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RESEARCH ARTICLE

Effects of provenance variation on nursery development of *Santalum album* L. in Himachal Pradesh

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Abstract

Provenance variation in *Santalum album L.* arises from both genetic and environmental influences, highlighting the need to identify superior seed sources for enhanced germination and growth. This study evaluated seeds from six sources across three forest divisions in Himachal Pradesh, viz. Changer (S_1), Kosariyan (S_2) and Samoh (S_3) in Bilaspur; Hiranagar (S_4) in Hamirpur and Jwalamukhi (S_5) and Sadwan (S_6) in Kangra. One-way analysis of variance (ANOVA) under a randomized block design (RBD) was applied to analyse seed weight and diameter, while two-way ANOVA (RBD) was used to assess seed germination and seedling growth parameters. Kosariyan (S_2) had the largest seed diameter (6.99 mm) and the highest 100-seed weight (14.58 g). Seeds with the largest sizes generally exhibited higher weights; however, their germination percentage was significantly lower compared to seeds with smaller diameters, except for Kosariyan (S_2). Seeds sown in April 2020 exhibited better germination (68.52 %) than those sown in May (47.61 %). Kosariyan (S_2) achieved the highest germination percentage (66.68 %) and energy (34.42 %). *In vitro* germination on Murashige and Skoog (MS) medium was higher compared to autoclaved sand. Sadwan (S_5) excelled in seedling growth, with half-sib seedlings achieving the maximum seedling height (21.62 cm), collar diameter (3.2 mm), leaf length (6.32 cm) and leaf width (2.3 cm) at one year of age. Seedling height demonstrated high heritability and genetic gain, making it a valuable trait for selection. The findings highlight significant provenance variation, with Kosariyan (S_2) and Jwalamukhi (S_5) emerging as superior for germination and growth performance respectively. These findings underscore the need to identify and utilize optimal seed sources to promote sustainable and productive cultivation of *S. album.*

Keywords: growth parameter; provenance variations; *Santalum album* L.; seed sources

Introduction

Santalum album L., commonly known as sandalwood, is a small yet highly valuable evergreen tree of the Santalaceae family. Renowned for its aromatic heartwood and essential oil, sandalwood carries deep cultural, medicinal and economic significance in India, where it has been traditionally harvested for centuries by diverse industries, including perfumery and pharmaceuticals (1). The species thrives under specific climatic and ecological conditions and is distributed across approximately 9600 km^2 of India, predominantly in the deciduous forests of the Deccan region, with Karnataka and Tamil Nadu being its principal natural habitats (2, 3). In Himachal Pradesh, *S. album* occurs sporadically in the mid-hill regions, particularly in the districts of Bilaspur, Hamirpur and Kangra (5). These areas present varied soil and climatic conditions, reflecting the species' adaptability across a range of ecological niches. Typically, *S. album* thrives in regions with annual rainfall ranging from 600—1600 mm and at elevations where temperatures are moderate. This moderate-sized tree can attain heights of 12–15 m and girths ranging from 1–2.4 m (4). The species undergoes two flowering and fruiting cycles annually, the principal one occurring between September and December, when seed production reaches its maximum (5). However, the altitudinal gradient significantly influences the phenology, as trees at lower elevations flower earlier than those at higher altitudes (6). Despite its ecological and economic importance, *S. album* is classified as a vulnerable species, largely due to illegal felling driven by high international demand for its heartwood and oil. Additionally, other threats include habitat degradation, climate change and insufficient conservation efforts. The species' natural regeneration is further constrained by morphophysiological dormancy, attributed to its hard seed coat, which delays germination (7). Artificial methods, including pre-sowing treatments are therefore critical for breaking dormancy and enhancing germination rates (8, 9).

Large-scale cultivation and conservation of *S. album* depend upon seed propagation. Although tissue culture and vegetative propagation provide alternatives, they are often resource-intensive and impractical for widespread application (10). Seed-based propagation represents an efficient and low-cost strategy; well-managed nursery practices play a pivotal role in securing the successful establishment of healthy seedlings (11). Various intrinsic and extrinsic factors including seed size, genetic quality and environmental conditions at the source are the main foundations of the germination potential of *S. album*. The concept of a seed source, referring to the geographical origin of seeds or propagules, is pivotal in determining seed traits and subsequent seedling performance (12). Additionally, seed quality including germination rates, vigour and seedling growth potential is significantly influenced by environmental factors. These factors, coupled with genetic variability among populations, make the selection of seed sources an essential component of tree improvement programs (13). Provenance variation in seed traits and seedling performance is particularly relevant for tree species like *S. album*, which are distributed across diverse ecological zones. These variations can profoundly affect nursery practices, including seed germination and seedling establishment. Despite the widespread distribution of *S. album* in India, research on the genetic and environmental factors affecting its seed quality remains limited. Few provenance trials have been conducted to assess the influence of seed source on germination and growth, leaving critical gaps in understanding the interplay between genetic potential and environmental adaptation. Given the species' extensive ecological range, it is reasonable to hypothesize that significant genetic and environmental variations exist among different seed sources of *S. album.* Such variations can influence traits like seed size, germination percentage, seedling vigor and growth patterns, making it imperative to identify superior seed sources for sustainable cultivation. Moreover, the interaction between genetic potential and environmental conditions can guide breeding programs and forest regeneration efforts, particularly in regions where the species is not naturally abundant (25, 27, 34).

The present study aims to address these research gaps by evaluating the effects of seed source and seed size on the nursery performance of *S. album* in the mid-hill zone of Himachal Pradesh. This region presents unique environmental conditions, offering an opportunity to study how geographical variations impact germination and seedling growth. By conducting seed source trials, this research seeks to identify superior seed sources with desirable traits for enhanced propagation and conservation. Furthermore, the findings will contribute to the broader goals of genetic resource management, sustainable forest regeneration and tree improvement programs for *S. album*. Understanding how seed source and seed size influence germination and growth will provide valuable insights for nursery management and breeding strategies. Ultimately, these efforts will support the sustainable cultivation and conservation of this economically and ecologically critical species.

