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Article

Annual Variability in Cone and Seed Yields Across Seed Stands of Taurus Cedar (*Cedrus libani*) and Its Impact on Gene Diversity of Seed Crops

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Abstract

Variation and comparison of annual cone and seed productions, and seed characteristics (number and percentage of filled seeds per cone) were examined for three consecutive years at three seed stand populations of Taurus cedar (*Cedrus libani* A. Rich.) with distinct structural characteristics. Fertility variation in cone and seed production was analyzed and discussed to inform for management practices of seed stands and for other silvicultural interventions. The analysis of variance showed the significant differences among populations and years, as well as among trees within a population and a year for both cone and seed production and seed characteristics. Population x year interactions were also significant ($p<0.05$), highlighting the importance of cone collecting stand and seed harvesting year. The parental balance curves showed that the cone production was much closer to equal contribution to the gamete gene pool than the production of filled seeds across years, suggesting that the number of cones is a better indicator of overall seed production. Fertility variation (Ψ) in cones and filled seeds ($1.10\leq\Psi\leq 1.71$ except 2.38 in a population and year) showed small deviation among seed stands and among years within a seed stand. Gene diversity of seed crops has increased through clustering populations and pooling years reaching values of 0.998 and 0.997, respectively.

Keywords: afforestation; fertility variation; genetic diversity; reproductive output; stand structural characteristics

1. Introduction

Taurus cedar (*Cedrus libani* A. Rich.), also called as the cedar of Lebanon, is an important forest tree species in its native range and extant, such as in Bulgaria [1], Argentina [2], Italy [3], Iran [4], France [5,6]. It is valued and exotic for valuable timber, resin production from seed, cone and wood, landscape purposes and social-cultural importance (i.e., ethnobotany, symbol of Lebanon flag). Natural forests of the species are mainly at Taurus Mountains in southern Türkiye together with remain populations in Lebanon and Syria [7,8].

Taurus cedar has been used widely in afforestation, reforestation and restoration practices in Turkish forestry. Over the past decade, the distribution area increased from 463,521 ha to 580,515 ha (of which 42.8% was unproductive) through seeding and planting practices [9]. A total of 60 million seedlings from 20 tones seeds were produced from 21 seed stands (3,304.2 ha) [9,10] selected phenotypically from natural forests [11]. There are 7 seed orchards (46.4 ha) but they are not suitable for seed harvesting because of juvenile age [9,10]. This highlights the importance of selection and management of seed stands in *C. libani* (i.e., estimation of production variation and genetic parameters).

The species can grow up to 50 m height and 2.5 m diameter or more than that in old forests and monumental forest and trees by slender trunks and over 1000 years old at various ecological conditions natural such as mainly between 800 and 2100 m asl., and between 500 m and 2400 for local populations [7,8]. *C. libani* generally bears cones at about 30 years old in natural stands [8]. Male strobili appear in July and elongate 3-5 cm in August, while female strobili can be seen in September according to location and altitude in *C. libani*. The female strobili convert to mature cones by brown color, 8.46 cm length and 4.9 cm width [12,13].

Opening of the cone scales begins in October and seed dispersal occurs in 25-26 months after fertilization [8]. Seed dispersal starts at end of November and continues during the winter in natural stands of *C. libani*. However, seeds of 23-24 months old cones collected in August had also germination percentage in the species [12]. The frequency of good seed years in this species is two to three years and varies with altitude [13,14]. However, the occurrence of good seed years is also highly variable among locations, ranging from intervals of two years to three or even six years [8,12]. Characteristics of abundant cone and seed yields deviate among provenances in *C. libani* i.e., [12,15,16].

Fertility variation is defined as a difference in the ability to produce progeny (i.e., reproductive success) among individuals [17]. Fertility variation is commonly estimated based on pollen, strobili, flower, cone, fruit and seed production [18–22], and it approaches 1 when individuals contribute equally to the gamete gene pool of a population. It is used for various purposes in plant science such as genetic management, population breeding and species conservation [17,18,21,23–27]. Although cone and seed yields, as well as fertility variation, have been studied in natural populations of *C. libani* [28] using short-term data, annual variation in cone and seed yields and related parameters have not been examined in detail using long term data for this species.

This study aims to: i) assess annual variation of cone and seed yields and associated fertility variation among seed trees and gene diversity of seed crops in seed stands of *Cedrus libani*, ii) compare these patterns across three consecutive years and three seed stands that bare different silvicultural characteristics, and iii) provide recommendations on the management and the cone harvest strategy in these seed stands.

