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Conversion loss among strobili, conelets, and cones and its impact on effective population size: a case study in *Cedrus libani*

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Taurus cedar (*Cedrus libani* A. Rich.), also known as cedar of Lebanon, is a target species in the Turkish National Tree Breeding and Seed Production Program. It is valued for its wood and non-wood products and sociocultural significance and occurs naturally across 580,515 ha, primarily in the Taurus Mountains of Türkiye. Conversion from strobili to the mature cone in Taurus cedar can take 24–26 months. The conversion, impacted by many abiotic and biotic factors, is essential for the sustainability of the species. In this case study, the production of female and male strobilus, conelets, and cones, their variation and conversion, and correlations among the characteristics, fertility variation, and linkage parameters (i.e., effective number of parents and gene diversity) were examined on 50 individual trees sampled from a natural population in southern Türkiye. Average numbers of female and male strobilus, conelets, and cones were 179, 653, 35, and 28, respectively, although individual trees showed large variations in characteristics. Conversion ratios of female strobili to conelets and mature cones, and from conelets to mature cones, were 21.7, 17.9 and 81.6%, respectively, despite the large differences among trees in the conversions. For instance, from the conversion of conelets to mature cones ranged from 48.6 to 100.0% among trees. The ratios of female to male strobilus, conelets, and cones changed. However, cone production was only significantly ($p < 0.01$) related to number of conelets ($r = 0.943$, $R^2 = 0.89$). The result showed that conelet production was a better indicator of cone production in Taurus cedar. Fertility variation was lower in female strobili (1.20, 42% of trees), conelets (1.17, 43%), and mature cones (1.20, 42%) compared to zygotic fertility (2.90, 35%) and male strobili (2.08, 24%). Female, conelet, and cone fertility pathways thus showed greater consistency across the sampled population than zygotic fertility and male strobilus production. Effective population size was about 48% larger in strobili than mature cone stages.

KEYWORDS
abortion, population, reproductive, seed, sibling, variation

1 Introduction

Taurus cedar, also known as the Lebanon cedar (*Cedrus libani* A. Rich.), is a forest tree species in the genus Cedrus of the Pineacea family (Yaltırık, 1988; Anşin and Özkan, 1993). Natural distribution of the species spans Lebanon and Syria, although the tree is mainly found in the Taurus Mountains of Türkiye, at 580515 ha, of which 43% is unproductive (Boydak,

2003; Anonymous, 2025a). The species grows up to 2.5 m in diameter at breast height and 50 m in height (Boydak, 1988).

Male strobilus appear in July and grow 3–5 cm in August, while female flowers can be seen in September. Female flowers convert to conelets in 6 months and to mature cones in 24–26 months after fertilization (Odabaşı, 1990; Boydak, 1996). Taurus cedar, which bears cones at about 30 years old in natural stands, experiences a good seed year every 2 or 3 years (Saatçioğlu, 1976; Odabaşı, 1990; Boydak, 1996). Taurus cedar is one of the target species of the National Tree Breeding and Seed Production Program of Türkiye because of its valuable wood product and social–cultural importance (Koski and Antola, 1993). Studies on its reproductive characteristics are one of the contributive tools for the program. However, while many studies have been carried out on Taurus cedar and other forest tree species (i.e., Odabaşı, 1990; Kang et al., 2003; Bilir et al., 2017, 2023; Çatal et al., 2018; Bilir, 2024), conversion among strobili, conelet, and cone were not examined in detail in *C. libani*. Fertility variation, defined as an individual's ability to fertilize (reproductive success), estimated by cones, flowers, pollen, fruit and seed production (Griffin, 1982; Savolainen et al., 1993; Kang, 2001; Kang et al., 2003, 2023; Bilir, 2011; Bilir et al., 2017), and linkage parameters (e.g., effective population size, gene diversity), are important guiders in plant science and forestry practices to produce improved seed crop (i.e., Bila, 2000; Kang, 2001; Kang et al., 2003, 2023). However, the parameters that change according to reproductive characteristics have not been estimated for *C. libani* (Kang et al., 2023).

The purposes of this case study were to examine variation in female and male strobili and their conversion to conelets and cones, estimate relationships among the reproductive characteristics, and estimate fertility variation and linkage parameters stratified by conversion success. The analysis was based on 50 individual trees sampled from a natural population of Taurus cedar to support genetic, breeding, silvicultural, and forestry management practices for the species.