Materials and Methods

The study area

The study was conducted in three forest divisions of the Himachal Pradesh State Forest Department, India. Three seed sources were selected from Bilaspur forest division viz., Changer (S_1), Kosariyan (S_2) and Samoh (S_3) of Bilaspur district; one from Hamirpur Forest Division, i.e, Hiranagar (S_4) of Hamirpur district and two from the Dehra Forest Divisions, viz., Jwalamukhi (S_5) and Sadwan (S_6) of Kangra district (Fig. 1). Fifteen phenotypically superior mother trees were selected from each seed source through systematic random

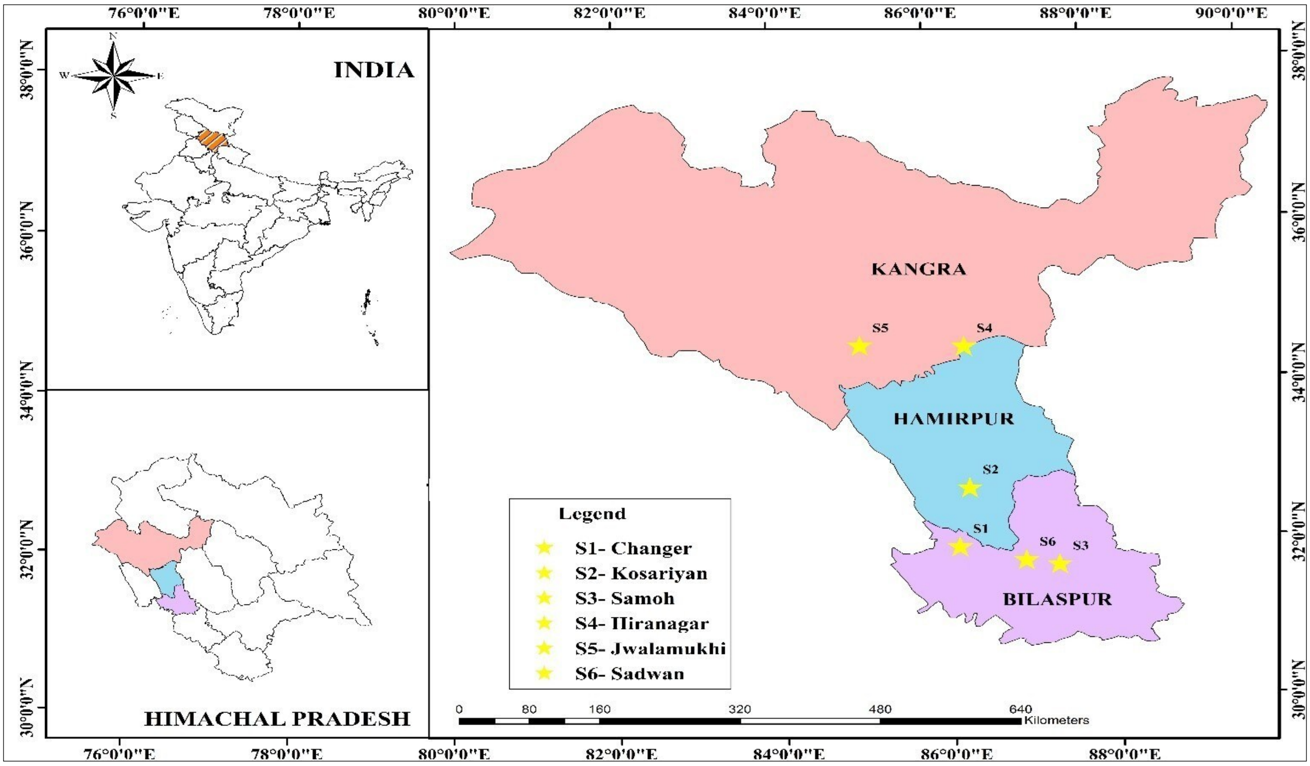

Fig. 1. Location of seed sources (Source: ArcGIS).

selection during December 2019–January 2020. These seeds were then used to record seed characteristics, seed germination and growth parameters by raising in the nursery.

Climate

The experiment was carried out in a glasshouse (controlled environmental conditions, Table 1) of the Department of Tree Improvement and Genetic Resources, College of Forestry, Dr Yashwant Singh Parmar University of Horticulture and Forestry, Nauni, Solan, Himachal Pradesh from April 2020 to May 2021 located between 30° 51' 44.74'' N latitude and 77° 10' 9.15'' E longitude, at 1200 m above mean sea level (Fig. 2). The Nauni falls under a subtropical to sub-temperate climate with an average annual rainfall of about 1000–1100 mm.

Table 1. Controlled glasshouse conditions for *S. album* L. seedlings during the study period

Parameters	Controlled conditions
Temperature (day)	25– 30 °C
Temperature (night)	15–18 °C
Humidity	70–80 %
Watering	Kept soil moist but not waterlogged
Air circulation	Good ventilation with roof vents, side vents and fans for air circulation
Protection from pests	Regular inspection and integrated pest management (IPM)
Disease management	Avoid overwatering, ensure good drainage and proper ventilation to prevent mold

The collected seeds from each seed source were sown in the polybags (5'' × 7'') during April and May 2020 in three replications under glasshouse conditions and germination was recorded and expressed as percentage germination (14). *In vitro* germination was recorded during the last week of March 2021. Seeds were pre-treated with 4 mM gibberellic acid for 12 hr. After pre-sowing treatments, all treated seeds were washed with Teepole under running water and treated with 2 % bavistin before being washed with autoclave-distilled water 2–3 times, then cultured on Murashige and Skoog basal medium (MS media) (S_1) and autoclaved sand (S_2). Table 2 presents the composition of the modified MS medium. Seeds cultured in autoclaved sand were placed in the germinator for 30 days with a temperature of 25 °C and humidity of 75–85 % (15). The time required for seed germination under *in vitro* conditions along with the germination percentage was determined by calculating the proportion of germinated seeds to the total number of seeds in the sample and expressing this value as a percentage.

Seed studies

Fruits collected from different seed sources were depulped, cleaned and dried. Variations in colours of fresh seeds were determined by matching them with the colour chart of the Royal Horticultural Society, London (16). Six seed sources representing three forest divisions of Himachal Pradesh, along with various factors, were studied. The weight of 100 seeds from each seed source was measured using an electronic balance, following the guidelines of the International Seed Testing Association (ISTA) (17). Twenty seeds were selected randomly per replication from each seed source and

Table 2. Composition of modified MS medium

Constituents	g/L
Inorganic constituents	
STOCK I {Major constituents (50 mL/L)}	
NH_4NO_3	33.00
KNO_3	38.00
$CaCl_2.2H_2O$	8.86
$MgSO_4.7H_2O$	7.40
KH_2PO_4	3.40
STOCK II {Minor constituents (1 mL/L)}	
H_3BO_3	6.20
$MnSO_4.4H_2O$	22.30
$ZnSO_4.7H_2O$	8.65
KI	0.80
$Na_2MoO_4.2H_2O$	0.25
$CuSO_4.5H_2O$	0.025
$CoCl_2.6H_2O$	0.025
STOCK III (5 mL/L)	
Na_2EDTA	7.46
$FeSO_4.7H2O$	5.56
STOCK IV {Organic constituents (5 mL/L)}	
Pyridoxine	0.020
Glycine	0.080
Thiamine	0.040
Nicotinic acid	0.020