2. Materials and Methods

2.1. Cone and Seed Collection, and Parental Balance Curve

Collection of mature cones was carried out during October for three consecutive years (2023-2025) from three seed stands, also known seed collection areas, of Taurus cedar, where the species have optimal and the largest natural distribution at Mediterranean regions in Türkiye. Although the seed stands occur at the same altitude, they exhibit distinct structural characteristics, including differences in tree age and stem density per hectare. (Table 1) [10]. Thirty-five trees were selected phenotypically (i.e., tree height, diameter at breast height, stem straight) [11] from each seed stand. The trees were randomly selected at least 100 m distance and should have mature cones [28,29]. The total number of mature cones were counted from the selected trees.

Table 1. Geographic information (latitude, longitude, altitude), age, size and stand density of the seed stands (populations P1, P2 and P3 from now on) of Taurus cedar.

Seed Stand code	Latitude (N)	Longitude (E)	Altitude (m)	Stand age (year)	Size (ha)	Density (trees/ha)
P ₁	38°05'23"	30°42'20"	1,600	60	77.0	800
P ₂	37°44'47"	30°49'21"	1,600	118	48.9	650
P ₃	37°51'00"	31°19'10"	1,550	149	23.0	450

All cones were thoroughly dissected to assess the number of seeds produced per cone. Average number and percentage of filled seeds per cone were calculated from four healthy cones harvested as much as possible from different directions of each tree. The cones were stored (at about 20 °C)

indoor for seed extraction during two weeks. The cutting test method was used for assessing the seed characteristics (i.e., whether they are filled or empty/damaged) [30]. The average number of filled seeds per tree was estimated by the average number of filled seeds/cone multiplied by the bearing mature cones per tree.

The parental balance curve was plotted as the cumulative proportion of reproductive output (e.g., cones, seed) against the cumulative proportion of parental seed trees [20,31]. The curves are very useful to identify highly fertile, underperforming, or infertile trees and manage seed stands to ensure maximum genetic diversity, which is crucial for establishing resilient forests.

2.2. Data Analysis

The differences in cone number and seed production among populations and years were performed by following model of ANOVA [32]:

$$Y_{ijk} = \mu + F_i + B(F)_{j(i)} + e_{ijk} \quad (1)$$

where Y_{ijk} is the observation from the k th tree of the j th stand in the i th year, μ is the overall mean of the characteristics, F_i is the effect of i th year, $B(F)_{j(i)}$ is the effect of the j th population in the i th year, and e_{ijk} is the random error.

Within a year, differences among seed trees in cone and seed yield per year in a stand were also compared by following model of one-way analysis of variance as:

$$Y_{ij} = \mu + P_i + e_{ij} \quad (2)$$

where Y_{ij} is the observation from the i th tree of the j th stand, μ is the overall mean of the cone or seed yields, P_i is the yield of the i th tree and e_{ij} is the random error.

The fertility variation also known sibling coefficient (Ψ) among seed trees was estimated based on the proportions of cone and filled seed/tree (Ψ_c & Ψ_s) representing the total contribution as zygotic parents within the population for the years [33] as:

$$\Psi_c = N \sum_{i=1}^N \text{Cone}_i^2 = CV_c^2 + 1, \text{ and} \quad (3a)$$

$$\Psi_s = N \sum_{i=1}^N \text{Seed}_i^2 = CV_s^2 + 1 \quad (4b)$$

where Cone_i and Seed_i represent the cone and seed fertility (relative proportion of cone and seed production in the seed stand) of the i th tree, and CV_c and CV_s stand for the coefficients of variation in cone and seed productions, respectively.

The effective number of parents for cone ($N_p^{(C)}$) and seed ($N_p^{(S)}$) productions were calculated based on the fertility variations (Ψ_c & Ψ_s) and the census number (N) of seed trees, respectively [26] as:

$$N_p^{(C)} = \frac{\Psi_c}{N}, \text{ and} \quad (4a)$$

$$N_p^{(S)} = \frac{\Psi_s}{N} \quad (4b)$$

The effective number of parents ($N_p^{(C)}$ & $N_p^{(S)}$) is also related to gene diversity (GD) for cone and seed productions (GD_c & GD_s) by Lindgren *et al.* [34] and Lindgren and Mullin [35] as:

$$GD_c = 1 - \frac{0.5}{N_p^{(C)}}, \text{ and } GD_s = 1 - \frac{0.5}{N_p^{(S)}} \quad (5a \& b)$$

3. Results

3.1. Cone and Seed Productions, and Parental Balance Curve

Cone and seed productions and related seed characteristics showed a large difference among populations (seed stands) and years, and also among trees within a population and a year (Table 2). The reproductive output increased with increasing of stand age and showed a negative relationship with stand density. In particular, during the whole studied period, cone production per tree, filled seed number per cone, and total filled seed production per tree were highest in the P3 seed stands, characterized by older age (145 years) and lower tree density (450 trees/ha).