2 Materials and methods

2.1 Sampling area and data collection

Female and male strobilus numbers (N_f and N_m; Figure 1) were counted on 50 phenotypically selected trees (based on tree height, diameter, and stem straightness; Zobel and Talbert, 2003) sampled in autumn 2023. Trees were collected from a natural population located in southern Türkiye (38°05′N, 30°42′E; elevation 1,590 m; Figure 2). The production of female and male strobilus was estimated by using the number of male strobili in a branch sampled from each direction and multiplying the branch number of each individual (i.e., Bila, 2000; Kang, 2001; Bilir et al., 2005; Bilir and Kang, 2021; Kang et al., 2023). The sampled population encompassed 52 ha, 80 years, 16 m height, and 620 tree ha^{-1} (Anonymous, 2025b). Numbers of conelets (Cn), which were 2–3 cm length in the summer of 2024, and numbers of mature cones (CN), which were about 8.5 cm length after 23–25 months in the autumn of 2025 (Figure 1), were counted on the marked trees depending on the cone maturation period of the species (Saatçioğlu, 1976; Odabaşı, 1990; Boydak and Çalıkoğlu, 2008). Data normality was not assumed in the study.

The soil in the area was Paleozoic, clayey-limestone (Atalay, 1987). Minimum, maximum, and average temperatures (°C), and total annual precipitation (mm = kg/m^2), obtained from General Directorate of Meteorology and Climatology of Türkiye (MGM, 2025), are given in Figure 3.

2.2 Data analysis

Pearson's phenotypic correlations (r_p) among the productions were estimated by the SAS software (SAS, 2004) as Equation 1 (Falconer, 1989):

$$r_p = \frac{COV_{f(x,y)}}{\sqrt{\sigma^2_{f(x)}}\sqrt{\sigma^2_{f(y)}}} \quad (1)$$

where $COV_{f(xy)}$ is the phenotypic covariance between the traits x and y and $\sigma^2_{f(x)}$ and $\sigma^2_{f(y)}$ are the phenotypic variances for the traits x and y, respectively.

Coefficient of variation (CV%) was estimated based on average ($\bar{x}$) and standard deviation (S) of the characteristics as Equation 2:

$$CV = (S/\bar{x}) * 100 \quad (2)$$

The variations of female and male fertility (ψ_f and ψ_m) among individuals were estimated for the strobilus production as Equations 3a and b (Kang and Lindgren, 1998):



FIGURE 1
Strobilus and mature cones of the species.

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FIGURE 2
A sampled tree and population.