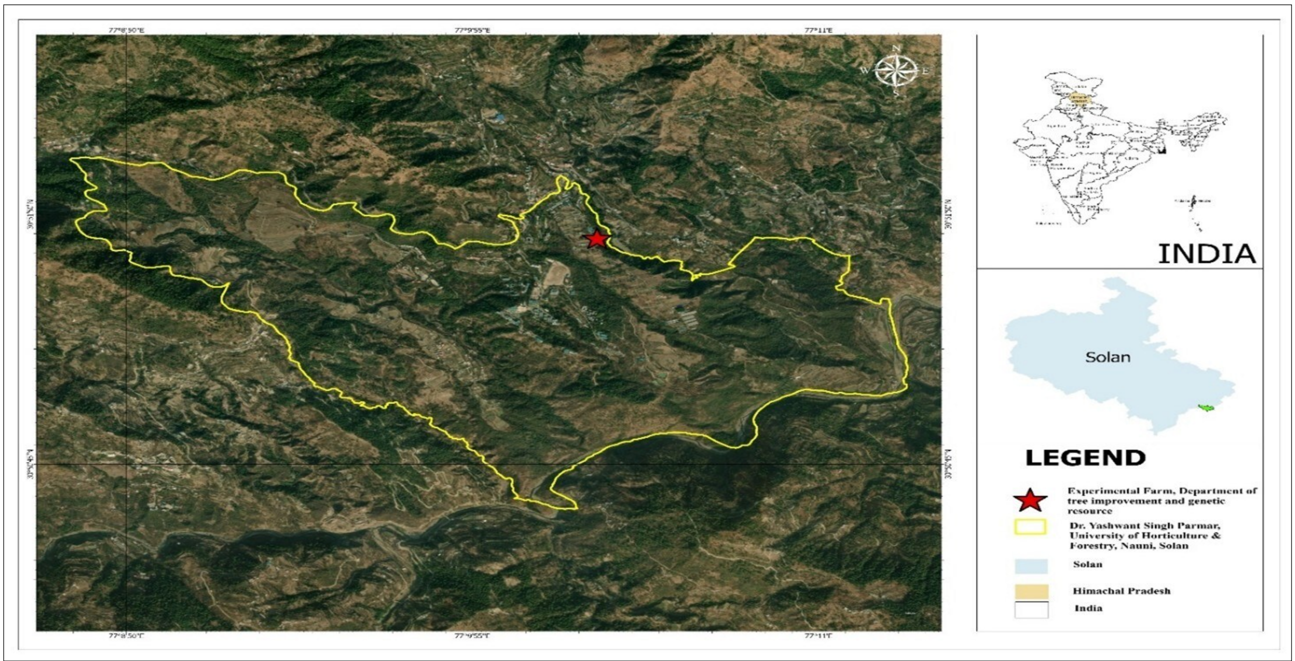

Fig. 2. Map of experimental area (Source: ArcGIS).

seed diameter was measured in mm using a digital Vernier caliper (Mitutoyo Corporation, Japan).

Growth performance

Seeds were treated with gibberellic acid (GA_3) at 500 ppm and were sown with appropriate tags containing codes assigned to their respective sources across two sowing dates: the first sowing was labelled as d_1(20–04–2020) and the second sowing as d_2(20–05–2020) in polybags maintained under glasshouse conditions. Various growth parameters of seedlings were measured at 3, 6, 9 months and at one year of age. Seedling height was determined by measuring the distance from the collar region to the tip of the main shoot using a ruler. The collar diameter was measured using a digital Vernier Calliper. Five leaves were selected randomly in three replications for measuring leaf length and leaf width with the help of a scale. Leaf length was recorded from the apex tip to the base, while leaf width was measured at the widest part of the leaf.

Genetic parameters

The genetic estimate is a useful technique for analysing data collected from mother trees of different genotypes and half-sib progenies. Phenotypic parameters of mother trees are also included with seed germination and nursery growth parameters for the estimation of different genetic parameters, including Genotypic coefficient of variation (GCV) percentage, Phenotypic coefficient of variation (PCV) percentage, repeatability coefficient, genetic advance and genetic gain. Phenotypic parameters of the mother tree included tree height, clear bole height and crown spread. The total height of a tree is measured as the straight-line distance from the tip of the leading shoot to the ground, whereas clear bole height is measured from ground level to the first branch of the tree. Both heights were measured using a multimeter (Ravi's Multimeter, India). The crown spread was assessed in two directions: north–south and east–west. The measurement involved using a plumb bob, a perpendicular staff and a measuring tape. The staff was aligned on the ground directly beneath the tip of the outermost branch with the help of the plumb bob. A measuring tape was then used to measure the distance between the outermost branches in the specified direction. This process was first carried out along the north–south direction and then repeated for the east–west direction. The major genetic parameters in any tree improvement work are heritability, genetic gain and genetic progress. The genotypic, phenotypic and environmental variance were calculated as follows:

$$Vp = Vg + Ve$$

where,

Vp = phenotypic variance

Vg = genotypic variance

Ve = environmental variance.

Coefficients of variability were calculated using the following formulae (18):

$$\text{PCV}(\%) = \frac{\sqrt{Vp}}{\bar{X}} \times 100$$

$$\text{GCV}(\%) = \frac{\sqrt{Vg}}{\bar{X}} \times 100$$

Where,

PCV (%) = phenotypic coefficient of variability

GCV (%) = genotypic coefficient of variability

Vp = phenotypic variance

Vg = genotypic variance

$\bar{X}$ = population mean

The repeatability coefficient represents the upper limit of the association between genetic and phenotypic variance (19). It also indicates how much of the total variation arises from differences within a population, as well as the extent to which variation among individual trees contributes to the overall population diversity.

$$\text{Mother tree repeatability coefficients } (\sigma_m^2) = \frac{\sigma_m^2}{\sigma_m^2 + \sigma_{w(m)}^2}$$

Where,

σ_m^2 = Mother tree variance

$\sigma_{w(m)}^2$ = within mother tree variance

Heritability in percentage was calculated by the formulae

$$h = \frac{Vg}{Vp}$$

Where,

h = heritability (broad sense)

Vp = phenotypic variance

Vg = genotypic variance

The anticipated genetic advance at a 5 % selection intensity was estimated using the following formula (21)

$$\text{Genetic advance} = \frac{Vg}{Vp} \times \sqrt{Vp} \times k$$

Where,

Vg = genotypic variance

Vp = phenotypic variance

k = Selection differential at 5 % selection intensity. The value of k = 2.06 (22)

The genetic gain was calculated by expressing the genetic advance as a percentage of the population mean (20).

$$\text{Genetic gain}(\%) = \frac{\text{Genetic advance}}{\bar{X}} \times 100$$

Where,

$\bar{X}$ = population mean

Statistical analysis

Morphological, germination and seedling growth parameters were analysed to assess variation among seed sources using ANOVA in R Studio (23). One-way ANOVA was applied to analyze seed weight and diameter, while two-way ANOVA was used to assess seed germination and seedling growth parameters. Additionally, a principal component analysis (PCA) biplot was generated using R Studio (23).

