

Genetic Evaluation and Selection of Superior Teak (*Tectona grandis*) Families Using BLUPs in a Progeny Trial

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Abstract

Teak (*Tectona grandis*) is a high-value timber species, and its genetic improvement is crucial for enhancing productivity in plantation forestry. This study evaluated 100 open-pollinated teak families in a progeny trial established in 1998 to assess genetic variation and identify superior genotypes using Best Linear Unbiased Prediction (BLUP). Significant variation was observed among families for all studied traits, including tree height, girth at breast height (GBH), clear bole length (CBL), crown traits, and wood volume. Estimates of narrow-sense heritability were higher for girth at breast height, crown height and tree height, indicating moderate additive genetic control. BLUP values revealed that 29 families had consistently positive genetic merit across traits, while 31 had uniformly negative values. Selection of the top 20–30 families based on wood volume BLUPs is projected to yield substantial genetic gains with reduced genetic erosion, supporting the establishment of a clonal seed orchard (CSO). The study demonstrates the effectiveness of BLUP in identifying elite teak families and emphasises the role of genetic evaluation in developing high-yielding, genetically diverse planting stock for long-term tree improvement programs.

Keywords: Heritability, Genetic advance, Breeding value, Forestry

Competing Interests

The authors declare no competing interests.

Introduction

A prized tropical hardwood, teak (*Tectona grandis*) is grown on more than 27 million hectares in more than 65 nations and is well-known for its quality timber and economic significance (Bahtiar et al. 2023). Natural teak forests are widely distributed throughout India, and various state forest departments as well as plantation owners have embraced the practice of planting this commercially significant tree species on a large scale (Bennett 2014). In order to increase the yields from the land, it has also been utilized as a tree component in a number of agroforestry systems (Shukla and Viswanath 2014).

Genetic improvement programs worldwide focus on enhancing growth rates, wood quality, and pest resistance through breeding, hybridization, and biotechnology (Nelson 2023). The success of tree improvement programs relies heavily on precise estimation of genetic parameters, including heritability, genetic correlations, and breeding values. Best Linear Unbiased Prediction (BLUP) has emerged as a robust statistical approach for estimating breeding values, particularly in forestry, as it allows for the accurate prediction of genetic merit by accounting for both fixed and random effects in complex data structures (Ling et al. 2021). Identifying families with consistently superior performance across economically and ecologically relevant traits enables the selection of elite genotypes for vegetative propagation and seed orchard development.

India is the centre of diversity for Teak, and the germplasm from India has been introduced into several tropical countries of the world. There were extensive surveys of the natural teak forests from the 1960s to 1990s, and several phenotypically superior trees were selected, and their progeny trials were undertaken at different locations (Kedharnath 1984). In this study, a progeny test was evaluated using BLUP methodology to estimate breeding values for key growth traits in teak. The objective was to identify genetically superior families suitable for clonal propagation and potential inclusion in clonal seed orchards, thereby accelerating genetic gains and enhancing productivity in teak plantations.

Materials and Methods

Location, progeny trial, and trait measurement

Morpho-metric data was recorded on all the trees in the progeny trials located at Lohara, Chandrapur, Maharashtra (Fig. 1). The trial site at Lohara, Chandrapur, Maharashtra, is characterised by a tropical monsoon climate with a mean annual rainfall of approximately 1,200–1,500 mm, a mean annual temperature range of 20–35°C, and a distinct wet season from June to September. The edaphic conditions include well-drained, loamy to sandy-loam soils with a pH range of 6.0–7.5, typical of teak-growing regions in central India.

The details of the progeny trial established at the test site have been given in Table 1. The families were sourced from four different states in India. The half-sib progeny test was established in 1998, with 100 open-pollinated families in Randomised Block Design with 4 replications, each with 3 individuals per half-sib family. The spacing between trees in the trial was 3m×4m, with families planted in rows. The data on morphological parameters was recorded in 2019. The assumption of a half-sib structure in this open-pollinated progeny trial implies

that progeny primarily result from crosses between the selected mother tree and unrelated pollen donors. Teak is primarily a self-incompatible species (Tangmitcharoen and Owens 1997) with predominant cross-pollination. However, the potential inclusion of full sibs or selfed progeny due to limited pollen flow or proximity of related trees could affect the coefficient of relationship and thus influence heritability estimates (h^2). While specific pollen flow or relatedness data were not collected, the design assumes minimal selfing and outcrossing with unrelated individuals, which may overestimate additive genetic variance if violated.

Individual tree data were averaged to obtain family means for each family per replication. The data was recorded on tree height (in meters), clear bole length (CBL in meters), and crown height (CRH in meters) using Leica DISTO™ S910. The girth (circumference) at breast height (GBH) was recorded (in cm) at 1.37 meters above the ground. Crown diameter (CRD, in meters) was measured in two perpendicular directions using a measuring tape. The number of primary branches was counted ocularly.

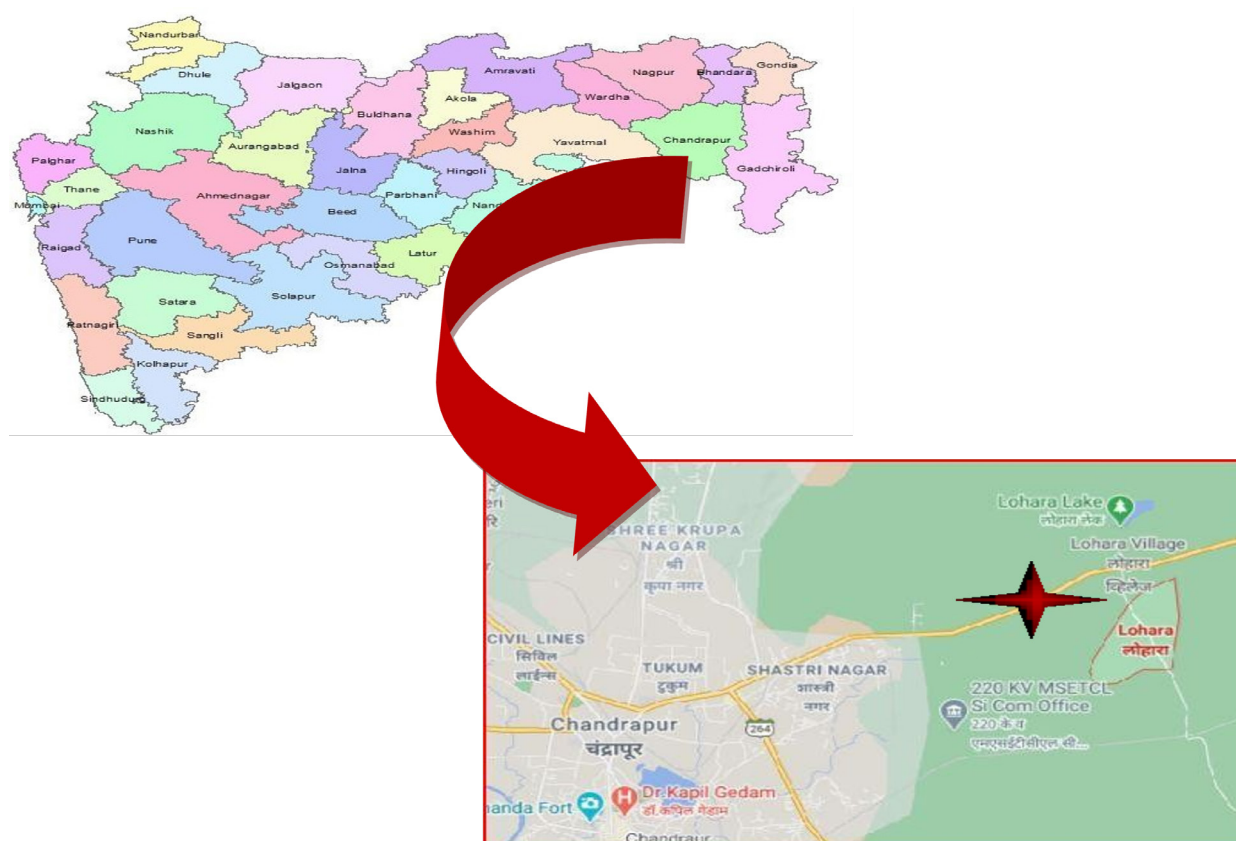


Figure 1
Location of the test site

Table 1

Plantation details of progeny trial of *Tectona grandis* located at Lohara, Chandrapur, Maharashtra. *Locality/state from where plus trees were selected

S.No.	Half-sib family	Family Code	Place of origin*
1	MHAL-A1	T-001	Allapalli, Maharashtra
2	MHAL-A2	T-002	Allapalli, Maharashtra
3	MHAL-A3	T-003	Allapalli, Maharashtra
4	MHAL-A4	T-004	Allapalli, Maharashtra
5	MHAL-A6	T-005	Allapalli, Maharashtra
6	MHAL-A8	T-006	Allapalli, Maharashtra
7	MHAL-P1	T-007	Allapalli, Maharashtra
8	MHAL-P2	T-008	Allapalli, Maharashtra
9	MHAL-P3	T-009	Allapalli, Maharashtra
10	MHAL-P4	T-010	Allapalli, Maharashtra
11	MHAL-P5	T-011	Allapalli, Maharashtra
12	MHAL-P6	T-012	Allapalli, Maharashtra
13	MHAL-P7	T-013	Allapalli, Maharashtra
14	MHAL-P8	T-014	Allapalli, Maharashtra
15	Angul MHAL-P8	T-015	Angul, Allapalli, Maharashtra
16	MHAL-P9	T-016	Allapalli, Maharashtra
17	MHSC-A1	T-017	Allapalli, Maharashtra
18	MHSC-A2	T-018	Allapalli, Maharashtra
19	MHSC-A4	T-019	Allapalli, Maharashtra
20	MHSC-J1	T-020	Maharashtra
21	MHSC-J2	T-021	Maharashtra
22	MHWY-K2	T-022	Maharashtra
23	MHWY-K3	T-023	Maharashtra
24	MHEM-R2	T-024	Maharashtra
25	T.S.O.Baitul Pt.1	T-025	Baitul, MP
26	T.S.O.Baitul Pt.45	T-026	Baitul, MP
27	Orissa 78 Pt.47	T-027	Odisha
28	Nepa T.S.O. 79 BBC-1	T-028	Nepanagar, MP
29	T.S.O.Baitul BBC-2	T-029	Baitul, MP
30	T.S.O.Baitul BBC-8	T-030	Baitul, MP
31	T.S.O.Baitul BBC-13	T-031	Baitul, MP
32	Nepa T.S.O.BBC-18	T-032	Nepanagar, MP
33	Nepa T.S.O.81 BBC-30	T-033	Nepanagar, MP
34	T.S.O.Baitul BBC-38	T-034	Baitul, MP
35	T.S.O.Baitul BBC-49	T-035	Baitul, MP
36	T.S.O.Baitul BBC-57	T-036	Baitul, MP
37	T.S.O.Baitul BHC-1	T-037	Baitul, MP
38	T.S.O.Baitul BHC-13	T-038	Baitul, MP
39	T.S.O.Baitul BHC-16	T-039	Baitul, MP
40	T.S.O.Baitul BHC-19	T-040	Baitul, MP
41	T.S.O.Baitul BSC-6	T-041	Baitul, MP
42	Nepa T.S.O.77 BSC-23	T-042	Nepanagar, MP
43	T.S.O.Baitul CSC-16	T-043	Baitul, MP
44	T.S.O.Baitul CSC-24	T-044	Baitul, MP
45	T.S.O. Control (Lohara)	T-045	Lohara, Maharashtra
46	T.S.O.Raipur C.NO.C8	T-046	Raipur, Chhattisgarh
47	T.S.O.Baitul C.NO.C78	T-047	Raipur, Chhattisgarh