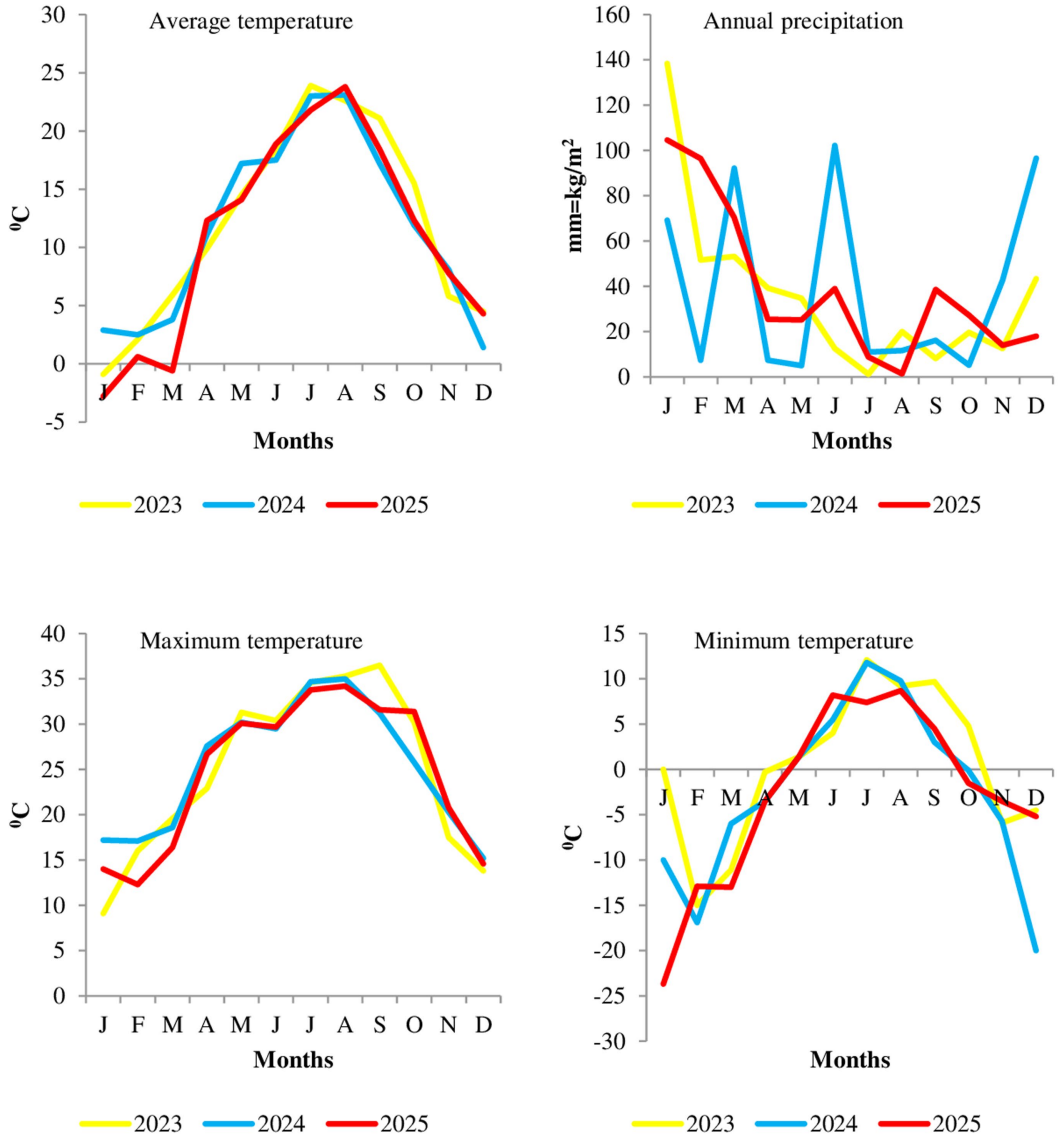


FIGURE 3
Monthly minimum, maximum, and average temperatures, and total annual precipitation.

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$$\psi_f = N\sum_{i=1}^{N} f_i^2 = CV_f^2 + 1 \quad (3a)$$

$$\psi_m = N\sum_{i=1}^{N} m_i^2 = CV_m^2 + 1 \quad (3b)$$

where N is the census number, f_i is the fertility as female of the ith tree, and m_i is the fertility as male of the ith tree in the studied population. CV_f and CV_m stand for the coefficients of variation in female and male strobili productions, respectively.

Total fertility variation, also known as the sibling coefficient (Ψ), was calculated depending on the census number (N) and numbers of female (f_i) and male (m_i) strobili of the ith individual by Kang and Lindgren (1999) Equation 4 as:

$$\Psi = N\sum_{i=1}^{N}\left(\frac{0.5f_i}{\sum f_i} + \frac{0.5m_i}{\sum m_i}\right)^2 \quad (4)$$

The variations of conelet (Cn) and cone (CN) fertility (Ψ_{cn} and Ψ_{CN}) among individuals were estimated for the yields as Equations 5a and b (Kang and Lindgren, 1999; Bilir, 2011):

$$\Psi_{c_n} = N\sum_{i=1}^{N} c_{ni}^2 = CV_{Cn}^2 + 1 \quad (5a)$$

$$\Psi_{C_n} = N\sum_{i=1}^{N} c_{Ni}^2 = CV_{CN}^2 + 1 \quad (5b)$$

where C_{ni} and C_{Ni} represent the conelet and cone fertility of the ith tree, and CV_{Cn} and CV_{CN} stand for the coefficients of variation in conelet and cone production, respectively.

The effective number of parents ($N_e^{(p)}$), the effective numbers of females ($N_e^{p(f)}$) and males ($N_e^{p(m)}$), and the effective numbers of conelets ($N_e^{p(cn)}$) and cones ($N_e^{p(CN)}$) were calculated based on the total fertility variation (Ψ), female (ψ_f) and male (ψ_m) fertility, and conelet (Ψ_{cn}) and cone fertility. (Ψ_{CN}) variations were estimated as Equations 6a, b, c, d and e (Kang et al., 2003; Bilir, 2011):