Results and Discussion

Seed characteristics

The seed sources of *S. album* L. exhibited a noticeable variation in the morphological traits of the seeds. Seed colour is an important factor influencing both seed quality and its growth potential. Seeds collected from Changer (S_1) matched to dark brown group (200C), Kosariyan (S_2) and Samoh (S_3) matched to brown group (200D), whereas the remaining seed sources, viz., Hiranagar (S_4), Jwalamukhi (S_5) and Sadwan (S_6) were matched to grey/light-brown group (N199D, N199C and N199C) (Fig. 3). Seeds matched with the brown group category demonstrated superior germination potential (grown in polybags) compared to those in the grey-brown category. This might be due to dark-colour seeds (brown group category) absorbing light and heat, which can potentially increase soil temperature around the seed, promoting faster germination as compared to light-coloured seeds (grey brown category). The findings of the present study are supported by previous reports, which also indicate that bright-coloured seeds exhibit greater vigour and higher seed quality than seeds of other colours (24). Significant differences in seed traits such as 100-seed weight and seed diameter were observed across various seed sources (Fig. 4A, B). Kosariyan recorded the highest seed weight (14.58 g), which was statistically comparable to Hiranagar (14.32 g) and Changer (14.14 g). In contrast, Jwalamukhi recorded the lowest seed weight at 10.56 g. The maximum seed diameter was observed in Kosariyan (S_2), with a mean value of 6.99 mm, which was statistically similar to that of Hiranagar (6.77 mm) and Changer (6.70 mm). Conversely, Jwalamukhi (S_5) exhibited the smallest seed diameter (6.32 mm). The variation observed in morpho-physiological characteristics of seeds of *S. album* collected from various seed sources may be attributed to genetic variation, reflecting adaptation to diverse environmental conditions prevailing throughout their distributional ranges (5, 13, 25). The bigger seed size and seed weight recorded from Kosariyan (S_2) revealed that the seed sources that had greater seed diameter (mm) resulted in maximum seed weights as well as higher seed germination percentages. This might be due to large reserves of nutritional matter present in seeds among various seed sources. Differences in seed mass among various seed sources may be influenced by environmental factors that vary across locations (26, 27). Similar results were reported by various researchers who found that the larger seeds with more seed weight promote greater seedling establishment because of higher nutritional reserves that offer an edge during selection and enable optimal germination percentage and seedling growth (28, 29). However, it was observed that for seed sources except Kosariyan (S_2), the seeds with bigger sizes do have the highest weight, but the germination percentage was significantly lower compared to the seeds with smaller diameters. This might be due to longer seed viability and fruit maturity period, thicker seed coats of larger seeds and moisture conditions of soils. These results indicate that an extended maturity period could potentially enhance the resource assimilation period, thereby facilitating lower germination in larger seeds relative to smaller ones (30, 31).

Seed germination parameters

Significant variations in germination percentage and germination energy were observed, influenced by both the seed source and the sowing dates. Among the various seed sources, S_2 showed the highest germination rate (79.23 %), while S_5 recorded the lowest at 40.58 %. Moreover, the highest germination energy was recorded for S_2 (34.42 %), followed by S_1 (28.26 %), whereas the minimum germination energy was recorded for S_4 (19.25 %). Among the two sowing dates, seeds sown during April exhibited higher germination percentage (68.52 %) and germination energy (35.00 %) in contrast to the seeds sown during May, which had a lower germination percentage of 47.61 % and germination energy of 14.11 % (Fig. 4C, D). The date of sowing significantly affects the germination percentage as well as germination energy. The seeds sown in April (35 %) exhibited significantly higher germination energy as compared to the seeds sown during May (14.11 %), which reflects the vigor of both the seed and the resulting seedling.

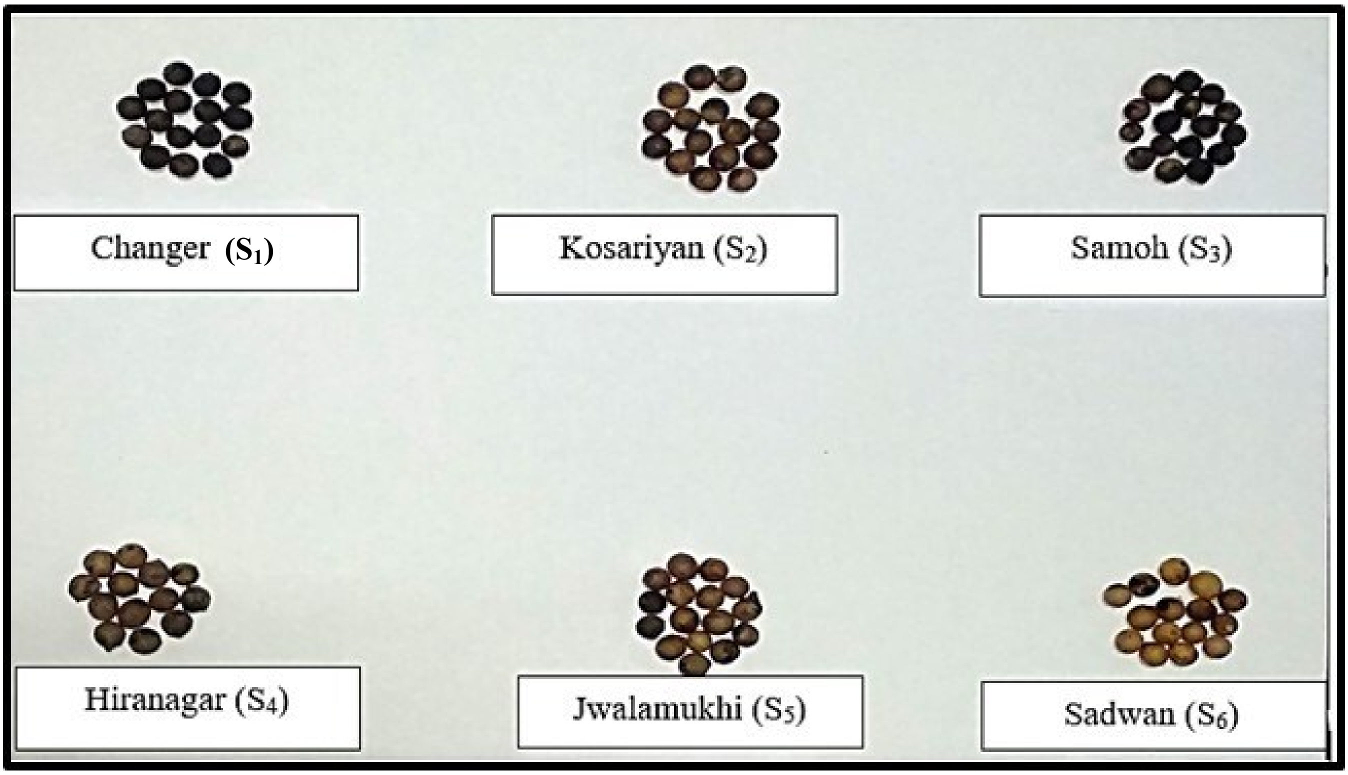

Fig. 3. Seed variation among different seed sources.