48	T.S.O.Raipur C.NO.6	T-048	Raipur, Chhattisgarh
49	T.S.O.Raipur C.NO.8	T-049	Raipur, Chhattisgarh
50	T.S.O.Raipur C.NO.12	T-050	Raipur, Chhattisgarh
51	T.S.O.Raipur C.NO.14	T-051	Raipur, Chhattisgarh
52	T.S.O.Baitul C.NO.15	T-052	Baitul, MP
53	T.S.O.Raipur C.NO.16	T-053	Raipur, Chhattisgarh
54	T.S.O.Raipur C.NO.19	T-054	Raipur, Chhattisgarh
55	T.S.O.Raipur C.NO.20	T-055	Raipur, Chhattisgarh
56	T.S.O.Raipur C.NO.24	T-056	Raipur, Chhattisgarh
57	T.S.O.Raipur C.NO.25	T-057	Raipur, Chhattisgarh
58	Orissa 79 I C.NO.26	T-058	Odisha
59	T.S.O.Baitul C.NO.27	T-059	Baitul, MP
60	T.S.O.Raipur C.NO.27	T-060	Raipur, Chhattisgarh
61	T.S.O.Raipur C.NO.28	T-061	Raipur, Chhattisgarh
62	T.S.O.Raipur C.NO.30	T-062	Raipur, Chhattisgarh
63	T.S.O.Raipur C.NO.43	T-063	Raipur, Chhattisgarh
64	T.S.O.Raipur C.NO.44	T-064	Raipur, Chhattisgarh
65	T.S.O.Baitul C.NO.45	T-065	Baitul, MP
66	T.S.O.Raipur C.NO.45	T-066	Raipur, Chhattisgarh
67	T.S.O.Raipur C.NO.46	T-067	Raipur, Chhattisgarh
68	T.S.O.Raipur C.NO.47	T-068	Raipur, Chhattisgarh
69	T.S.O.Raipur C.NO.48	T-069	Raipur, Chhattisgarh
70	Orissa 79 I C.NO.48	T-070	Odisha
71	T.S.O.Raipur C.NO.49	T-071	Raipur, Chhattisgarh
72	T.S.O.Raipur C.NO.50	T-072	Raipur, Chhattisgarh
73	T.S.O.Raipur C.NO.51	T-073	Raipur, Chhattisgarh
74	T.S.O.Raipur C.NO.55	T-074	Raipur, Chhattisgarh
75	T.S.O.Raipur C.NO.58	T-075	Raipur, Chhattisgarh
76	T.S.O.Baitul C.NO.60	T-076	Baitul, MP
77	ORPUB-3	T-077	Odisha
78	ORPUB-8	T-078	Odisha
79	ORPUB-9	T-079	Odisha
80	ORPUB-10	T-080	Odisha
81	ORPUB-18	T-081	Odisha
82	ORPUB-19	T-082	Odisha
83	ORPUB-24	T-083	Odisha
84	ORAN-R1	T-084	Angul, Odisha
85	ORAN-R2	T-085	Angul, Odisha
86	ORAN-R4	T-086	Angul, Odisha
87	ORAN-R5	T-087	Angul, Odisha
88	ORAN-R6	T-088	Angul, Odisha
89	ORANP-2	T-089	Angul, Odisha
90	ORANP-4	T-090	Angul, Odisha
91	ORANP-7	T-091	Angul, Odisha
92	ORANP-11	T-092	Angul, Odisha
93	ORANP-12	T-093	Angul, Odisha
94	ORANP-13	T-094	Angul, Odisha
95	ORPNB-12	T-095	Odisha
96	Nepa T.S.O. KEAC-2	T-096	Nepanagar, MP
97	Nepa T.S.O. KEAC-4	T-097	Nepanagar, MP
98	Nepa T.S.O. KEAC-9	T-098	Nepanagar, MP
99	C.NO.182 Sironcha F.D.	T-099	Sironcha, Maharashtra
100	T.S.O. Raipur C.NO.21	T-100	Raipur, Chhattisgarh

Statistical analysis

Statistical analysis was carried out with freely available R software (<https://www.r-project.org/>). The phenotypic dataset was analyzed using a multi-trait mixed linear model framework implemented in the breedR package in R (Muñoz F and Sanchez L 2025). The analysis was conducted using family means averaged per replication to reduce environmental noise and focus on genetic differences among families. While this approach enhances precision by minimizing within-replication environmental variation, it aggregates individual tree data, thereby losing resolution on within-family genetic variation and individual performance, which could be captured in full individual-tree mixed models.

Six traits viz., tree height (Height), clear bole length (CBL), girth at breast height (GBH), crown diameter (CRD), crown height (CRH), and number of primary branches (PRB)—were included in the model. All traits were standardised prior to analysis (mean-centered and scaled by trait-specific standard deviations) to facilitate convergence and ensure comparability across traits. The following model was fitted jointly for all traits:

$$y = X\beta + Z_f u_f + Z_r u_r + \epsilon$$

where y is the vector of standardized observations, β is the vector of fixed effects (overall mean per trait), u_f represents random family effects, u_r represents random replication effects, and ϵ denotes residual errors. Family and replication were modeled as independent random factors with unstructured covariance matrices across traits. Model parameters were estimated by residual maximum likelihood (REML) using the expectation–maximisation algorithm.

Variance–covariance matrices for the family and residual terms were extracted, and family-level best linear unbiased predictors (BLUPs) were obtained in the standardized scale. These BLUPs and intercepts were then back-transformed into the original measurement units using the means and standard deviations of each trait. Predicted family values were computed by combining the fixed intercepts and family BLUPs. From the predicted GBH, family-level stem volume was calculated using the local volume equation of the Forest Survey of India (Singh et al. 2023):

$$V = (6.102843 \times D^2 - 0.13475 \times \sqrt{D}) \times 1000$$

where $D = \text{GBH} / \pi \times 100$, with GBH expressed in centimetres. Family-mean heritability (h^2) was estimated for each trait following:

$$h^2 = \sigma_f^2 / (\sigma_f^2 + \sigma_e^2 / r)$$

where σ_f^2 is the family variance component, σ_e^2 is the residual variance component, and r is the number of replications per family mean. Standard errors of heritability were approximated using a nonparametric bootstrap procedure, in which families

were resampled with replacement and models were refitted 1000 times.

Genetic correlations among traits were calculated by converting the family variance–covariance matrix into a correlation matrix. The contribution of family effects was further assessed using likelihood ratio tests by comparing full and reduced models with and without the family term.

Finally, graphical exploration was performed using bar plots, heatmaps, and scatterplots to visualize predicted family performance across traits and relationships among traits. The plots were obtained using the package ggplot2 (Wickham et al. 2016).

Genetic advance was calculated as $h^2(X_s - X_p)$, where h^2 is the estimate of heritability, X_s is the mean of selected families, and X_p is the mean value for the population (Falconer 1996). Group coancestry (Θ) and status number (N_s) were calculated to assess the genetic diversity of the selected clones. Group coancestry was computed as the probability that two alleles randomly drawn from the population are identical by descent, defined as $\Theta = \sum_{i=1}^n p_i^2 = 1/n$ where p_i is the proportional contribution of the i^{th} clone, and n is the number of selected clones. The status number, representing the effective number of unrelated and equally contributing clones, was derived as $N_s = 1/2\Theta$

Results

Variation among families and their BLUPs

The boxplot of families for studied traits (Fig. 2 a-f) revealed variation for all traits, both within and between families. The p-value for the likelihood ratio test was 4.957371×10^{-09} , suggesting significant genetic differences between families in the trial. Residual diagnostics (Suppl. Fig 1) indicated no obvious deviations from model assumptions. The residuals were centred around zero with no apparent trends against fitted values, supporting the adequacy of the mixed model for inference. BLUP is used to estimate the breeding values of a family in a progeny trial. The BLUP values centred around 0 for height, clear bole length, crown diameter, crown height and number of primary branches (Fig. 3). The median BLUP value was negative for wood girth at breast height, suggesting that a greater number of families had negative BLUP values for the aforementioned traits in the study.

Fig. 2a)

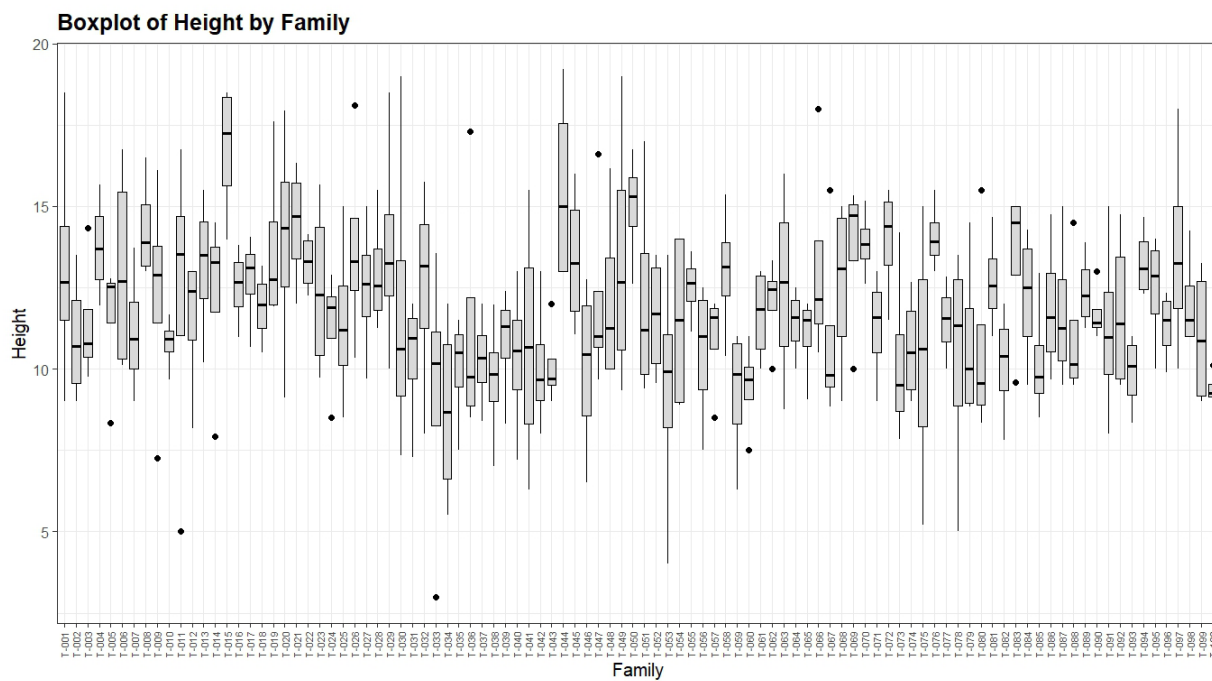


Fig. 2 b)

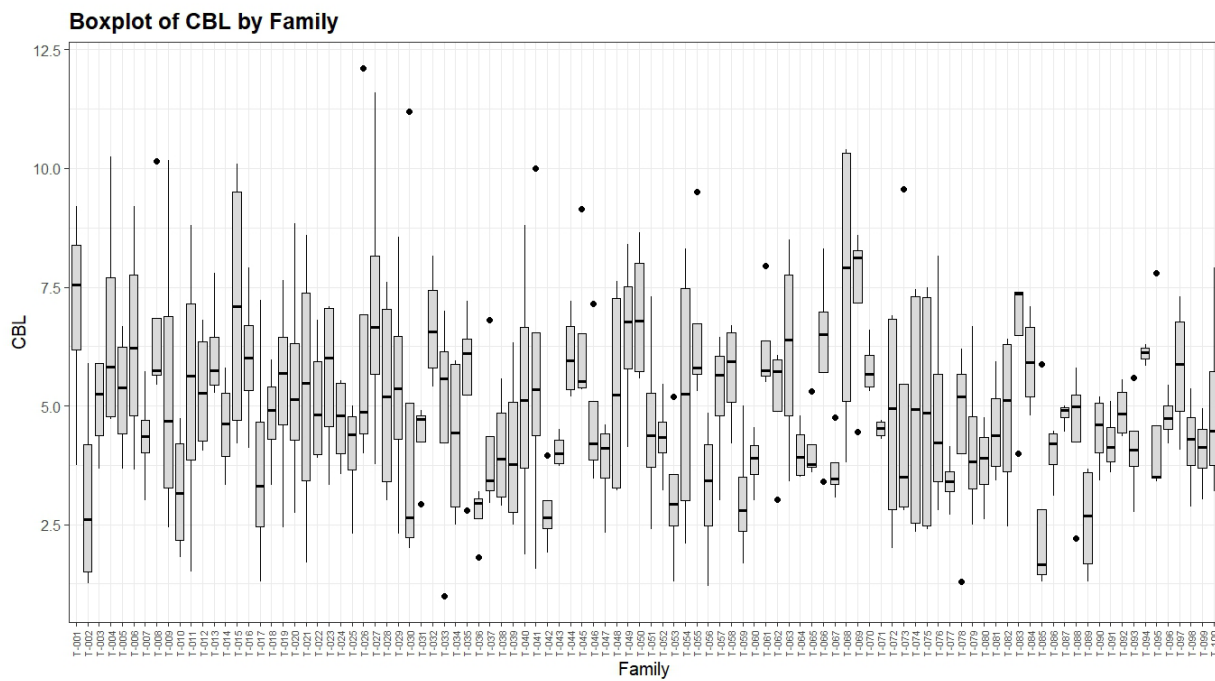


Fig. 2 c)