Table 2. Mean, coefficient variation (CV) and range for the number of cones (Nc), percentage (NSc%) and number (NSc) of filled seeds per cone, and total number of filled seeds (NS_T) per tree in the three seed stands (P₁, P₂ and P₃) during three studied years (2023-2025).

Years	P ₁			P ₂			P ₃			Pooled	
	Mean	CV	Range	Mean	CV	Range	Mean	CV	Range	Mean	CV
<u>2023</u>											
Nc	28	0.48	12-90	23	0.58	12-86	36	0.58	14-110	29	0.59
NSc%	73	0.17	37-95	93	0.04	83-100	94	0.04	80-98	87	0.14
NSc	75	0.30	22-120	56	0.44	12-140	82	0.32	19-131	71	0.38
NS _T	2135	0.55	374-5940	1240	0.51	192-3080	2906	0.62	742-8580	2094	0.70
<u>2024</u>											
Nc	20	0.85	8-72	29	0.61	12-98	27	0.50	14-60	25	0.65
NSc%	90	0.11	66-100	89	0.11	65-100	95	0.04	84-100	91	0.09
NSc	44	0.59	13-110	88	0.53	18-177	93	0.43	16-173	75	0.59
NS _T	895	1.19	156-5040	2325	0.62	396-6109	2715	0.69	320-6688	1978	0.85
<u>2025</u>											
Nc	18	0.45	10-48	20	0.31	12-40	28	0.63	12-90	22	0.57
NSc%	85	0.14	51-100	91	0.06	72-97	94	0.04	85-100	90	0.01
NSc	61	0.53	16-120	75	0.43	18-130	90	0.37	19-164	75	0.45
NS _T	1165	0.85	160-5472	1482	0.62	288-5000	2518	0.76	760-10152	1722	0.85
<u>Pooled</u>											
Nc	22	0.63	8-90	24	0.58	12-98	31	0.59	12-110	26	0.61
NSc%	83	0.16	37-100	91	0.07	65-100	94	0.04	80-100	89	0.11
NSc	60	0.50	13-120	73	0.51	12-177	88	0.38	16-173	74	0.48
NS _T	1399	0.86	156-5940	1682	0.68	192-6109	2713	0.68	320-10152	1931	0.80

Cone production (Nc) was also greatest in P3 in 2023, while the lowest was observed in P1 in 2024. Similarly, both the percentage of filled seed per cone (NSc%) and the total number of filled seeds per tree (NS_T) were also highest in P3 in 2023 (Table 2, Figures 1 and 2). Cone and filled seed production in P3 in 2023 were 100% and 149% higher, respectively, than the lowest values recorded in P1 in 2025 (18 cones and 1165 filled seeds per tree). Besides, the percentage of filled seeds per cone (NSc%) ranged from 73% in the P1 in 2023 to 95% in P3 in 2024 (Table 2).