In vitro germination

In the present study, the longest germination time (19.55 days) was observed for S_6, followed by S_5 (18.92 days) and S_1 (18.75 days), whereas the shortest germination time (12.83 days) was observed for S_3 (Fig. 4E, F). Furthermore, a marked difference was noted among different seed sources and sowing dates for *in vitro* germination percentage. S_1 exhibited the highest germination percentage (77.77 %) followed by S_5 (66.66 %). In contrast, S_2 showed the lowest germination percentage at 38.49 %. Between the sowing media, seeds cultured on MS media had a higher germination percentage (66.21 %) as compared to seeds cultured in autoclaved sand (40.39 %). MS media provides optimal nutrients and a controlled environment, resulting in higher germination rates. Our findings on *in vitro* germination are consistent with previous studies, which reported higher germination parameters on MS medium (15, 32).

Nursery growth performance

Seeds from six distinct sources were sown in polybags under glasshouse conditions during April and May of 2020. To evaluate differences among seed sources and sowing dates, nursery growth traits such as seedling height, collar diameter, leaf length and leaf width were recorded at intervals of three, six, nine and twelve months (Fig 5). There were no significant differences recorded among seed sources, sowing dates and the interaction between seed sources and sowing dates within 3 months of seedlings. A significant difference was recorded between sowing dates, whereas there was no significant difference recorded between seed sources and seed sources × sowing dates interaction within 6 months of seedlings. Maximum seedling height was recorded during April sowing (13.85 cm) as compared to the May sowing (10.90 cm). At 9 months of growth, notable differences were observed among the

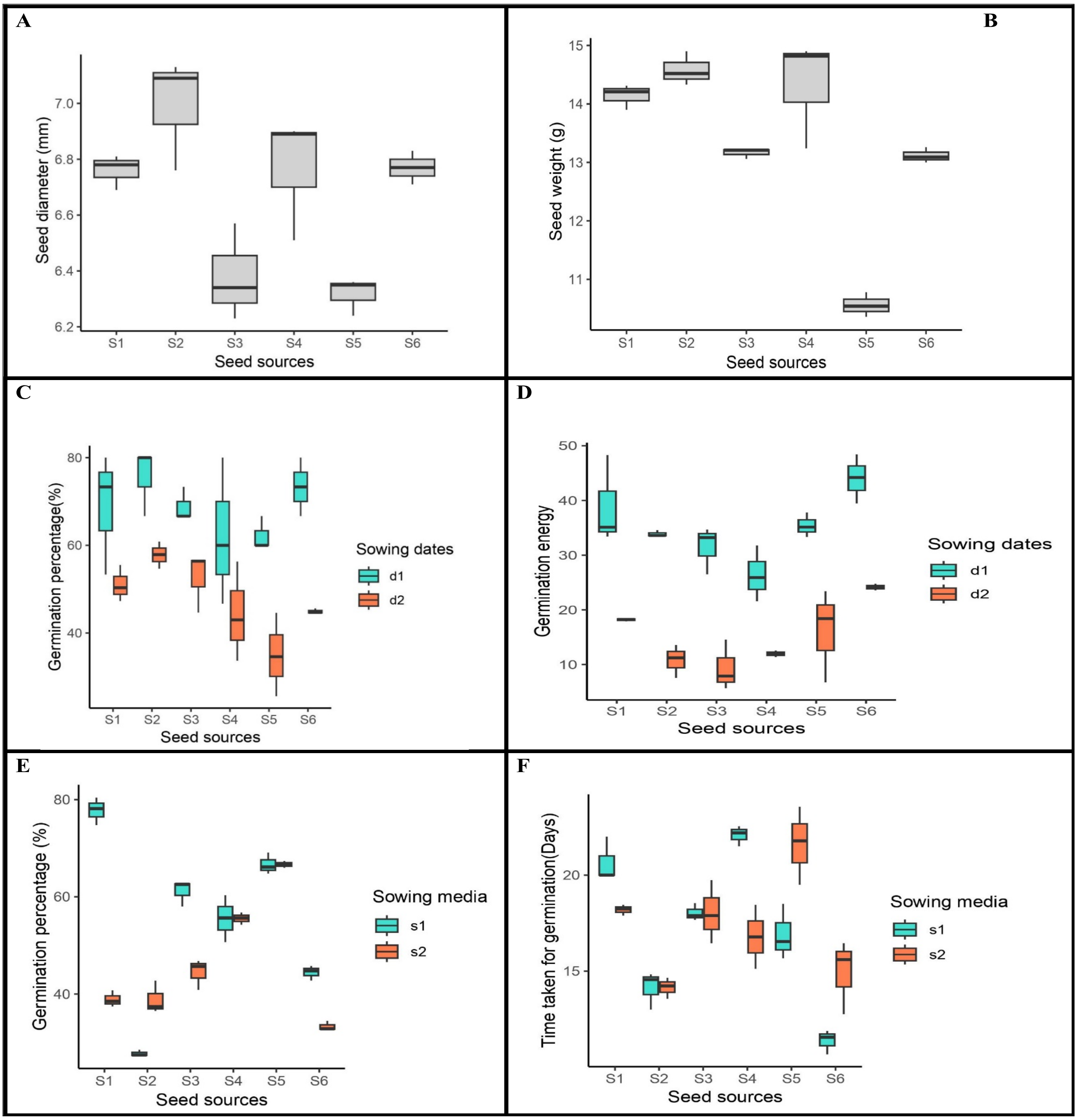

Fig. 4: Seed parameters A: Seed diameter (mm), B: Seed weight (g); Germination parameters (Field): C: Germination percentage (%), D: Germination energy; Germination parameters (*In vitro*) E: Germination percentage (%), F: Time taken for germination.

S_1: Changer S_2: Kosariyan, S_3: Samoh, S_4: Hiranagar, S_5: Jwalamukhi and S_6: Sadwan; d_1: First date of sowing, d_2: Second date of sowing; s_1: MS media, s_2: Autoclaved sand.