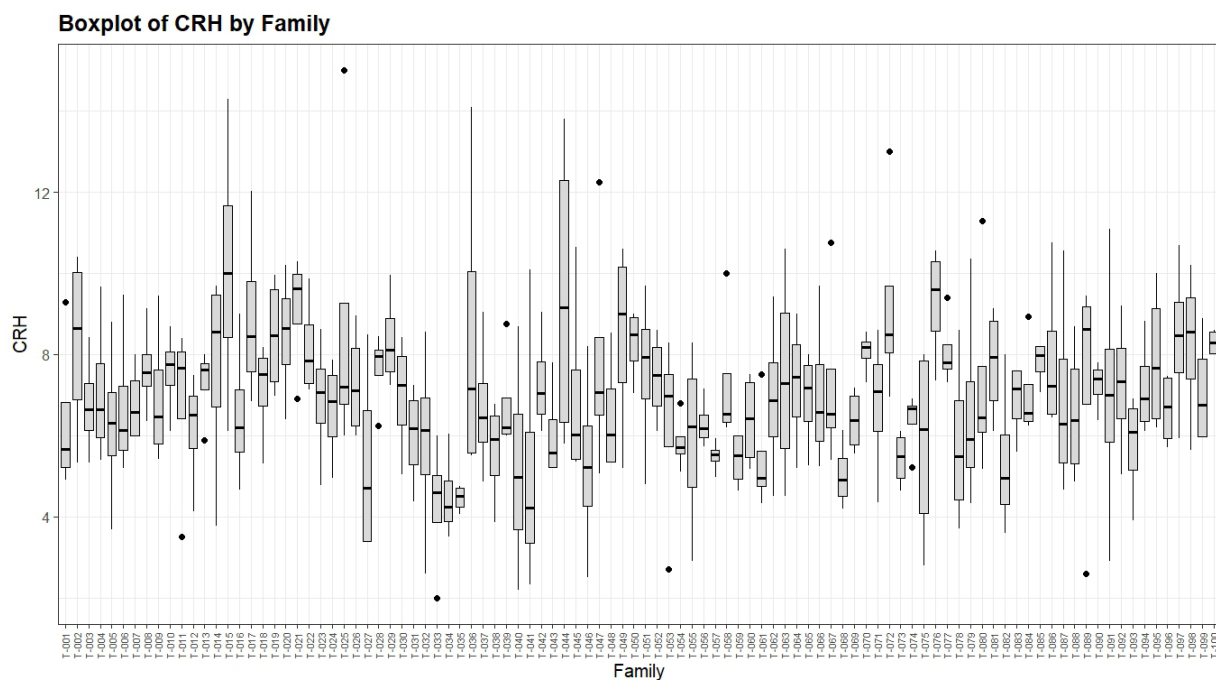


Fig. 2 d)

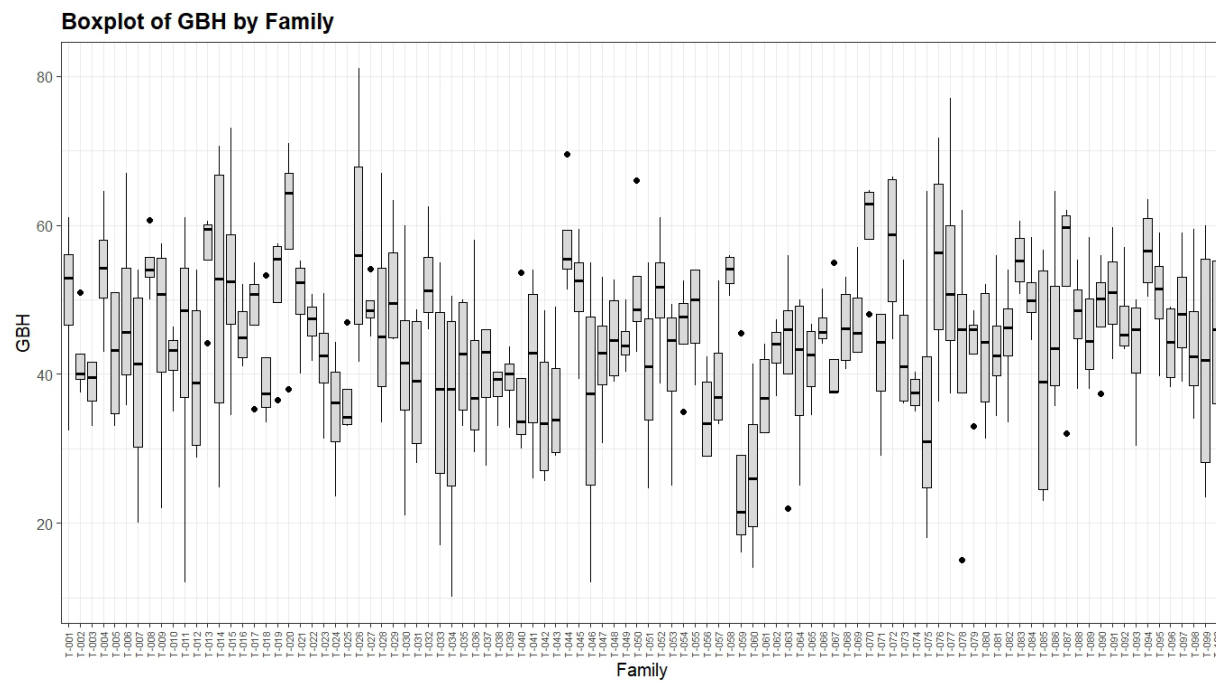


Fig. 2 e)

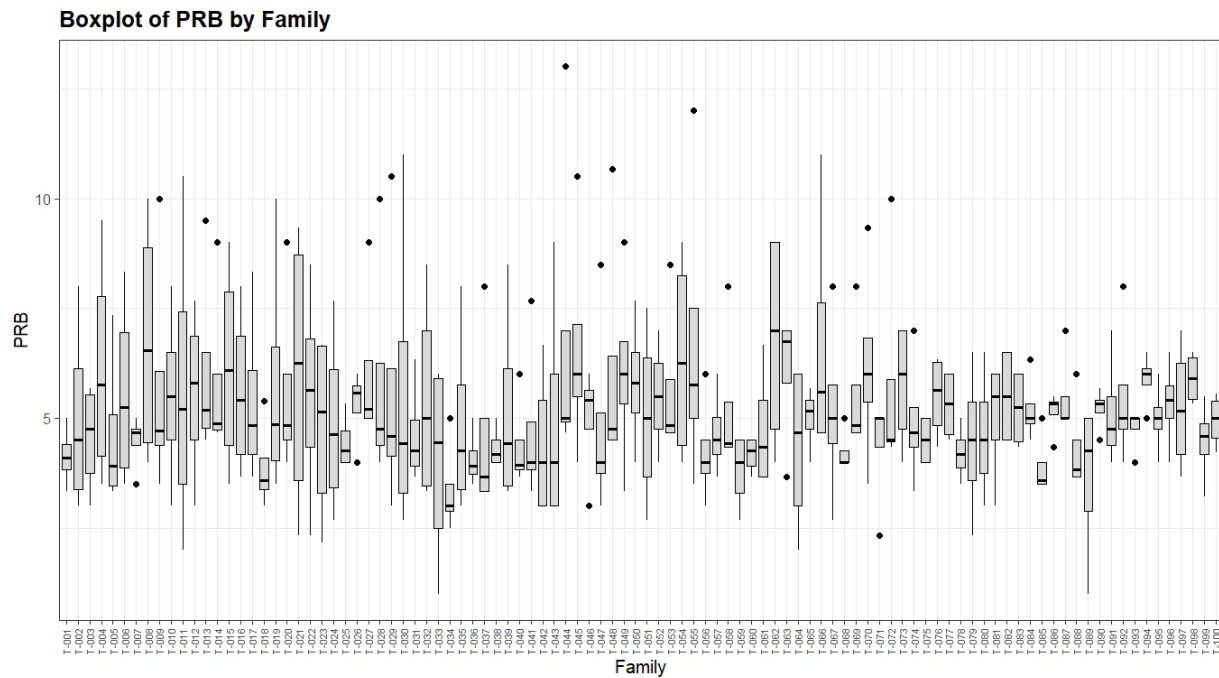


Fig. 2 f)

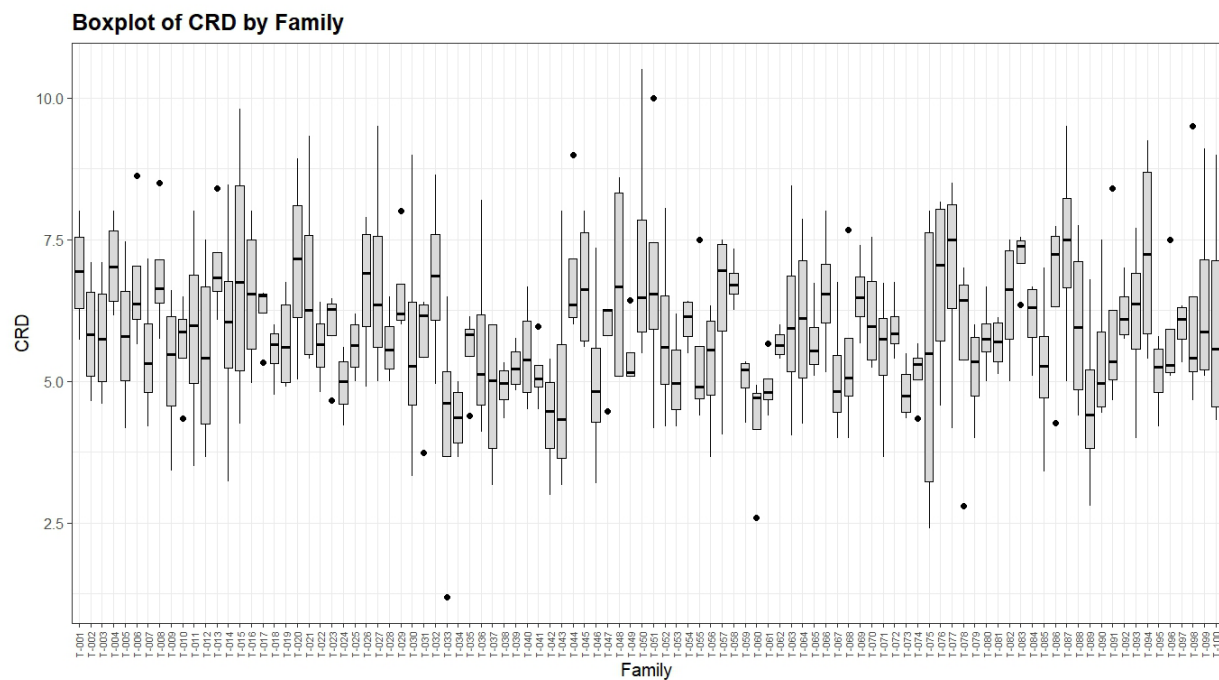


Figure 2 a-f

Box and whisker plot showing the mean and distribution of families for (a) Tree height (b) Clear bole length (c) Crown height (d) Girth at breast height (e) Number of primary branches and (f) Crown diameter.

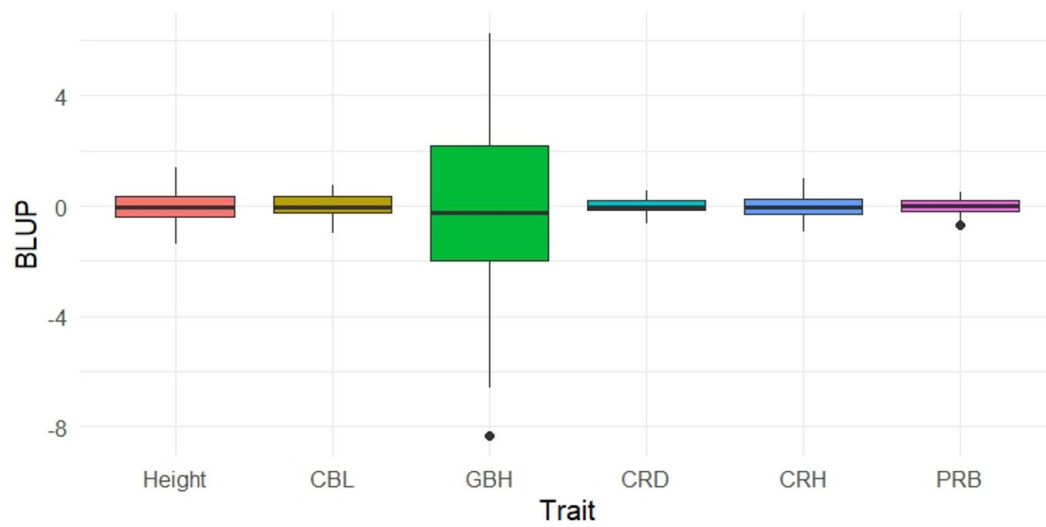


Figure 3

Box and whisker plot for distribution of BLUPs across traits. CBL; Clear bole length, GBH; Girth at breast height, CRD; Crown diameter, CRH; Crown height, PRB; Number of primary branches.