$$N_e^{(p)} = \frac{\Psi}{N} \quad (6a)$$

$$N_e^{p(f)} = \frac{\psi_f}{N} \quad (6b)$$

$$N_e^{p(m)} = \frac{\psi_m}{N} \quad (6c)$$

$$N_e^{p(cn)} = \frac{\Psi_{cn}}{N} \quad (6d)$$

$$N_e^{p(CN)} = \frac{\Psi_{CN}}{N} \quad (6e)$$

The gene diversity (GD) of seeds was estimated based on the total effective number of parents ($N_e^{(p)}$) (GD_Ψ), conelet effective number of parents ($N_e^{p(cn)}$) (GD_{cn}), and the cone effective number of parents ($N_e^{p(CN)}$) (GD_{CN}) as Equations 7a, b and c (Kang and Lindgren, 1998; Park et al., 2017):

$$GD_\Psi = 1 - \frac{0.5}{N_e^{(p)}} \quad (7a)$$

$$GD_{cn} = 1 - \frac{0.5}{N_e^{p(cn)}} \quad (7b)$$

$$GD_{CN} = 1 - \frac{0.5}{N_e^{p(CN)}} \quad (7c)$$

The parental balance curve was composed using the cumulative proportion of the productions by El-Kassaby and Reynolds (1990).

3 Results

3.1 Strobili, conelet, and cone productions

Large differences in strobilus production were found among the trees (Table 1 and Figure 4). Coefficient of the variation was the highest (105.1%) for the number of male strobili, while it was the lowest (41.0%) for the number of conelets (Table 1). The results were in accordance with the parental-balance curve shown by means of cumulative gamete contribution in Figure 5. The results indicated the importance of individual selection for higher and balanceable reproductivity in *Cedrus libani*.

Overall conversion ratios were 21.7% for female strobili to conelet, 17.9% for female strobili to mature cone, and 81.6% for conelet to mature cone. However, conversion rates varied substantially among individual trees across all three pathways. For instance, the conversions varied between 48.6 and 100.0% among trees for conelets to mature cones. It could be said that number of conelets is a better predictor for cone production. A low conversion ratio (15.8%) was estimated between female and mature cone stages.

3.2 Fertility variation, effective population size, and gene diversity

The fertility variations ranged from 1.17 (Ψ_{cn}, 86% of census number) to 2.90 (Ψ, 35%) and showed large deviations (Table 2). The gametic female (1.20, 87% of census number) and male (2.08, 48%) fertility variations increased to 2.90 (35%) in zygotic/total fertility (Table 2). The results also reflected the effective number of parents, as seen in Table 2. The deviation of gene diversity was 0.017 between GD_Ψ (0.971

TABLE 1 Descriptive statistics (averages, range, coefficient of variation, and standard error) for female (N_f) and male (N_m) strobili, conelets (Cn), and mature cones (CN).

Parameters	N_f	N_m	Cn	CN
Averages	179.4	652.8	34.6	28.4
Ranges	48–420	60–2,800	14–90	10–68
CV%	44.8	105.1	41.0	45.4
SE	11.4	96.9	2.0	1.8

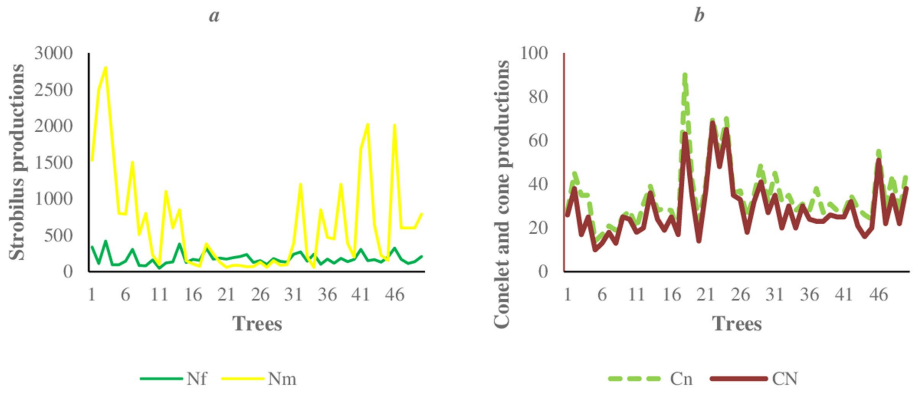


FIGURE 4
Numbers of female (N_f) and male (N_m) strobilus **(a)**, and conelet (Cn) and mature cone (CN) **(b)** in trees.