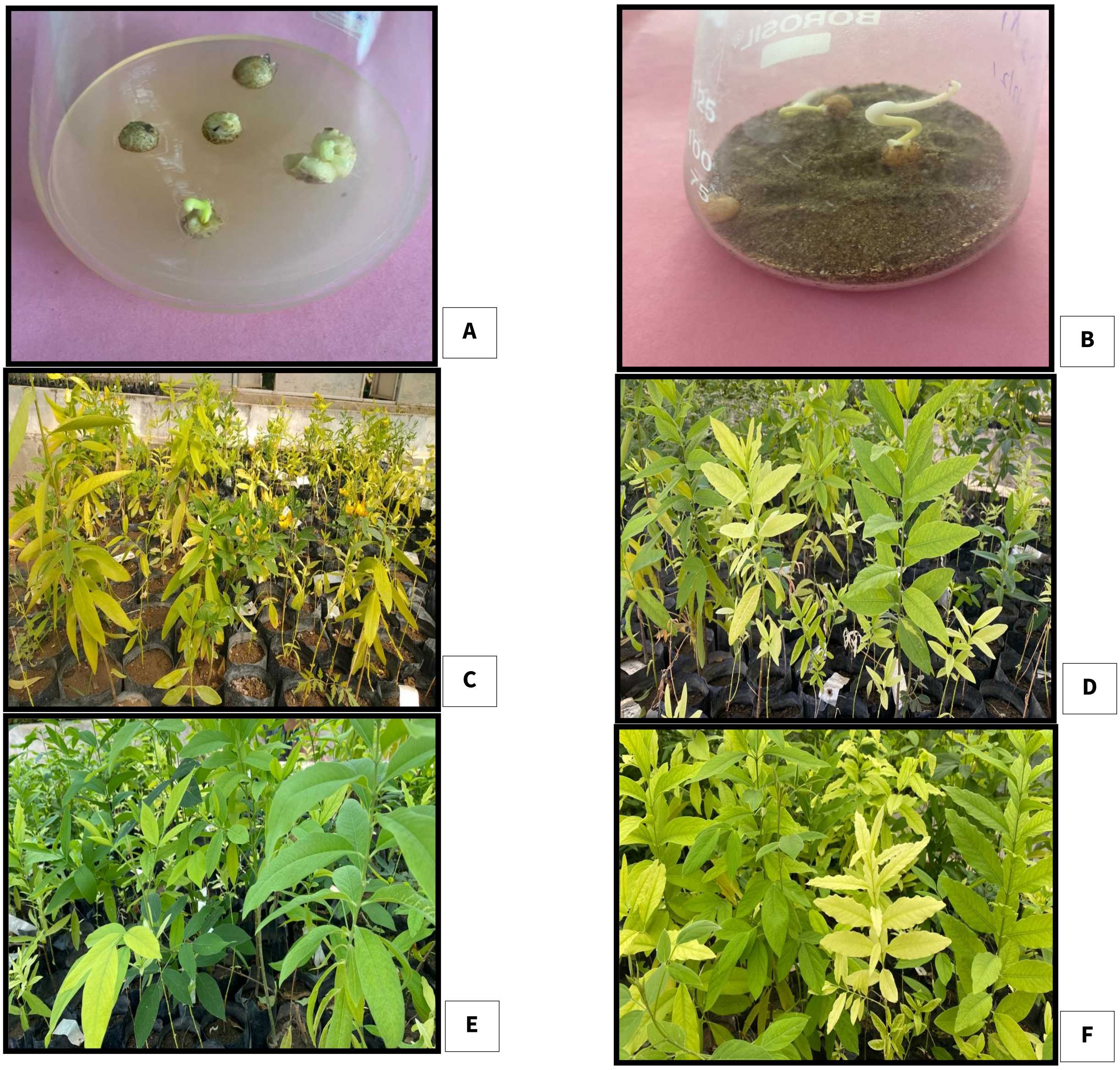

Fig. 5. *In vitro* germination of seeds (A: MS media, B: Autoclaved sand), Seedling growth (IC: 3 months, D: 6 months, E: 9 months, F: one year)

seed sources and sowing dates. The average seedling height was highest in S_5 (16.04 cm), followed by S_3 (15.15 cm) and S_1 (14.93 cm). In contrast, S_4 recorded the shortest seedlings with a mean height of 13.71 cm, closely followed by S_2 (13.79 cm) and S_6 (13.82 cm). Regarding sowing dates, seedlings of April had maximum height (16.27 cm) compared to seedlings of May (12.88 cm). In the seed source × sowing date interaction, no significant difference was recorded. In one year of seedling, significant differences were observed among seed sources, sowing dates and their interactions. Mean values across seed sources showed that S_5 exhibited the highest seedling height at 21.62 cm, followed by S_3 and S_1 with values of 18.05 cm and 17.53 cm respectively, whereas S_4 showed the minimum seedling height with a mean value of 16.68 cm. Seedlings sown in April attained greater height (18.85 cm) compared to those sown in May (17.28 cm). In the interaction between seed source and sowing date, the tallest seedlings were observed in S_5d_2 with an average height of 24.73 cm, while the shortest were recorded in S_4d_2, averaging 14.96 cm (Table 3).

Collar diameter (mm)

There were significant differences recorded between seed sources, sowing dates and the interaction between seed sources and sowing dates. After three months, S_3 recorded the highest collar diameter (1.51 mm), which was statistically similar to S_2 (1.47 mm) and S_6 (1.44 mm). In contrast, S_1 showed the lowest collar diameter at 1.18 mm. Seedlings raised in April recorded a greater collar diameter (1.51 mm) compared to those raised in May (1.26 mm). In the interaction between seed source and sowing date, the highest collar diameter was observed in S_2d_1 (1.71 mm), while the lowest was recorded in S_1d_2 (0.97 mm). At six months, seed sources and their interaction with sowing dates did not show any significant differences; however, a significant variation was noted between the two sowing dates. More collar diameter was recorded in April month seedlings (2.05 mm) as compared to May month seedlings(1.33 mm). At 9 months, S_1 had a maximum collar diameter of 2.55 mm and was statistically at par with S_5 (2.42 mm), whereas S_6 had a minimum collar diameter (1.92 mm). Among the two sowing dates, the maximum collar diameter was observed in the April month seedling (2.59 mm) as compared to the May month (1.88 mm). In the seed source × sowing date interaction, maximum collar diameter was recorded for S_3d_1 with a mean value of 2.76 mm and minimum was recorded for S_4d_2 with a mean value of 1.46 mm. At one year, mean values among seed sources revealed that S_5 had a maximum collar diameter of 3.20 mm and was statistically at par with S_1 (3.11 mm). S_4 had a minimum collar diameter with a mean value of 2.70 mm. Among the two sowing dates, more collar diameter was found in seedlings of April (3.21 mm) as compared to seedlings of May (2.72 mm) (Table 4).