Fig. 4 a)

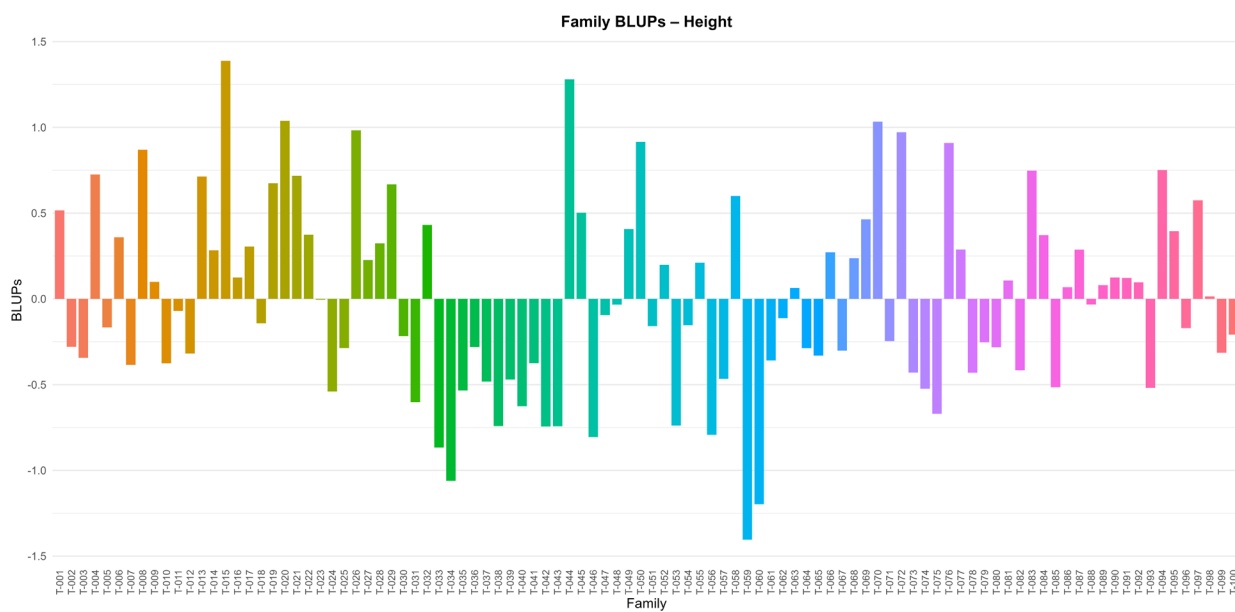


Fig. 4 b)

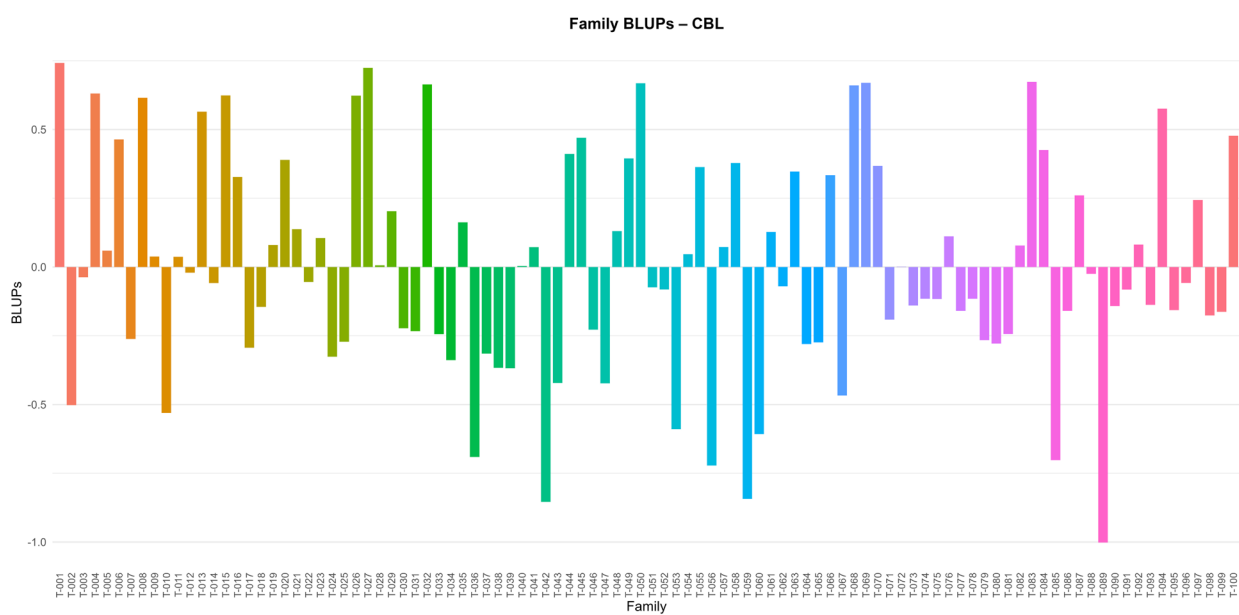


Fig. 4 c)

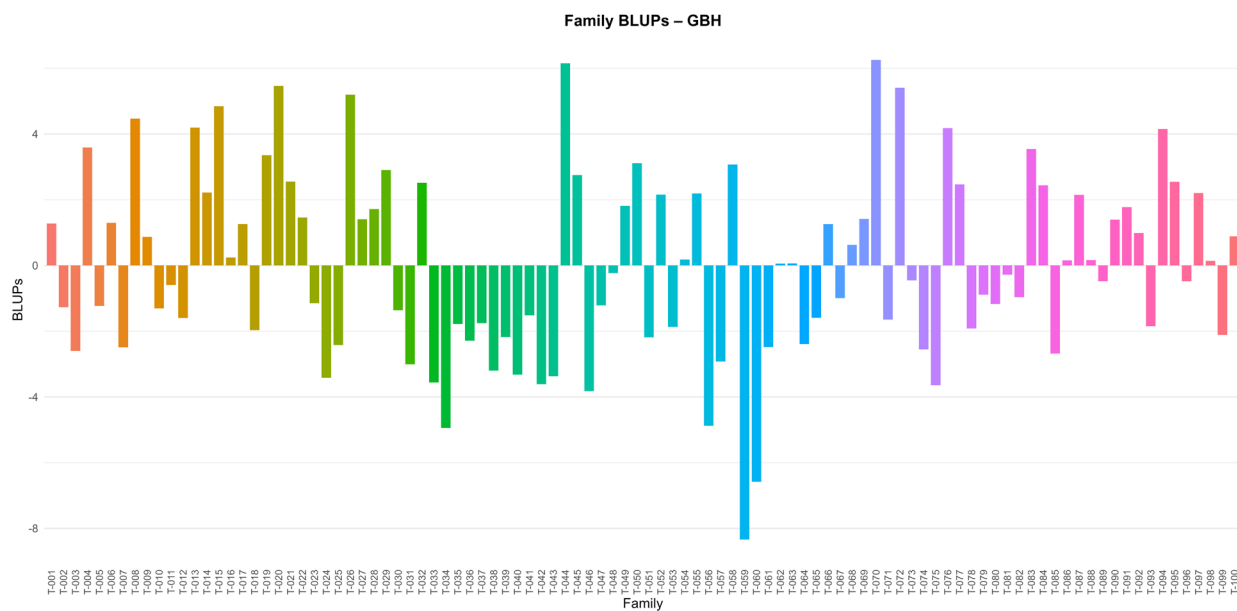


Fig. 4 d)

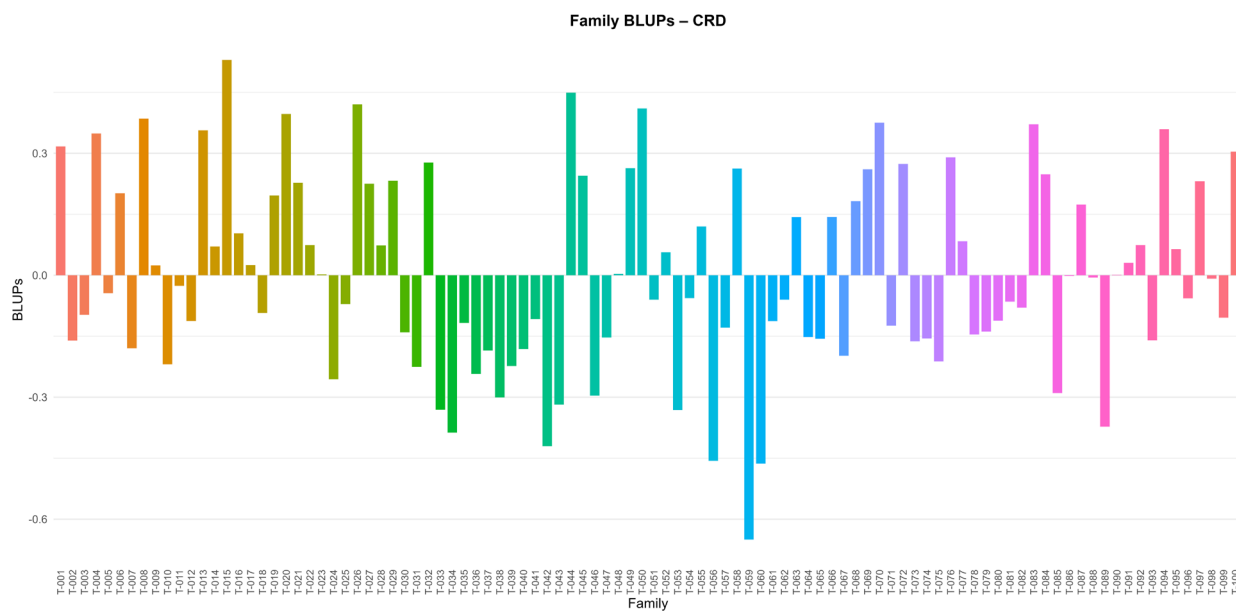


Fig. 4 e)

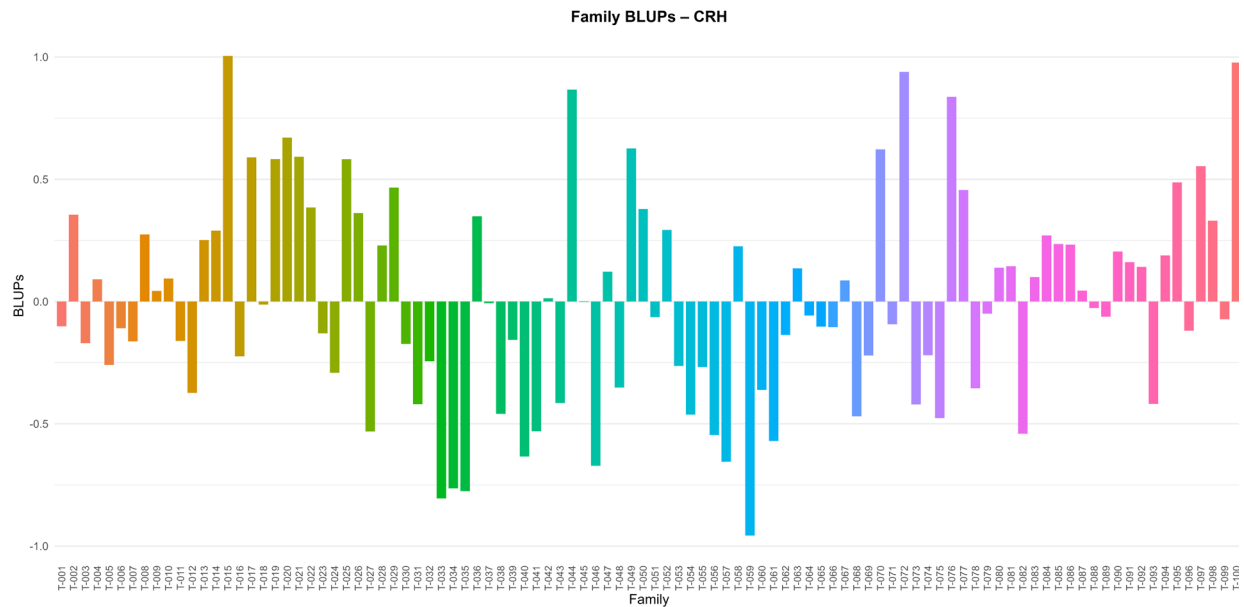


Fig. 4 f)