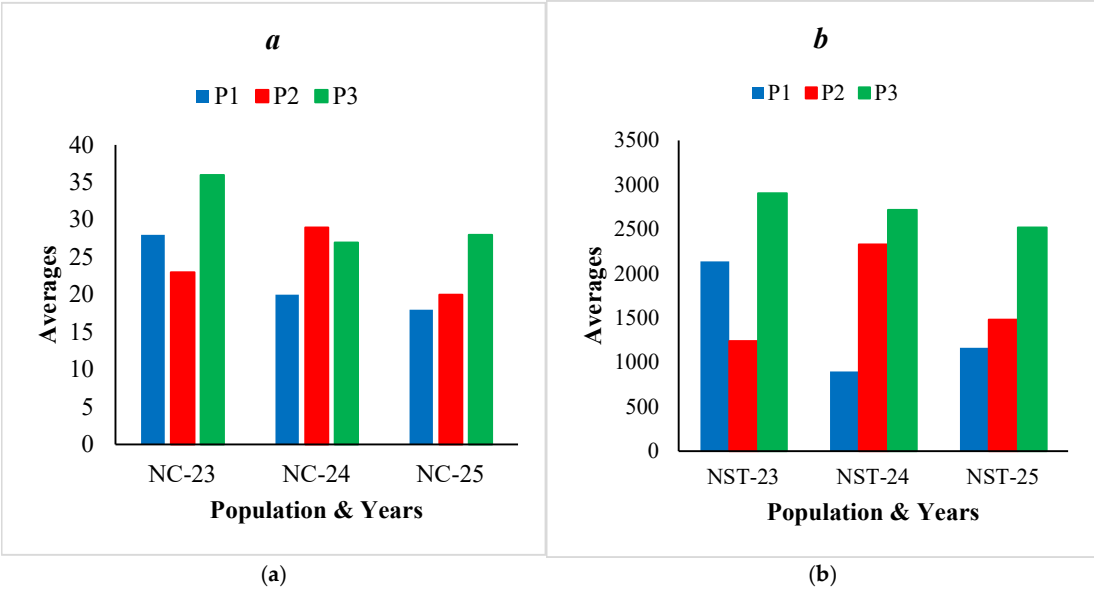


Figure 1. Number of cones (Nc) (a) and number of filled seeds per tree (NSr) (b) for the studied period (2023-2025) in the seed stands of Taurus cedar.

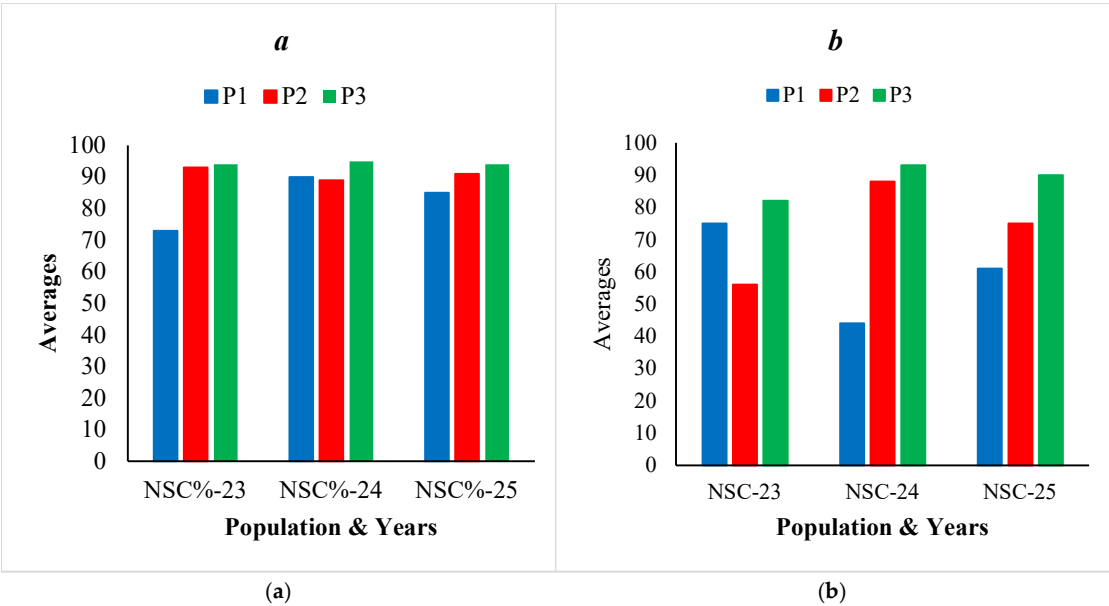


Figure 2. The percentage of filled seeds per cone (NSc%) (a) and number of filled seeds per cone (NSc) (b) for the studied period (2023-2025) in the seed stands of Taurus cedar.

When pooled the three stands, in year 2023 the mean number of cones (29) and the filled seeds per tree (2094) were the highest, while the percentage of filled seeds per cone (NSc%) and number of filled seeds per cone (NSc) were the lowest i.e., 87% and 71%, respectively (Table 2, Figures 1 and 2).

The seed stands (populations) showed significant differences ($p<0.05$) in cone production and seed yield, whereas the effect of year was significant only for the number of cones (Nc) and the percentage of filled seeds per cone (NSc%) (Table 3). In addition, population x year interactions were significant ($p<0.01$ or $p<0.05$) for the reproductive potential (Table 3).