Table 3. Seedling height (cm) of *S. album* L. seedlings at different age intervals

	Age of seedling (months)											
	Three months			Six months			Nine months			One year		
	d_1	d_2	Mean	d_1	d_2	Mean	d_1	d_2	Mean	d_1	d_2	Mean
S_1	10.00 ± 0.50	9.01 ± 0.30	9.51	13.03 ± 0.57	11.81 ± 0.48	12.42	15.83 ± 0.38	14.03 ± 0.92	14.93	18.22 ± 0.46	16.83 ± 1.19	17.53
S_2	10.47 ± 0.59	8.48 ± 0.34	9.47	14.13 ± 0.44	10.38 ± 0.12	12.26	15.46 ± 0.16	12.13 ± 0.56	13.79	18.63 ± 0.36	15.57 ± 1.41	17.10
S_3	9.75 ± 0.51	11.32 ± 1.45	10.5	14.29 ± 0.32	11.73 ± 1.09	13.01	17.36 ± 1.41	12.93 ± 0.70	15.15	20.12 ± 1.89	15.98 ± 1.26	18.05
S_4	9.89 ± 0.66	9.06 ± 0.14	9.49	13.96 ± 1.32	9.89 ± 1.38	11.93	16.17 ± 1.80	11.24 ± 0.80	13.71	18.41 ± 2.13	14.96 ± 0.66	16.68
S_5	9.88 ± 1.25	9.70 ± 0.40	9.79	13.95 ± 1.24	11.19 ± 0.38	12.57	16.85 ± 0.53	15.22 ± 0.12	16.04	18.51 ± 0.11	24.73 ± 0.65	21.62
S_6	10.66 ± 0.80	8.56 ± 0.76	9.61	13.77 ± 0.65	10.36 ± 0.08	12.07	15.93 ± 0.41	11.72 ± 0.25	13.82	19.20 ± 0.53	15.59 ± 0.28	17.40
Mean	10.11	9.35		13.85	10.90		16.27	12.88		18.85	17.28	
$CD_{0.05}$												
S		2.28			NS			NS			1.70	
d		1.32			NS			0.96			0.98	
S × d		3.23			NS			NS			NS	

Mean value ± standard error (SE); S: Seed sources; S_1: Changer; S_2: Kosariyan; S_3: Samoh; S_4: Hiranagar; S_5: Jwalamukhi; S_6: Sadwan; d: Date of sowing; d_1: First date of sowing; d_2: Second date of sowing; NS: Not significant.

Table 4. Collar diameter (mm) of *S. album L.* seedlings at different age intervals

Seed sources	Age of seedling (Months)											
	Three months			Six months			Nine months			One year		
	d_1	d_2	Mean	d_1	d_2	Mean	d_1	d_2	Mean	d_1	d_2	Mean
S_1	1.40 ± 0.12	0.97 ± 0.05	1.18	2.07 ± 0.05	1.15 ± 0.01	1.61	2.69 ± 0.15	2.41 ± 0.21	2.55	3.33 ± 0.13	3.08 ± 0.33	3.11
S_2	1.71 ± 0.04	1.23 ± 0.05	1.47	2.19 ± 0.02	2.53 ± 1.49	2.36	2.75 ± 0.14	1.56 ± 0.16	2.16	3.18 ± 0.06	2.49 ± 0.18	2.84
S_3	1.70 ± 0.08	1.32 ± 0.09	1.51	2.39 ± 0.16	1.16 ± 0.03	1.77	2.76 ± 0.24	1.52 ± 0.08	2.14	3.33 ± 0.11	2.69 ± 0.23	3.01
S_4	1.54 ± 0.03	1.22 ± 0.12	1.38	2.07 ± 0.14	0.86 ± 0.05	1.46	2.37 ± 0.17	1.46 ± 0.13	1.92	2.87 ± 0.16	2.53 ± 0.09	2.70
S_5	1.35 ± 0.07	1.29 ± 0.04	1.32	1.72 ± 0.09	1.14 ± 0.03	1.43	2.59 ± 0.09	2.24 ± 0.01	2.42	3.36 ± 0.05	2.85 ± 0.06	3.20
S_6	1.35 ± 0.08	1.53 ± 0.16	1.44	1.83 ± 0.08	1.13 ± 0.04	1.48	2.38 ± 0.11	2.08 ± 0.07	2.23	3.19 ± 0.11	2.70 ± 0.11	2.95
Mean	1.51	1.26		2.05	1.33		2.59	1.88		3.21	2.72	
$CD_{0.05}$												
S		0.18			NS			0.30			0.32	
d		0.10			0.52			0.17			0.19	
S × d		0.25			NS			0.42			NS	

Mean value ± standard error (SE); S: Seed sources; S_1: Changer; S_2: Kosariyan; S_3: Samoh; S_4: Hiranagar; S_5: Jwalamukhi; S_6: Sadwan; d: Date of sowing; d_1: First date of sowing; d_2: Second date of sowing; NS: Not Significant.

Leaf length (cm)

As shown in Table 5, no significant differences in leaf length were observed at 3 months among seed sources or their interaction with sowing dates. However, a significant effect of sowing date was noted, with seedlings sown in May exhibiting greater leaf length (5.65 cm) compared to those sown in April (5.10 cm). At 6 months, leaf length showed no significant variation across seed sources, sowing dates or their interactions. By 9 months, significant differences were recorded among seed sources, sowing dates and their interactions. The maximum leaf length was observed in seed source S_6 (5.83 cm), followed by S_3 (5.77 cm) and S_5 (5.50 cm), while the minimum was recorded in S_2 (5.04 cm), followed by S_4(5.51 cm) and S_1 (5.31 cm). Seedlings from the May sowing continued to exhibit maximum leaf length (5.61 cm) compared to April (5.39 cm). In the interaction between seed source and sowing date, the maximum leaf length was found in S_6d_2(6.28 cm) and the lowest in S_2d_2(4.96 cm). At one year, significant differences were recorded among seed sources, with S_5(6.25 cm) showing the maximum leaf length, followed closely by S_6(6.13 cm) and S_4 (6.06 cm). The lowest values were noted in S_2 (5.63 cm), S_3 (5.70 cm) and S_1 (5.75 cm). No significant difference was observed between sowing dates, though the interaction effect revealed maximum leaf length in S_5d_1 (6.41 cm) and minimum in S_1d_1 (5.18 cm).

Table 5. Leaf length (cm) of *S. album* seedlings at different age intervals

Seed sources	Age of seedling (months)											
	Three months			Six months			Nine months			One year		
	d_1	d_2	Mean	d_1	d_2	Mean	d_1	d_2	Mean	d_1	d_2	Mean
S_1	4.66 ± 0.15	5.23 ± 0.23	4.94	5.37 ± 0.14	5.51 ± 0.11	5.44	5.12 ± 0.23	5.51 ± 0.27	5.31	5.18 ± 0.12	6.32 ± 0.25	5.75
S_2	5.15 ± 0.14	5.73 ± 0.17	5.44	5.68 ± 0.05	5.11 ± 0.38	5.39	5.13 ± 0.12	4.96 ± 0.28	5.04	5.56 ± 0.03	5.71 ± 0.23	5.63
S_3	5.25 ± 0.30	6.65 ± 0.45	5.95	5.54 ± 0.15	5.52 ± 0.19	5.53	5.53 ± 0.10	6.00 ± 0.02	5.77	5.43 ± 0.12	5.96 ± 0.50	5.70
S_4	4.92 ± 0.23	5.78 ± 0.57	5.35	5.67 ± 0.12	5.32 ± 0.21	5.49	5.60 ± 0.05	5.43 ± 0.30	5.51	6.14 ± 0.20	5.99 ± 0.14	6.06
S_5	5.50 ± 0.20	5.63 ± 0.72	5.56	5.51 ± 0.21	5.41 ± 0.14	5.46	5.56 ± 0.15	5.45 ± 0.13	5.50	6.41 ± 0.14	6.09 ± 0.08	6.25
S_6	5.16 ± 0.24	4.90 ± 0.36	5.03	5.26 ± 0.21	5.40 ± 0.02	5.33	5.39 ± 0.05	6.28 ± 0.17	5.83	6.33 ± 0.17	5.92 ± 0.23	6.13
Mean	5.10	5.65		5.50	5.38		5.39	5.61		5.84	6.00	
$CD_{0.05}$												
S		0.44			NS			NS			0.37	
d		NS			0.43			NS			0.22	
S × d		0.63			NS			NS			0.53	