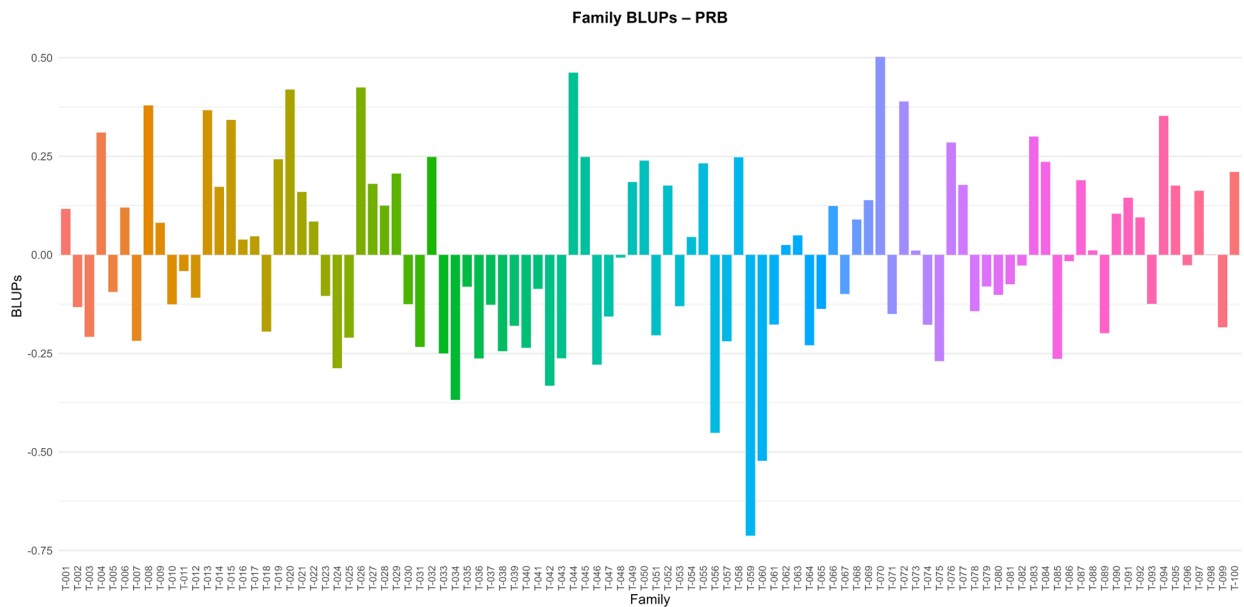


Figure 4 a-f

BLUPs of families for (a) Tree height(m), (b) Clear bole length (CBL;m), (c) Crown height (CRH;m), (d) Crown diameter (CRD;m), (e) Girth at breast height (GBH;cm), (f) Number of primary branches (PRB) and (g) Wood volume (dm³). T-001, T-002, T-003..., are half sib families.

Fig. 5 a)

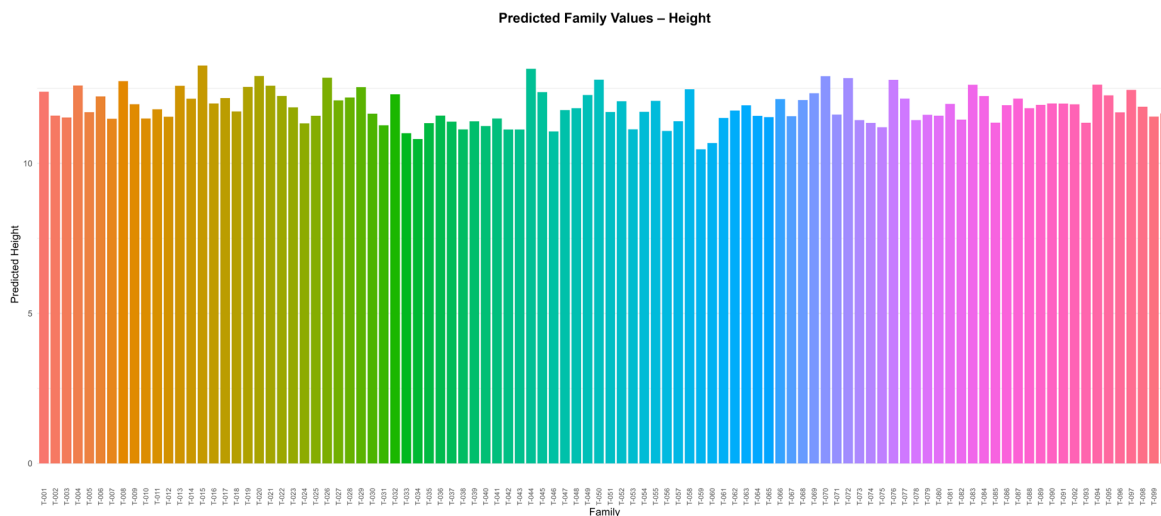


Fig. 5 b)

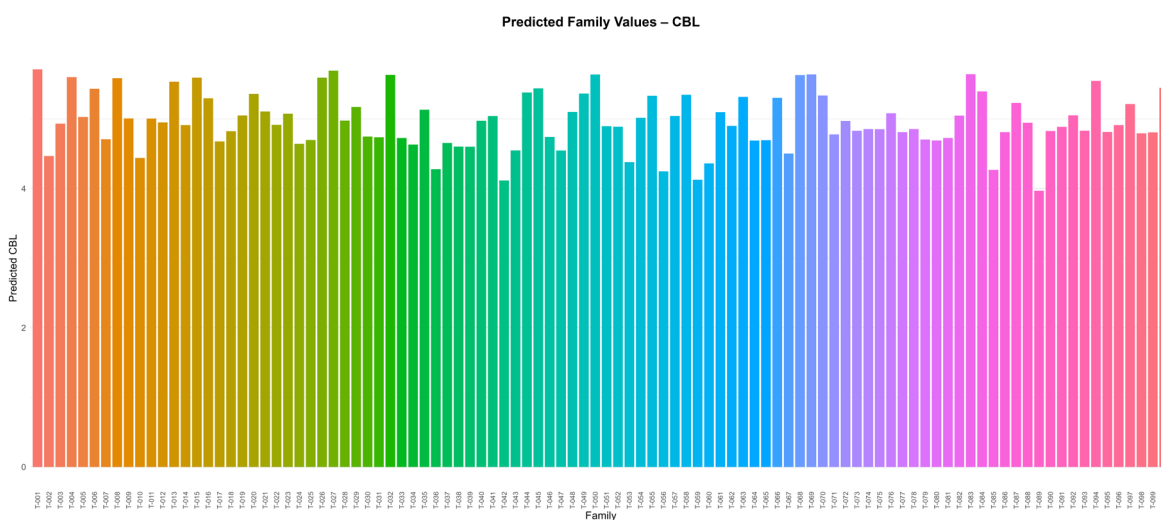


Fig. 5 c)

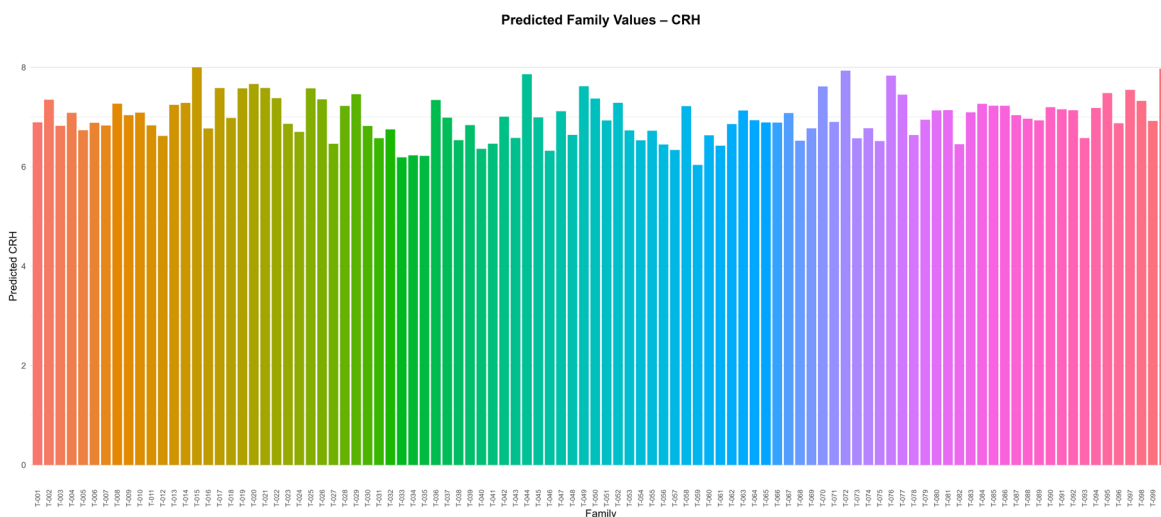


Fig. 5 d)

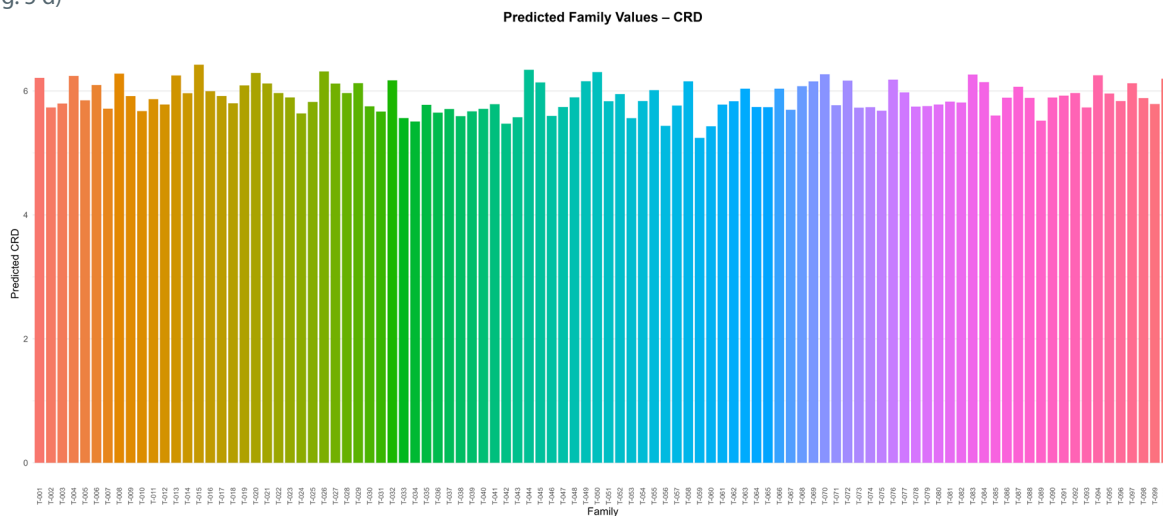


Fig. 5 e)