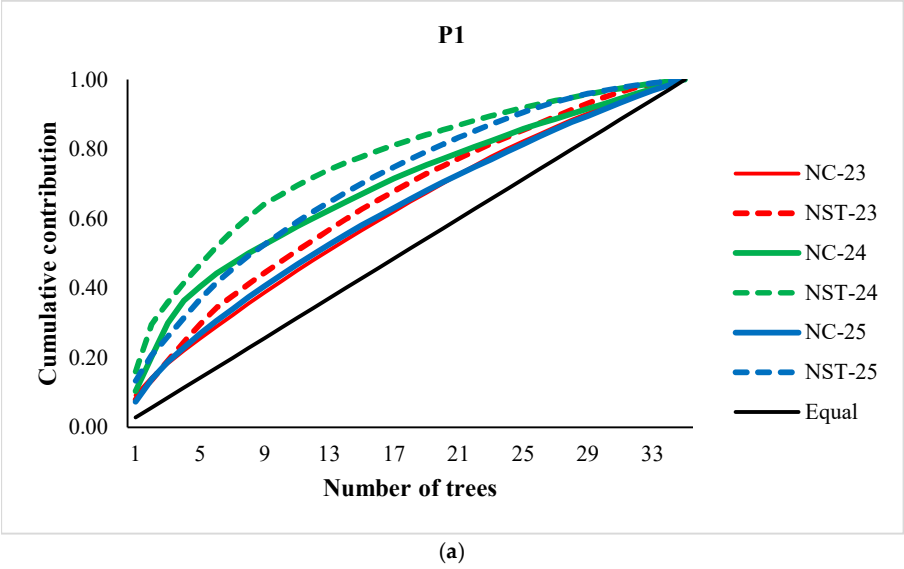
Table 3. Analysis of variance (ANOVA) for the number of cones (Nc), percentage (NSc%) and number of filled seeds per cone (NSc) and number of filled seeds per tree (NSr) among years and seed stands.

Source	Variable	d.f.	Mean square	F	P
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Stand (S)	Nc	2	2103.581	9.427	**
	NSc%	2	3774.421	60.731	**
	NSc	2	20765.343	19.774	**
	NSr	2	50229040.060	26.239	**
Year (Y)	Nc	2	1287.114	5.768	*
	NSc%	2	661.029	10.636	**
	NSc	2	557.867	.531	NS
	NSr	2	3811994.994	1.991	NS
S x Y interaction	Nc	4	625.881	2.805	*
	NSc%	4	1204.025	19.373	**
	NSc	4	8862.324	8.439	**
	NSr	4	11881578.603	6.207	**
Error	Nc	306	223.147		
	NSc%	306	62.150		
	NSc	306	1050.127		
	NSr	306	1914322.016		

** , * , and ^{NS} indicate statistically significant difference at the probability level 0.01, 0.05 and non-significant, respectively.

The parental balance curves in P1 showed more deviation from the ideal equal contribution for cone and seed characteristics compared to the stands of P2 and P3 (Figure 3). The observed parental balance curves for numbers of cone (Nc) and filled seeds per tree (NSr) were not deviated dramatically from equal production among individuals in the seed stands and years when pooled, while they showed different figures for the individual seed stands (Figure 3 and Figure 4). For instance, cone productions of the years of pooled population were much closer to equal contribution to the gamete gene pool than that of filled seeds (Figure 4).