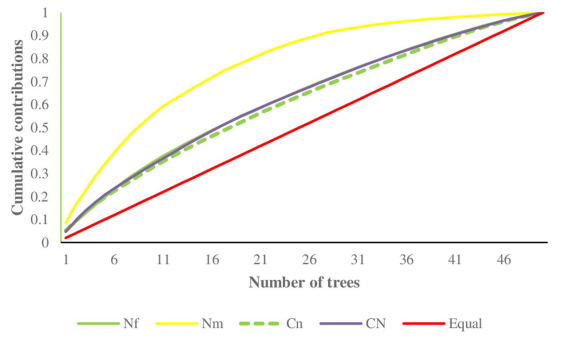


FIGURE 5
Parental-balance curves of the individuals.

for $\Psi = 17.26$) and GD_{cn} (0.988 for $\Psi_{cn} = 42.88$). The results demonstrate the importance of reproductive characteristics in the estimations included for gene diversity. Male and zygotic fertility variations need to be balanced by forestry practices to increase gene diversity of seed crop.

3.3 Relations between productions

The relations between productions deviated (Table 3). However, cone production (CN) showed only a significant ($p < 0.01$) relation to number of conelet (Cn) ($r = 0.943$, $R^2 = 0.89$) (Table 2 and Figure 6a). Conelet production appears to be a better indicator of cone production in *Cedrus libani*. It is interesting that strobilus production had no significant ($p > 0.05$) effect on cone production (Table 3). The results indicate the importance of pollinators other than the mother tree.

There was also significant ($p < 0.01$) and positive correlation between female (N_f) and male (N_m) strobilus ($r = 0.390$) ($R^2 = 0.32$) (Table 2 and Figure 6b). The result could be a guide for the selection, establishment, and management of other forestry practices in the species.

TABLE 2 The female and male fertility variations (ψ_f & ψ_m), and zygotic fertility variations for strobilus (Ψ), conelet (Ψ_{Cn}), and cone (Ψ_{CN}) productions, and effective number of parents ($N_e^{(p)}$, $N_e^{p(f)}$, $N_e^{p(m)}$, $N_e^{p(cn)}$ and $N_e^{p(CN)}$).

ψ_f*	ψ_m	Ψ	Ψ_{Cn}	Ψ_{CN}
1.20	2.08	2.90	1.17	1.20
$N_e^{p(f)}$	$N_e^{p(m)}$	$N_e^{(p)}$	$N_e^{p(cn)}$	$N_e^{p(CN)}$
41.77 (0.84)**	24.02 (0.48)	17.26 (0.35)	42.88 (0.86)	41.61 (0.84)

*f, m, Cn, and CN represent numbers of female strobilus, male strobilus, conelet production, and cone productions, respectively.
**Relative effective number of parent (N_r) calculated as $N_r = N_e/N$ (Lindgren et al., 1996) in the parentheses.

TABLE 3 Correlations among the female (N_f) and male (N_m) strobilus, conelet (Cn), and mature cone (CN) productions.

r	N_f	N_m	Cn
N_m	0.390**	—	
Cn	0.293*	-0.038^{NS}	—
CN	$.223^{NS}$	-0.090^{NS}	0.943**

*Correlation is significant at 95% significance. **Correlation is significant at 99% significance. ^{NS}Correlation is not significant.

4 Discussion

4.1 Strobili, conelet, and cone productions

Many biotic (i.e., good flowering year, species, populations) and abiotic (year, edaphic, geographic and climatic characteristics) factors could have contributed to the large variation among the trees for the production (Table 1 and Figure 4), and conversion ratios (i.e., Bila and Lindgren, 1998; Kang et al., 2003; Bilir, 2011; Varol et al., 2017; Çatal et al., 2018; Bilir and Kang, 2021; Bilir et al., 2023, 2005, 2025a,b; Eser, 2024; Oktan, 2026; Kaytanlıoğlu Tığlı, 2026). The variation could also be related to the higher gene diversity of seed to establishment and management practices of seed sources (Kang and Lindgren, 1999; Kang, 2001; Kang et al., 2023). For instance, the variations of conversion indicated the importance of the prediction of a good seed year, which occurs every 2 to 6 years (Saatçioğlu, 1976; Odabaşı, 1990; Boydak and Çalıkoğlu, 2008), for the planning of forestry practices. However, desynchronization between female and male strobilus could also impact on the low conversion ratio (15.8%) from female strobili to mature cone together with the abiotic and biotic factors.