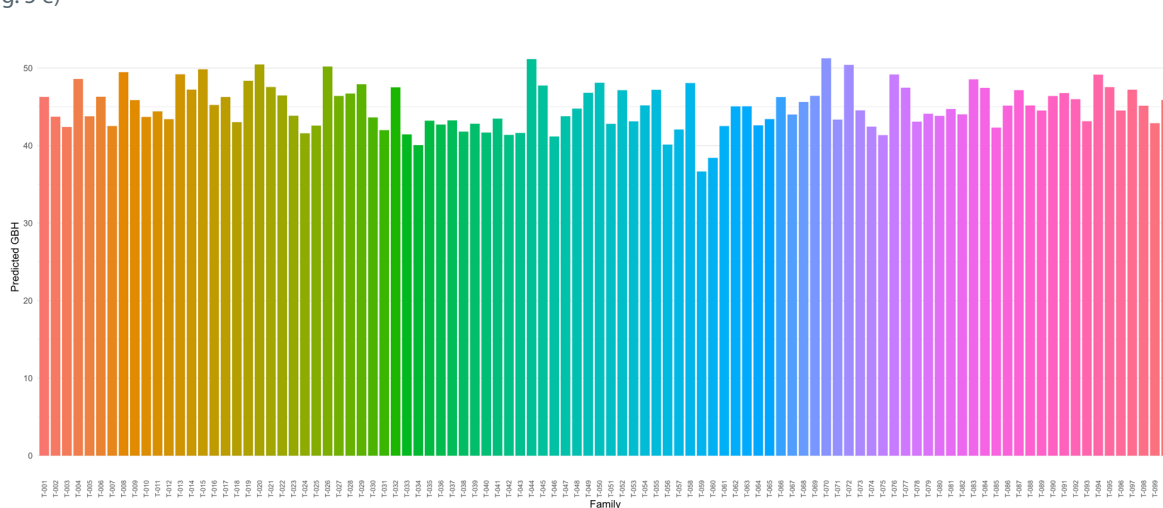


Fig. 5 f)

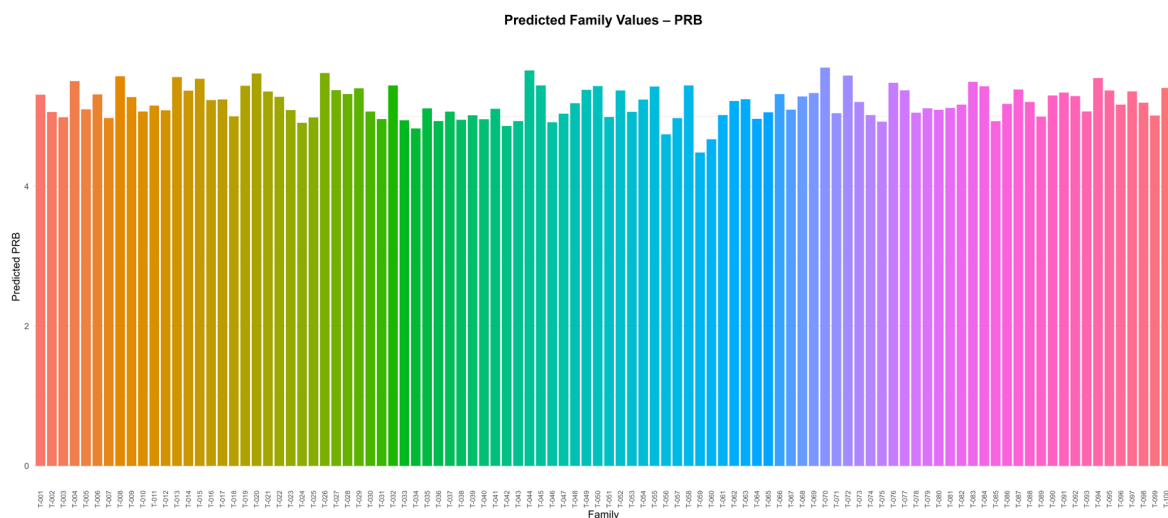


Fig. 5 g)

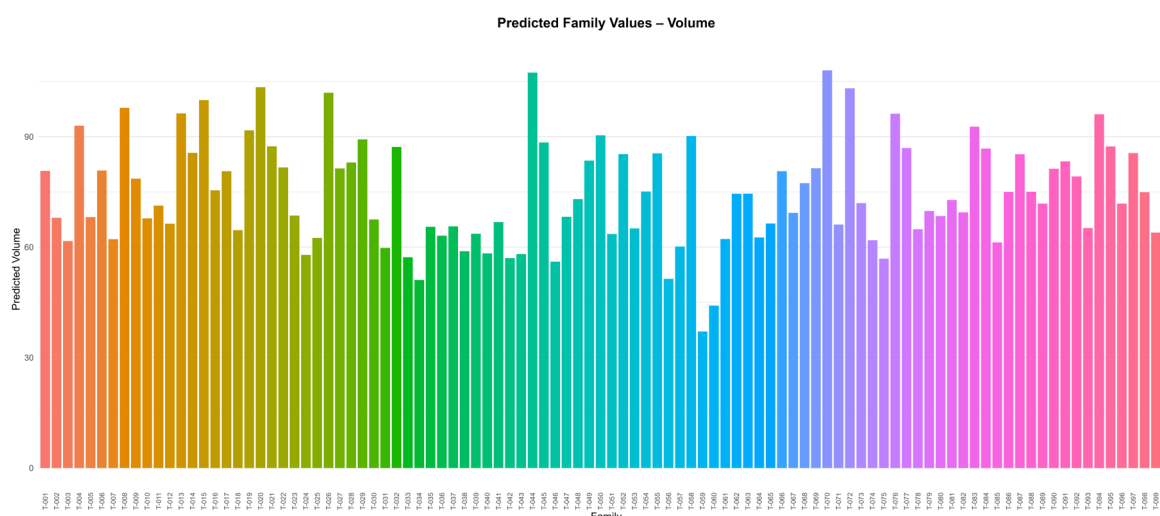


Figure 5 a-g: Predicted family values for (a) Tree height (m), (b) Clear bole length (CBL;m), (c) Crown height (CRH;m), (d) Crown diameter (CRD;m), (e) Girth at breast height (GBH;cm), (f) Number of primary branches (PRB) and (g) Wood volume (dm³). T-001, T-002, T-003..., are half-sib families.

The BLUP values for families across all measured traits are shown in Figure 4 a-f. Predicted family values for these traits, along with wood volume, are presented in Figure 5 a-g. Detailed BLUPs and predicted family values for all studied traits are provided in Supplementary Table 1. Table 2 summarizes the BLUPs and predicted family values for the top 20 and bottom 20 families for measured traits and predicted wood volume.

For tree height, the highest predicted family value was recorded in Angul MHAL-P8 (T-015, 13.26 m; Table 2). The lowest was observed in T.S.O.Baitul C.NO.27 (T-059, 10.47 m; Table 2). Four families had BLUP values greater than 1 m for tree height (Table 2). In total, 48 families had positive BLUP values (Supplementary Table 1). Angul MHAL-P8 (T-015) exhibited the maximum BLUP value (1.39 m), followed by T.S.O.Baitul CSC-24 (T-044, 1.28 m), MHSC-J1 (T-020, 1.04 m), and Orissa 79 I C NO.48 (T-070, 1.03 m). These families showed strong genetic potential for tree height (Table 2). Families with the lowest BLUPs, such as T.S.O.Baitul C.NO.27 (T-059, -1.4 m), T.S.O.Raipur C.NO.27 (T-060, -1.2 m), and T.S.O.Baitul BBC-38 (T-034, -1.06 m), exhibited lower genetic potential compared to the population mean (Table 2).

For clear bole length, the highest predicted value was 5.71 m (MHAL-A1, T-001), and the lowest was 3.97 m (ORANP-2, T-089; Table 2). Forty-five families had positive BLUP values for clear bole length (Supplementary Table 1). The remaining families showed zero or negative BLUPs, indicating no contribution or negative contribution towards bole length (Supplementary Table 1).

For girth at breast height (GBH), the highest and lowest predicted family values were 51.26 cm (T.S.O.Baitul CSC-24,

T-070) and 36.66 cm (T.S.O.Baitul C.NO.27, T-059), respectively. For crown diameter (CRD), the range was from 6.42 m (Angul MHAL-P8, T-015) to 5.24 m (T.S.O.Baitul C.NO.27, T-059). For crown height (CRH), the values ranged from 8 m (Angul MHAL-P8, T-015) to 6.04 m (T.S.O.Baitul C.NO.27, T-059). For the number of primary branches (PRB), the maximum was 5.70 (Orissa 79 I C.NO.48, T-070) and the minimum was 4.48 (T.S.O.Baitul C.NO.27, T-059). For wood volume, predicted values ranged from 108.02 dm³ (T.S.O.Baitul CSC-24, T-070) to 37.07 dm³ (T.S.O.Baitul C.NO.27, T-059; Table 2).

The number of families with positive BLUPs varied across traits. There were 49 for GBH and PRB, 46 each for CRH and CRD (Supplementary Table 1).

Wood volume, being an economically important trait, showed clear variation among families. The best-performing families with higher predicted values were Orissa 79 I C.NO.48 (T-070; 108.02 dm³), T.S.O.Baitul CSC-24 (T-044; 107.42 dm³), T.S.O.Baitul BBC-2 (T-020; 103.46 dm³), T.S.O.Raipur C.NO.47 (T-072; 103.15 dm³), and T.S.O.Baitul Pt.45 (T-026; 101.94 dm³) (Table 2). These families were genetically superior for wood volume compared to others.

By contrast, lower predicted values were found in families such as T.S.O.Baitul C.NO.27 (T-059, 37.07 dm³), ORPUB-8 (T-060, 44.12 dm³), T.S.O.Baitul BBC-38 (T-034, 51.1 dm³), T.S.O.Raipur C.NO.24 (T-056, 51.38 dm³) and T.S.O.Raipur C.NO. C8 (T-046, 56.04 dm³), (Table 2).

The families with positive and negative BLUP values for all traits, and mixed BLUP values have been given in Table 3. Among 100 families, 29 families were observed to have positive BLUP values for all traits, 31 families had negative BLUP values for all traits, and 40 families had mixed BLUP values.

Table 2: BLUPs and predicted family values for top 20 and bottom 20 families for measured traits and predicted family values for wood volume.