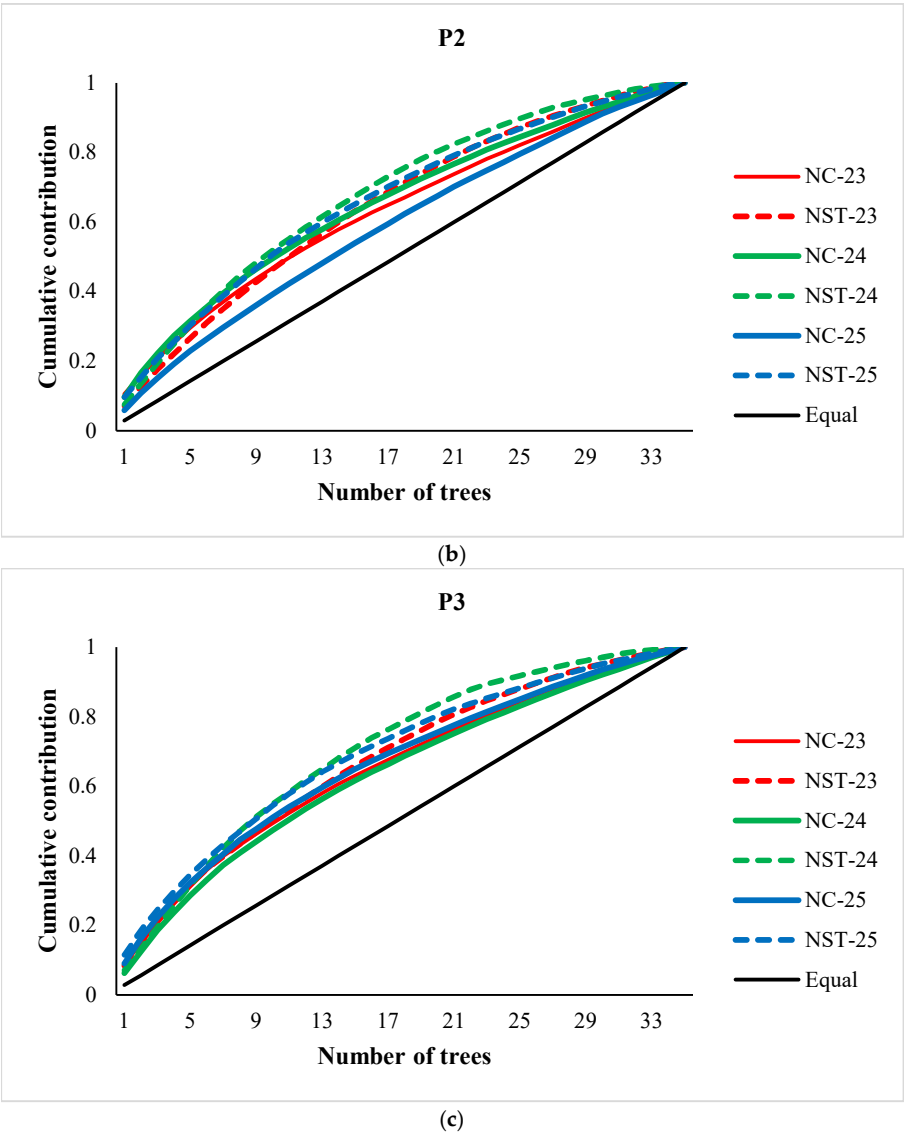


Figure 3. Parental-balance curves for cone (Nc) and seed production (number of filled seeds per tree: NSTr) during the studied years (2023-2025) in the seed stands P1, P2 and P3 of Taurus cedar.

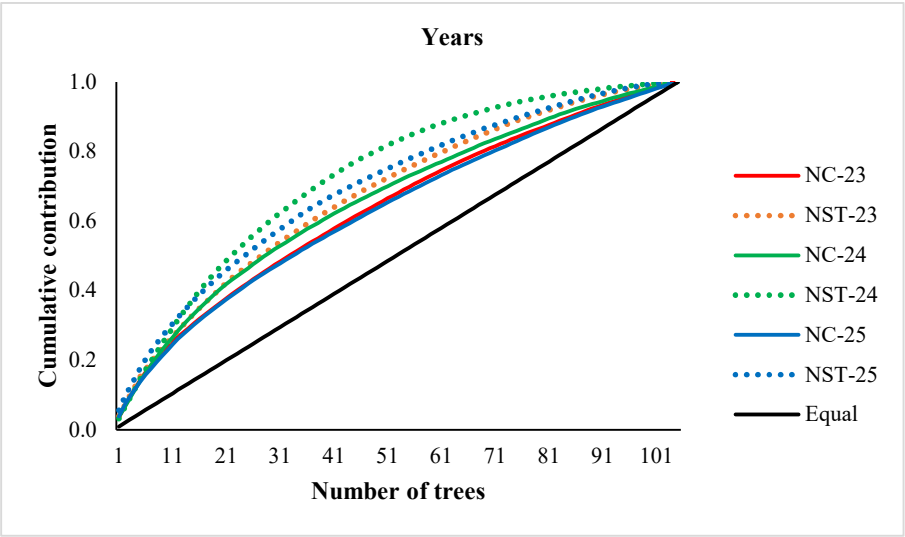


Figure 4. Parental-balance curve in the bulked individuals and years of the three seed stands.