4.2 Fertility variation, effective population size, and gene diversity

Fertility variations in *C. libani* may also be influenced by various biotic and abiotic factors, as in other forest tree species (i.e., Kang et

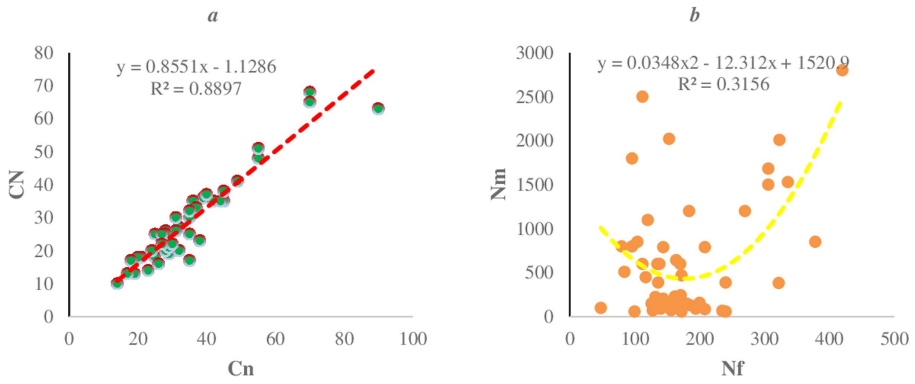


FIGURE 6
Relation between cone (CN) and conelet (Cn) productions **(a)**, and between female (N_f) and male (N_m) strobilus **(b)**.

al., 2003; Boydak and Çalıkoğlu, 2008; Bilir and Kang, 2021; Bilir et al., 2005, 2023, 2025a,b; Eser, 2024; Oktan, 2026; Kaytanlıoğlu Tığlı, 2026; Kang et al., 2026). The variations of female and male fertility (ψ_f and ψ_m) could also be related to the results found by Kang and Lindgren (1998). They suggested as a rough generalized heuristic rule that Ψ should be lower than 3 (CV $\leq$ 140%) for natural populations (Kang, 2001; Kang and Bilir, 2021; Kang et al., 2023). The studied population and characteristics had an ideal variation. However, male and zygotic fertility variations need to be balanced through forestry practices (e.g., genetic or common thinning, collecting seeds from a larger number of trees, supplemental pollination, or hormone application) to increase gene diversity of seed crop. A 48% larger effective population size from strobili to mature cone indicated the importance of balancing by forestry practices such as genetic or traditional tending in seed collection areas.

4.3 Relations between productions

The significant ($p < 0.01$) and positive correlation between cone (CN) and conelet (Cn) productions ($r = 0.943$, $R^2 = 0.89$) (Table 2 and Figure 6A) emphasized that conelet production was a better indicator of cone production in *Cedrus libani*, while strobili production was also suggested for estimation of seed crop (Saatçioğlu, 1976; Odabaşı, 1990; Boydak and Çalıkoğlu, 2008). It was interesting that strobilus production had no significant ($p > 0.05$) effect on cone production (Table 3). The results indicated the importance of pollinators other than mother tree. Similar significant ($p < 0.01$) and positive correlations between female (N_f) and male (N_m) strobilus were also reported in different forest tree species (i.e., Jonsson et al., 1976; Bhumibhamon, 1978; Burczyk and Chalupka, 1997; Bilir et al., 2002; Bilir and Kang, 2021). The result guide the selection, establishment, and management of other forestry practices in the species.

5 Conclusion

Female and male strobilus, conelet, and mature cone yields varied among the trees. The variation was the highest for male strobili, depending on a coefficient of variations (CV = 105.1%). Conversion ratios of female to conelet and to mature cone varied. The number of conelets could be a predictor of cone yield. The correlations between the reproductive characteristics changed for the productions. However, cone production was only significantly related to number of conelets. Fertility variations were at an acceptable level.

The studied population had an ideal variation for the characteristics. However, male and zygotic fertility variations need to be balanced by forestry practices to increase the gene diversity of seed crop.

This study was limited to 5 trees from a single population sampled over 1 year. This sampling design represents a constraint given the wide natural distribution of Taurus cedar across diverse environmental conditions in the Taurus Mountains. So, new studies should be involve long-term data and large numbers of populations and individuals. However, results of the case study could be used locally for the selection, establishment, and management or other forestry practices such as natural regeneration in the species.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

DÇ: Writing – original draft. EO: Writing – original draft, Data curation, Methodology. NB: Data curation, Writing – original draft, Formal analysis, Writing – review & editing.

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