Top 20 families																			
Fa- mily	Height (m)		Fa- mily	CBL (m)		Fami- ly	GBH (cm)		Fa- mily	CRD (m)		Fa- mily	CRH (m)		Family	PRB		Fa- mily	Wood Volume (dm3)
	BLUPs	PFVs		BLUPs	PFVs		BLUPs	PFVs		BLUPs	PFVs		BLUPs	PFVs		BLUPs	PFVs		PFVs
T-015	1.39	13.26	T-001	0.74	5.71	T-070	6.26	51.26	T-015	0.53	6.42	T-015	1.00	8.00	T-070	0.50	5.70	T-070	108.02
T-044	1.28	13.15	T-027	0.72	5.69	T-044	6.15	51.15	T-044	0.45	6.34	T-100	0.98	7.97	T-044	0.46	5.66	T-044	107.42
T-020	1.04	12.91	T-083	0.67	5.64	T-020	5.47	50.46	T-026	0.42	6.31	T-072	0.94	7.93	T-026	0.42	5.62	T-020	103.46
T-070	1.03	12.91	T-069	0.67	5.64	T-072	5.41	50.41	T-050	0.41	6.30	T-044	0.87	7.86	T-020	0.42	5.62	T-072	103.15
T-026	0.98	12.86	T-050	0.67	5.64	T-026	5.20	50.20	T-020	0.40	6.29	T-076	0.84	7.83	T-072	0.39	5.59	T-026	101.94
T-072	0.97	12.84	T-032	0.66	5.63	T-015	4.85	49.84	T-008	0.39	6.28	T-020	0.67	7.66	T-008	0.38	5.58	T-015	99.95
T-050	0.92	12.79	T-068	0.66	5.63	T-008	4.47	49.47	T-070	0.38	6.27	T-049	0.63	7.62	T-013	0.37	5.56	T-008	97.84
T-076	0.91	12.78	T-004	0.63	5.60	T-013	4.20	49.19	T-083	0.37	6.26	T-070	0.62	7.62	T-094	0.35	5.55	T-013	96.32
T-008	0.87	12.74	T-015	0.62	5.59	T-076	4.18	49.18	T-094	0.36	6.25	T-021	0.59	7.59	T-015	0.34	5.54	T-076	96.24
T-094	0.75	12.63	T-026	0.62	5.59	T-094	4.15	49.15	T-013	0.36	6.25	T-017	0.59	7.58	T-004	0.31	5.51	T-094	96.09
T-083	0.75	12.62	T-008	0.62	5.58	T-004	3.59	48.59	T-004	0.35	6.24	T-019	0.58	7.58	T-083	0.30	5.50	T-004	93.00
T-004	0.72	12.60	T-094	0.58	5.55	T-083	3.54	48.54	T-001	0.32	6.21	T-025	0.58	7.58	T-076	0.28	5.48	T-083	92.74
T-021	0.72	12.59	T-013	0.56	5.53	T-019	3.36	48.36	T-100	0.30	6.20	T-097	0.55	7.55	T-045	0.25	5.44	T-019	91.73
T-013	0.71	12.59	T-100	0.48	5.45	T-050	3.11	48.11	T-076	0.29	6.18	T-095	0.49	7.48	T-032	0.25	5.44	T-050	90.38
T-019	0.67	12.55	T-045	0.47	5.44	T-058	3.07	48.07	T-032	0.28	6.17	T-029	0.47	7.46	T-058	0.25	5.44	T-058	90.18
T-029	0.67	12.54	T-006	0.46	5.43	T-029	2.90	47.90	T-072	0.27	6.17	T-077	0.46	7.45	T-019	0.24	5.44	T-029	89.28
T-058	0.60	12.47	T-084	0.43	5.40	T-045	2.75	47.75	T-049	0.26	6.16	T-022	0.38	7.38	T-050	0.24	5.43	T-045	88.44
T-097	0.57	12.45	T-044	0.41	5.38	T-021	2.55	47.55	T-058	0.26	6.16	T-050	0.38	7.37	T-084	0.24	5.43	T-021	87.39
T-001	0.52	12.39	T-049	0.40	5.36	T-095	2.55	47.55	T-069	0.26	6.15	T-026	0.36	7.36	T-055	0.23	5.43	T-095	87.36
T-045	0.50	12.38	T-020	0.39	5.36	T-032	2.52	47.52	T-084	0.25	6.14	T-002	0.36	7.35	T-100	0.21	5.41	T-032	87.21
Bottom 20 families																			
Fa- mily	Height (m)		Fa- mily	CBL (m)		Fami- ly	GBH (cm)		Fa- mily	CRD (m)		Fa- mily	CRH (m)		Family	PRB		Fa- mily	Wood Volume (dm3)
	BLUPs	PFVs		BLUPs	PFVs		BLUPs	PFVs		BLUPs	PFVs		BLUPs	PFVs		BLUPs	PRB		PFVs
T-059	-1.40	10.47	T-089	-1.00	3.97	T-059	-8.34	36.66	T-059	-0.65	5.24	T-059	-0.96	6.04	T-059	-0.71	4.48	T-059	37.07
T-060	-1.20	10.68	T-042	-0.85	4.12	T-060	-6.58	38.41	T-060	-0.46	5.43	T-033	-0.80	6.19	T-060	-0.52	4.67	T-060	44.12
T-034	-1.06	10.81	T-059	-0.84	4.13	T-034	-4.94	40.06	T-056	-0.46	5.44	T-035	-0.78	6.22	T-056	-0.45	4.74	T-034	51.10
T-033	-0.87	11.01	T-056	-0.72	4.25	T-056	-4.88	40.12	T-042	-0.42	5.47	T-034	-0.76	6.23	T-034	-0.37	4.83	T-056	51.38
T-046	-0.81	11.07	T-085	-0.70	4.27	T-046	-3.83	41.17	T-034	-0.39	5.51	T-046	-0.67	6.32	T-042	-0.33	4.86	T-046	56.04
T-056	-0.79	11.08	T-036	-0.69	4.28	T-075	-3.64	41.35	T-089	-0.37	5.52	T-057	-0.65	6.34	T-024	-0.29	4.91	T-075	56.86
T-042	-0.74	11.13	T-060	-0.61	4.36	T-042	-3.61	41.39	T-053	-0.33	5.56	T-040	-0.63	6.36	T-046	-0.28	4.92	T-042	57.00
T-043	-0.74	11.13	T-053	-0.59	4.38	T-033	-3.56	41.44	T-033	-0.33	5.56	T-061	-0.57	6.42	T-075	-0.27	4.93	T-033	57.25
T-038	-0.74	11.13	T-010	-0.53	4.44	T-024	-3.42	41.58	T-043	-0.32	5.58	T-056	-0.55	6.45	T-085	-0.26	4.93	T-024	57.89
T-053	-0.74	11.13	T-002	-0.50	4.47	T-043	-3.37	41.63	T-038	-0.30	5.59	T-082	-0.54	6.45	T-036	-0.26	4.93	T-043	58.11
T-075	-0.67	11.20	T-067	-0.47	4.50	T-040	-3.32	41.67	T-046	-0.30	5.60	T-027	-0.53	6.46	T-043	-0.26	4.93	T-040	58.32
T-040	-0.63	11.25	T-047	-0.42	4.55	T-038	-3.20	41.80	T-085	-0.29	5.60	T-041	-0.53	6.46	T-033	-0.25	4.95	T-038	58.89
T-031	-0.60	11.27	T-043	-0.42	4.55	T-031	-3.01	41.99	T-024	-0.26	5.64	T-075	-0.48	6.52	T-038	-0.24	4.95	T-031	59.77
T-024	-0.54	11.33	T-039	-0.37	4.60	T-057	-2.92	42.08	T-036	-0.24	5.65	T-068	-0.47	6.52	T-040	-0.24	4.96	T-057	60.16
T-035	-0.53	11.34	T-038	-0.37	4.60	T-085	-2.68	42.32	T-031	-0.23	5.67	T-054	-0.46	6.53	T-031	-0.23	4.96	T-085	61.27
T-074	-0.52	11.35	T-034	-0.34	4.63	T-003	-2.60	42.40	T-039	-0.22	5.67	T-038	-0.46	6.53	T-064	-0.23	4.97	T-003	61.65
T-093	-0.52	11.35	T-024	-0.33	4.64	T-074	-2.56	42.44	T-010	-0.22	5.67	T-073	-0.42	6.57	T-057	-0.22	4.98	T-074	61.86
T-085	-0.51	11.36	T-037	-0.31	4.65	T-007	-2.49	42.51	T-075	-0.21	5.68	T-031	-0.42	6.57	T-007	-0.22	4.98	T-007	62.17
T-037	-0.48	11.39	T-017	-0.29	4.68	T-061	-2.48	42.52	T-067	-0.20	5.70	T-093	-0.42	6.58	T-025	-0.21	4.99	T-061	62.20
T-039	-0.47	11.40	T-064	-0.28	4.69	T-025	-2.42	42.58	T-037	-0.19	5.71	T-043	-0.41	6.58	T-003	-0.21	4.99	T-025	62.49

Table 3
Segregation of BLUP values for studied traits.

S.No.	Positive BLUP values for all traits		Negative BLUP values for all traits		Positive and Negative BLUP values for one or more traits	
	Code	Family	Code	Family	Code	Family
1	T-004	MHAL-A4	T-003	MHAL-A3	T-001	MHAL-A1
2	T-008	MHAL-P2	T-007	MHAL-P1	T-002	MHAL-A2
3	T-009	MHAL-P3	T-010	MHAL-P4	T-012	MHAL-P6
4	T-013	MHAL-P7	T-011	MHAL-P5	T-005	MHAL-A6
5	T-015	Angul MHAL-P8	T-018	MHSC-A2	T-006	MHAL-A8
6	T-019	MHSC-A4	T-024	MHEM-R2	T-014	MHAL-P8
7	T-020	MHSC-J1	T-030	T.S.O.Baitul BBC-8	T-016	MHAL-P9
8	T-021	MHSC-J2	T-031	T.S.O.Baitul BBC-13	T-017	MHSC-A1
9	T-026	T.S.O.Baitul Pt.45	T-033	Nepa T.S.O.81 BBC-30	T-022	MHWY-K2
10	T-028	Nepa T.S.O. 79 BBC-1	T-034	T.S.O.Baitul BBC-38	T-023	MHWY-K3
11	T-029	T.S.O.Baitul BBC-2	T-037	T.S.O.Baitul BHC-1	T-025	T.S.O.Baitul Pt.1
12	T-044	T.S.O.Baitul CSC-24	T-038	T.S.O.Baitul BHC-13	T-027	Orissa 78 Pt.47
13	T-045	T.S.O. Control Lohara	T-039	T.S.O.Baitul BHC-16	T-032	Nepa T.S.O.BBC-18
14	T-049	T.S.O.Raipur C.NO.8	T-040	T.S.O.Baitul BHC-19	T-035	T.S.O.Baitul BBC-49
15	T-050	T.S.O.Raipur C.NO.12	T-043	T.S.O.Baitul CSC-16	T-036	T.S.O.Baitul BBC-57
16	T-058	Orissa 79 I C.NO.26	T-046	T.S.O.Raipur C.NO.C8	T-041	T.S.O.Baitul BSC-6
17	T-063	T.S.O.Raipur C.NO.43	T-051	T.S.O.Raipur C.NO.14	T-042	Nepa T.S.O.77 BSC-23
18	T-070	Orissa 79 I C.NO.48	T-053	T.S.O.Raipur C.NO.16	T-047	T.S.O.Baitul C.NO.C78
19	T-072	T.S.O.Raipur C.NO.50	T-056	T.S.O.Raipur C.NO.24	T-048	T.S.O.Raipur C.NO.6
20	T-076	T.S.O.Baitul C.NO.60	T-059	T.S.O.Baitul C.NO.27	T-052	T.S.O.Baitul C.NO.15
21	T-083	ORPUB-24	T-060	T.S.O.Raipur C.NO.27	T-055	T.S.O.Raipur C.NO.20
22	T-084	ORAN-R1	T-064	T.S.O.Raipur C.NO.44	T-054	T.S.O.Raipur C.NO.19
23	T-087	ORAN-R5	T-065	T.S.O.Baitul C.NO.45	T-057	T.S.O.Raipur C.NO.25
24	T-090	ORANP-4	T-071	T.S.O.Raipur C.NO.49	T-062	T.S.O.Raipur C.NO.30
25	T-092	ORANP-11	T-074	T.S.O.Raipur C.NO.55	T-061	T.S.O.Raipur C.NO.28
26	T-094	ORANP-13	T-075	T.S.O.Raipur C.NO.58	T-066	T.S.O.Raipur C.NO.45
27	T-095	ORPNB-12	T-078	ORPUB-8	T-067	T.S.O.Raipur C.NO.46
28	T-097	Nepa T.S.O. KEAC-4	T-079	ORPUB-9	T-068	T.S.O.Raipur C.NO.47
29	T-100	T.S.O. Raipur C.NO.21	T-093	ORANP-12	T-069	T.S.O.Raipur C.NO.48
30			T-096	Nepa T.S.O. KEAC-2	T-073	T.S.O.Raipur C.NO.51
31			T-099	C.NO.182 Sironcha F.D.	T-077	ORPUB-3
32					T-080	ORPUB-10
33					T-081	ORPUB-18
34					T-082	ORPUB-19
35					T-085	ORAN-R2
36					T-086	ORAN-R4
37					T-088	ORAN-R6
38					T-089	ORANP-2
39					T-091	ORANP-7
40					T-098	Nepa T.S.O. KEAC-9

Heritability estimates and Correlation among traits

The narrow sense heritability estimates varied across the traits, indicating differences in the genetic control of each parameter (Fig. 6, Table 4). The highest heritability was observed for GBH, followed by tree height and CRH, suggesting moderate additive genetic effects for these growth traits. Conversely, PRB exhibited the lowest heritability, implying a greater influence of environmental factors on primary branching patterns. Moderate heritability values were recorded for CBL and CRD, suggesting a mix of genetic and environmental contributions. Pearson's correlation coefficients among the studied traits (Fig. 7) showed significant positive genetic associations (p values < 0.05) between measured growth parameters. GBH was observed to have high genetic correlations with the number of primary branches (NPB), tree height and crown diameter (CRD). Tree height was observed to have a high positive genetic correlation with girth at breast height (GBH) and crown diameter (CRD), reinforcing its role as a key determinant of tree productivity. All the growth traits were observed to have significant and positive associations with each other.

Correlated response to selection for wood volume

The expected genetic advance as a response to selection for wood volume on different traits at 5 %, 10 %, 15 %, 20 %, 25 %, 30 %, 35 %, and 40 % selection intensities has been presented in Table 4 and Supplementary Fig. 2 a-f. It was observed that increasing the proportion of selected families for wood volume reduced the selection differential significantly for wood volume (from 30.07 at 5 % to 14.4 at 40 %). The genetic advance of traits such as height (from 0.79 m at 5 % to 0.43 m at 40 %), CRH (from 0.52 m at 5 % to 0.23 m at 40 %), GBH (from 5.42 cm at 5 % to 2.67 cm at 40 %) exhibited generally decreasing trends across intensities despite minor fluctuations in tree height (Table 4). However, appreciable reduction was not observed for CBL (from 0.24 m at 5 % to 0.23 m at 40 %) and CRD (from 0.16 m at 5 % to 0.13 m at 40 %), where values remained relatively stable amid small fluctuations. The genetic advance increased from 0.13 at 5 % to 1.03 at 10 % selection intensity and remained relatively constant near 1 thereafter for PRB. Additionally, group coancestry decreased markedly with increasing selection proportions (from 0.2 at 5 % to 0.025 at 40 %), reflecting reduced average relatedness among selected families as more individuals are included. Conversely, status number increased substantially (from 2.5 at 5 % to 20 at 40 %), indicating a larger effective population size under broader selection, which could help maintain genetic diversity while trading off against genetic gains.