3.2. Fertility Variation, Effective Number of Parents and Gene Diversity

Cone (Ψ_c) and filled seed (Ψ_s) fertility did not vary substantially among populations and years, nor among years within population (Table 4). For instance, pooled-year cone fertility (Ψ_s) in P2 was 1.46 ($N_{p(S)}= 72.0$, 69% of census number in the population) ranging from 1.25 (28.0, 80% in year-23) to 1.38 (25.4, 73% in year-24). For pooled years and populations, Ψ_c values were 1.36 (231.5, 74% of census number), 1.32 (79.6, 76% in year-25) and 1.42 (74.0, 71% in year-24) for pooled year and populations of Ψ_c (Table 5).

Table 4. Fertility variation among seed trees in cone (Ψ_c) and filled seed (Ψ_s) fertility, and effective number of parents for cone ($N_{p(C)}$) and filled seed ($N_{p(S)}$), and gene diversity for cone (GDc) and seed (GDs) in the seed stand for the years of 2023, 2024 and 2025.

	P ₁				P ₂				P ₃				Pooled			
Years	23	24	25	Total	23	24	25	Total	23	24	25	Total	23	24	25	Total
Ψ_c^*	1.22	1.71	1.20	1.40	1.33	1.36	1.10	1.33	1.33	1.24	1.38	1.34	1.34	1.42	1.32	1.36
Ψ_s	1.29	2.38	1.71	1.73	1.25	1.38	1.37	1.46	1.38	1.46	1.56	1.46	1.48	1.71	1.71	1.63
$N_{p(C)}$	28.7	20.5	29.2	75.6	26.4	25.7	32.0	79.0	26.3	28.6	25.3	78.3	78.4	74.0	79.6	231.5
$N_{r(C)**}$	0.82	0.59	0.84	0.72	0.75	0.73	0.91	0.75	0.75	0.81	0.72	0.75	0.74	0.71	0.76	0.74
$N_{p(S)}$	27.1	14.7	20.5	60.9	28.0	25.4	25.5	72.0	25.4	24.0	22.5	71.9	71.0	61.3	61.5	193.8
$N_{r(S)}$	0.77	0.42	0.59	0.58	0.80	0.73	0.73	0.69	0.73	0.69	0.64	0.69	0.68	0.58	0.59	0.62
GDc	0.983	0.976	0.983	0.993	0.981	0.981	0.984	0.994	0.981	0.982	0.980	0.994	0.994	0.993	0.994	0.998
GDs	0.982	0.966	0.976	0.992	0.982	0.980	0.980	0.993	0.980	0.979	0.978	0.993	0.993	0.992	0.992	0.997

*; C and S represent cone and filled seed productions, respectively, **; relative effective number $N_r = N_p/N$.

Years, populations and years within population had different reflections to high and low crop years (Table 2) depend on fertility variation, effective number of parents and gene diversity (Table 4).

Effective number of parents was 18% higher in the highest crop year (year-24) to the poorest (year-25) for $N_{p(C)}$ in P2, while it was 7% opposite from the highest crop year (year-24) to poor year (year-23) for $N_{p(S)}$ in the population (Table 4). Similar results were also found for the years of the populations by 2% decreasing for $N_{p(C)}$ and 9% increasing for $N_{p(S)}$ in the polled populations of the years between the highest (year-23) and lowest (year-25) production years. The results indicated importance of seed harvesting year.

The highest gene diversity (GD) was estimated for pooled years of the populations (0.998 for GDc and 0.997 for GDs) and within population for both cone (GDc) and seed (GDs) than individual population and year (Table 4). As seen from the Table, the lowest gene diversity (GDc= 0.976 and GDs= 0.966) in year-23 of P1 increased to 0.993 (GDc) and 0.992 (GDs) in bulked years of the population. Loss of gene diversity was up to 0.013 in seeds of individual year to bulked seeds of years in P2 (Table 4).

4. Discussion

The present study demonstrates pronounced variation in cone and seed production among seed stands, years, and individual trees, highlighting the complex and heterogeneous nature of reproductive output. Such variability was evident not only at the population (seed stand) level but also within populations across years, indicating that reproductive potential is shaped by both stand-level characteristics and temporal factors. The reproductive characteristics of forest tree species are influenced by numerous biotic (e.g., tree growth, age, and crown closure) and abiotic factors (e.g., light, temperature, humidity, and site quality) i.e., [11,12,25,36–38]. In natural stands of *C. libani*, good seed years occur approximately every two to three years [7], and the position of individual trees within the population can also affect reproductive output [12]. It has been reported that even during

good seed years, not all trees in a population are expected to produce abundant seed crops [12]. Similar variations in cone and seed productions were reported in *C. libani* by Bilir *et al.* [28] who reported higher values for two populations than the present study; numbers of cones and seeds were 90 and 33, and 5321 and 3115 per tree, respectively.

