p<0.05*) relations between female and male strobili within year in all orchards both ramet and clone levels, while they were significant (*p<0.05*) relations among years for cone production in the orchards. Among clones and among years within orchard showed significant (*p<0.05*) differences for the characters. Year x clone and clone x ramet interactions were generally significant. Female strobili seemed a better predictor for cone production. However, the heritability in broad sense was generally on average below 0.5 for the characters in each seed orchard. The primary results obtained from three years' data in three seed orchards could be used as a guide in managing of seed orchards of the species. Further observations should be carried out in other seed orchards by including new characters like number of filled seeds from different orchards and years to arrive at an accurate conclusion. The clonal variation of the reproductive traits could be reduced by adopting suitable management practices like tending or seed harvest from similar productivity trees for higher gene diversity in seed orchard crop, while the variations of the study were acceptable level.

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Conflict of interest

The authors declare no financial or personal interests could influence the work presented in this paper.

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