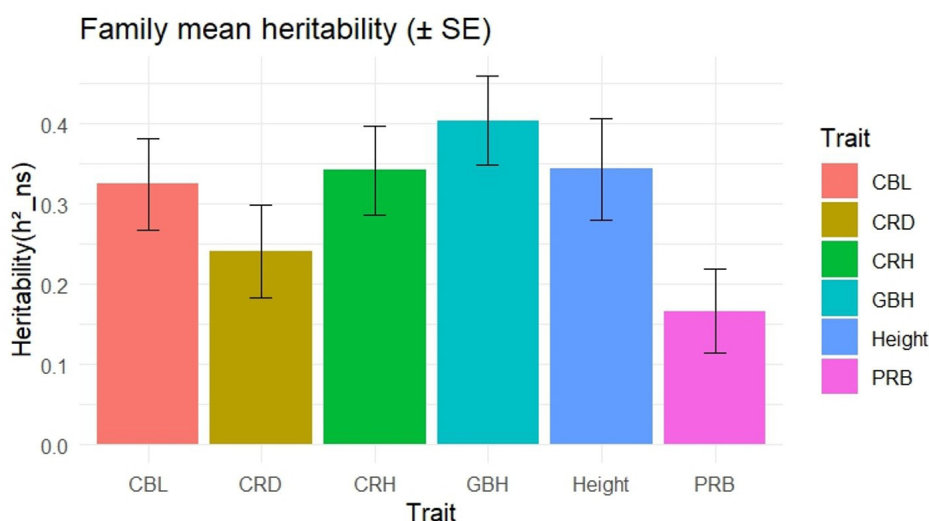


Figure 6.

Narrow sense heritability with standard error bar for studied traits. CBL; Clear bole length, GBH; Girth at breast height, CRD; Crown diameter, CRH; Crown height, PRB; Number of primary branches.

Table 4

Heritability, genetic advance under varying selection intensities, and diversity indices for growth and yield traits

Traits	Heritability (h^2_{ns})	Genetic Advance at Selection intensity							
		5%	10%	15%	20%	25%	30%	35%	40%
Height (m)	0.34	0.79	0.81	0.76	0.69	0.59	0.51	0.48	0.43
CBL (m)	0.32	0.24	0.32	0.35	0.32	0.27	0.23	0.25	0.23
GBH (cm)	0.40	5.42	4.73	4.25	3.80	3.47	3.18	2.91	2.67
CRD (m)	0.24	0.16	0.21	0.21	0.19	0.16	0.14	0.13	0.13
CRH (m)	0.34	0.52	0.48	0.39	0.35	0.31	0.28	0.23	0.23
PRB	0.17	0.13	1.03	1.00	1.00	0.99	0.98	0.98	0.97
Selection differential for predicted family wood volume		30.07	26.31	23.17	20.68	18.81	17.23	15.71	14.40
Group Coancestry		0.2	0.1	0.0667	0.05	0.04	0.0333	0.0286	0.025
Status Number (Ns)		2.5	5	7.5	10	12.5	15	17.5	20

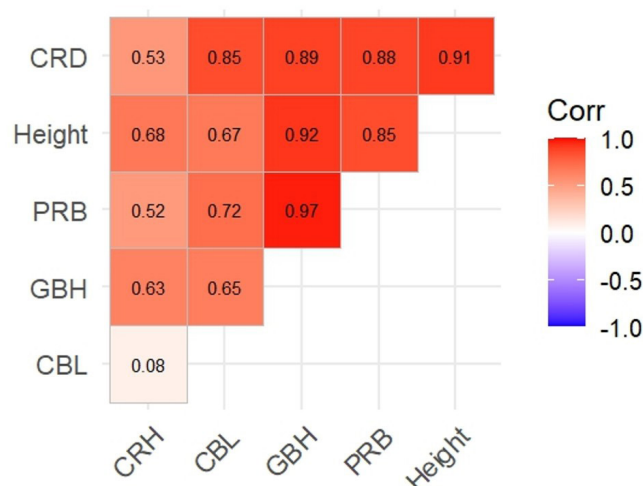


Figure 7

Genetic correlation among studied traits. CBL; Clear bole length, GBH; Girth at breast height, CRD; Crown diameter, CRH; Crown height, PRB; Number of primary branches.

Discussion

The progeny trial had a large number of families evaluated for different traits, of which wood volume, clear bole length, and girth at breast height are economically important traits from the tree growers' perspective. Traits such as the number of primary branches, crown diameter, and canopy height are not economically important but influence the seed-bearing ability and amount of carbon sequestered by trees. The families evaluated in this study also showed variation between them, for growth traits as observed by other workers in Teak populations (Bhat and Priya 2004; Narayanan et al. 2009; Sreekanth et al. 2014; Varghese et al. 2000). Similarly, in other studies on

genetic analysis of different teak progeny trials, significant variations were reported among families for all the quantitative traits studied (Swain et al. 1996; Gogate et al. 1997; Swain et al. 1999).

Higher heritability values were observed for tree girth and tree height in the present study, as previously observed by Narayanan et al. (2009). We observed a significant genetic correlation between tree height and girth as reported by Narayanan et al. (2009). The number of primary branches is an easily measurable trait. It had higher genetic correlation values with growth traits such as tree height, CBH and GBH. However, it could not be used as an aid to selection as it had low heritability values (Table 4). Lower heritability values of branching traits

for forest trees were also observed by Cornelius (1994). Furthermore, greater branching is not a desirable trait for the wood industries. The moderate narrow-sense heritability estimates (ranging from 0.17 for PRB to 0.40 for GBH; Table 4) likely reflect a combination of genetic and environmental influences, including potential dominance and epistatic effects that reduce additive variance, the advanced age of the trial, which may amplify micro-site heterogeneity in soil fertility and competition, and measurement errors inherent to field assessments of crown traits in mature stands (Cornelius, 1994; White et al., 2007). These moderate h^2 values imply reliable but tempered expected genetic gains under selection, with advances of 5–15 % achievable for GBH and height at 10 % intensity, aligning with ranges reported in an earlier teak progeny trial (Narayanan et al., 2009).

The family BLUP values are a measure of the breeding values of the mother tree (White and Hodge 1988). The reliance on open-pollinated families assumes a half-sib structure, which may not fully account for potential full-sib or selfed progeny due to localised pollen flow. This could introduce bias in the estimated coefficient of relationship, potentially inflating or underestimating heritability (h^2) and breeding values. Future studies incorporating genetic markers or pollen flow analysis could refine these estimates, enhancing the accuracy of selection decisions for clonal seed orchards. It was observed that 29 families had positive BLUP values for all studied traits, suggesting that the mother tree contributed favourable alleles/genes in crosses. The mother trees of families with negative BLUP values for all traits contributed alleles/genes towards a reduction in trait value. The roguing out of such families from the progeny trial would lead to genetic improvement in offspring generation. Conversion of progeny trial to a seedling seed orchard is a regular practice in which inferior families are rogued out to achieve genetic gain in offspring (White et al. 2007). The evaluated progeny trial is more than 25 years old now, and seed yield is expected to decline with age (Pardos et al. 2022). The single-site trial at Lohara, while representative of central Indian teak-growing conditions, limits the ability to assess genotype-by-environment (G×E) interactions, which are essential for validating the wide environmental adaptation. The climatic (tropical monsoon, 1,200–1,500 mm rainfall, 20–35°C) and edaphic (loamy to sandy-loam, pH 6.0–7.5) conditions at the site may not fully reflect the variability encountered in other teak regions, such as the drier teak forests of Thailand or the humid coastal areas of Indonesia. Consequently, the superior families identified (e.g., Orissa 79 I C.NO.48, T.S.O.Baitul CSC-24) may exhibit differential performance elsewhere, necessitating multi-site trials to confirm their stability and adaptability. Until such data are available, the results should be applied cautiously to other regions, with consideration for local environmental factors.

Thus, a clonal seed orchard (CSO) can be established through vegetative propagation of elite mother trees identified based on higher family BLUP values. The establishment of CSO with 5 elite mother trees (5 % selection intensity) selected for wood volume i.e. Orissa 79 I C.NO.48 (T-070; 108.02 dm³),

T.S.O.Baitul CSC-24 (T-044; 107.42 dm³), T.S.O.Baitul BBC-2 (T-020; 103.46 dm³), T.S.O.Raipur C.NO.47 (T-072; 103.15 dm³), and T.S.O.Baitul Pt.45 (T-026; 101.94 dm³), is expected to result in genetic gain of 79 cm for height, 52 cm for crown height, and 24 cm for clear bole height over population mean (Table 4). The current study relied on family mean BLUPs to identify elite families, which provides a robust initial selection for CSO establishment. However, the use of family averages rather than individual tree data may overlook within-family genetic variation, potentially affecting the choice of the most superior individuals for cloning. This reliance on family means may upwardly bias heritability estimates by underestimating residual variance through averaging, though the effect is typically modest in balanced designs with few progeny per family (White and Hodge, 1988). Incorporating individual-level genetic evaluations in future studies, possibly through repeated measurements or genetic marker data, could refine the selection process, ensuring the propagation of the highest-performing clones and maximising genetic gains in subsequent generations.

Selection of 10 best mother trees for wood volume is expected to result in genetic gain of 81 cm for height, 48 cm for crown height, and 32 cm for clear bole length over the population mean (Table 4). The genetic advance for economically important traits such as girth and tree height progressively decreases as the proportion of selection increases. The population average in this case is expected to be greater than the mean values in natural forests, as the progenies had been established using plus trees identified from the natural populations. Thus, significant gains can be observed by the establishment of clonal seed orchards using elite mother trees.

While a reduced number of clones can maximise genetic gain, this approach concomitantly elevates the risk of genetic erosion and inbreeding depression, primarily due to the decline in effective population size under intensified selection pressure (Chaloupková et al. 2019) as observed in Table 4. To mitigate such risks, the European Forest Genetic Resources Programme (EUFORGEN) advocates the deployment of 50–100 clones in clonal seed orchards (CSOs) as a means of simultaneously enhancing genetic gain and safeguarding genetic diversity. Conversely, Wu (2019) posited that a smaller cohort of clones (5–30) may be sufficient to secure substantial genetic gain while maintaining acceptable levels of genetic diversity in CSOs. In alignment with these findings, the selection of approximately 20–30 elite trees, prioritized on the basis of predicted family volume, may constitute an optimal strategy for the establishment of CSOs, with projected genetic gains exceeding 23 cm in clear bole length, 51 cm in total height, and 3.18 cm in girth at breast height.

Conclusions

The present study revealed substantial genetic variability among 100 teak families for key growth traits, with BLUPs effectively capturing family breeding values. High heritability

estimates for tree height, girth at breast height, and wood volume highlight strong additive genetic control and offer promising targets for selection in genetic improvement programs. Significant positive correlations among growth traits, particularly between GBH and wood volume, reinforce the potential for indirect selection. Families such as Orissa 79 I C.NO.48 and T.S.O.Baitul CSC-24 consistently showed superior genetic potential across traits. The identification of families with uniformly positive BLUPs suggests they can serve as elite sources for future breeding. Conversely, families with negative BLUPs across traits may be considered for roguing to enhance genetic gain. Establishing a clonal seed orchard using 20–30 elite mother trees is suited to balance genetic gain with long-term diversity. The expected improvement in wood volume and other growth parameters through selective propagation underscores the utility of progeny trials in tree breeding. Overall, this study provides a robust framework for deploying genetic selection and clonal propagation to sustainably enhance productivity and quality in teak plantations.

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Author contributions

Conceptualization: FS; Methodology: FS; Formal analysis and investigation: FS; Writing - original draft preparation: DP; Writing - review and editing: DP, FS; Funding acquisition and Supervision: FS; AM and IAS performed the experiments and collected the data. All authors reviewed, edited, and approved the final manuscript.

Data Availability Statement

The associated raw data and R code have been submitted as a supplementary Excel sheet and supplementary file.