The reproductive output in this study was found increased with stand age and exhibited a clear negative relationship with stand density. The consistently higher cone production per tree, filled seed number per cone, and total filled seed production per tree observed in the P3 seed stand across the whole study period suggest that older seed stands with lower tree density provide more favorable conditions for reproductive development. Reduced competition for resources such as light, water, and nutrients in lower-density stands likely enhances individual tree vigor, thereby supporting increased reproductive investment. The superior reproductive performance of P3 seed stand, particularly during 2023, underscores the importance of stand structure in determining reproductive potential. Similarly, previous studies, were reported that tree size, age and provenance could impact on cone and seed yields [12,39] and their characteristics (i.e., germination percentage~ filled seeds) [12,15,16,40].

Interannual variation was also substantial, with 2023 emerging as the most productive year in terms of mean cone number and total filled seed production per tree when the three seed stands were pooled. However, this year was also characterized by lower values of filled seed percentage and filled seed number per cone, indicating a trade-off between cone quantity and seed quality.

The significant population $\times$ year interactions ($p < 0.05$) observed for reproductive output (Table 3) underscore the importance of both the seed collection stands and the year of collection, indicating that environmental conditions prevailing in a forest stand and temporal variation can differentially affect reproductive performance among populations [26]. Given that a planting spacing 1.5 m $\times$ 3 m (~2222 seedlings/ha) or about 13 kg seeds/ha are required for seeding in reforestation, afforestation and restoration practices of *C. libani* [13], the abundant seed production of per tree (Table 2) indicates its representation rate in future generation. High seed production can provide a simple and cost-effective guide for seed harvesting and selection of mother trees, and management of seed collection areas.

Coefficients of variations of cone and seed productions (Table 2) were at acceptable level for an ideal natural population ($CV < 140\% = \Psi < 3$) [27] in both population and years, while cone and seed productions varied for the productions in the population and year. However, cone productions of the years were much closer to equal contribution to the gamete gene pool than that of filled seeds (Figures 3 and 4). Genetic contributions can be explained by parental balance curves, and the cumulative percentage curve is often used to quantify fertility variation in forest populations [18,31]. Unequally contributions of the parents to the gamete gene pool were not pronounced, indicating that they can be balanced through silvicultural practices such as tending or equal seed collection per tree.

The parental balance curve is a graphical tool primarily used in forest genetics to visualize the variation in reproductive success among individual parent trees within a seed-producing population (e.g., seed stands, seed orchards). It helps assess the gene diversity of the resulting seed crop. The sibling coefficient (Ψ) is a related measure that quantifies this variation in fertility; a value of 1 indicates equal contribution, while higher values indicate greater disparity. This study implied that the gene diversity of the seed crops could be improved when the cones (seeds) are pooled across seed stands and/or collection years (Figures 3 and 4).

Variation in cone (Ψ_c) and filled seed (Ψ_s) fertility among populations and years, as well as among years within population (Table 4) remained within acceptable limits and below the threshold of $\Psi < 3$ for natural stands [25]. However, the results indicated importance of seed harvesting year and population. Loss of gene diversity can be mitigated by pooling seeds from different populations and years supporting afforestation practices in adaptive areas and enhancing resistance to biotic and abiotic stresses. This approach relies on higher gene diversity in seed crops, which depends on the seed transfer region of the species [41]. However, we suggest that a trade-off between the effective number of parents (gene diversity) and the number of populations and/or years should be carefully

considered to ensure a sustainable seed supply in the seed stands of Taurus cedar. The long term seed storage capacity of the species, up to 5-6 years [12,40] could be used for this purpose.

5. Conclusion

Author Contributions: NB conducted data collection. KSK, MT and NB conducted data validation. KSK and NB performed data analysis. MT, KSK and NB prepared draft paper, figures and tables. MT, KSK and NB conducted review & editing All authors participated in the discussion and approved the submitted version.

Institutional Review Board Statement: Not applicable.

Data Availability Statement: The data presented in this study are available on request from the corresponding author.

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Conflicts of Interest: The authors declare no conflicts of interest.

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