Mean value ± standard error (SE); S: Seed sources; S_1: Changer; S_2: Kosariyan; S_3: Samoh; S_4: Hiranagar;,S_5: Jwalamukhi; S_6: Sadwan; d: Date of sowing; d_1: First date of sowing; d_2: Second date of sowing; NS: Not Significant.

Leaf width (cm)

At 3- and 6-month-old seedlings, no significant variations were recorded in leaf width, but at 9 months, there were significant variations in leaf length among seed sources, sowing dates and their interaction. Maximum leaf width was recorded for S_5 (1.61 cm) and minimum was recorded for S_3 (1.26 cm) among seed sources. Seedlings of May month showed more Leaf width (1.43 cm) as compared to seedlings of April month (1.32 cm). In the source × sowing date interaction, maximum leaf width was recorded in S_1d_1 (1.24 cm) and minimum was recorded for S_5d_2(1.89 cm). At one year, no significant differences were observed among seed sources or in their interaction with sowing dates. However, seedlings sown in May exhibited greater leaf width (2.28 cm) compared to those planted in April (1.96 cm) (Table 6). A significant variation among seed sources and date of sowing was observed for different growth parameters from six months onward after seed germination. However, the variation in collar diameter and leaf length was recorded as prominent from three months onward after seed germination.

The growth performance of sandalwood seedlings after germination followed trends similar to those reported by previous studies (13, 25, 27, 33, 34), where seedling height, collar diameter, leaf length and leaf width tend to increase significantly after six months of germination, influenced by both environmental conditions and genetic factors (25, 27). Similarly, in the present study, seeds collected from different localities with varying environments and genetic traits showed variations in germination and growth parameters. Moreover, several researchers have reported significant variation in seed and seedling traits as well as growth performance among different seed sources of *Dalbergia sissoo*, *Pinus roxburghii*, *Jatropha curcas*, *Celtis australis*, *Elaeocarpus prunifolius* and *Ulmus villosa*, which has been attributed to differences in environmental factors, phenotypic characters and the genetic makeup of the mother trees (13, 35–39).

Genetic parameters

In this study, the genetic parameters analysed included the GCV (%), PCV (%), repeatability coefficient, heritability, genetic gain and genetic advance. For all the traits examined, PCV was consistently higher than GCV (Table 7). A similar trend with higher PCV values than GCV has been reported previously (40). Among phenotypic characters of mother trees, maximum GCV (22.43 %), PCV (24.24 %), repeatability coefficient (0.85) and genetic gain (42.74) were noted for tree height, whereas the minimum was noted for crown spread (N-S) with GCV values of 4.53 %, PCV values of 10.42 %, repeatability coefficient-0.18 and genetic gain-4.06. Additionally, maximum genetic advance was also recorded for tree height (4.43), but minimum was recorded for bole height (0.9). Among the different seed traits, seed weight showed the highest values for GCV (14.6 %), PCV (15.2 %), repeatability coefficient (0.92), genetic advance (2.89) and genetic gain (28.90). Genetic estimates for nursery stage performance of progenies from different seed sources showed that maximum GCV (13.17 %), PCV (17.15 %), heritability (0.62) and genetic gain (21.80) were recorded for seedling height, statistically at par with collar diameter with mean values of GCV-9.39 %, PCV-13.07 %, heritability-0.62 and genetic gain-13.90 respectively (Table 8). Furthermore, maximum genetic advance was also recorded for seedling height (3.94), followed by leaf length (0.43) and collar diameter (0.41). Genetic variability among mother trees from different seed sources exhibited higher phenotypic than genotypic coefficients, indicating a close association between tree growth and seed traits, consistent with earlier findings (25, 27). Heritability estimates are generally categorized as low (< 0.3), moderate (0.3–0.6) and high (> 0.6). In the present study, tree height exhibited the highest repeatability (0.82) among phenotypic traits, while seed weight showed the highest repeatability (0.92) among seed-related traits. The highest heritability was recorded for seedling height (0.62), followed by collar diameter (0.52), indicating a moderate to high genetic influence on these characteristics. Similar ranges of

Table 6. Leaf width (cm) of *S. album* seedlings at different age intervals

Seed sources	Age of seedling (Months)											
	Three months			Six months			Nine months			One year		
	d_1	d_2	Mean	d_1	d_2	Mean	d_1	d_2	Mean	d_1	d_2	Mean
S_1	1.20 ± 0.07	1.35 ± 0.09	1.28	1.39 ± 0.03	1.32 ± 0.03	1.35	1.24 ± 0.06	1.35 ± 0.05	1.30	2.24 ± 0.07	1.97 ± 0.15	2.11
S_2	1.26 ± 0.04	1.33 ± 0.07	1.29	1.36 ± 0.02	1.27 ± 0.09	1.31	1.36 ± 0.04	1.29 ± 0.05	1.33	2.36 ± 0.15	1.83 ± 0.03	2.10
S_3	1.22 ± 0.04	1.38 ± 0.03	1.30	1.30 ± 0.05	1.27 ± 0.05	1.28	1.27 ± 0.05	1.25 ± 0.08	1.26	2.20 ± 0.19	1.88 ± 0.09	2.04
S_4	1.22 ± 0.05	1.18 ± 0.15	1.20	1.23 ± 0.02	1.41 ± 0.08	1.32	1.28 ± 0.07	1.44 ± 0.12	1.36	2.20 ± 0.06	2.03 ± 0.17	2.12
S_5	1.48 ± 0.14	1.19 ± 0.03	1.34	1.27 ± 0.05	1.39 ± 0.04	1.33	1.33 ± 0.02	1.89 ± 0.23	1.61	2.51 ± 0.12	2.10 ± 0.04	2.30
S_6	1.21 ± 0.05	1.24 ± 0.04	1.22	1.22 ± 0.03	1.25 ± 0.04	1.24	1.44 ± 0.03	1.34 ± 0.05	1.39	2.19 ± 0.09	1.94 ± 0.06	2.06
Mean	1.27	1.28		1.30	1.32		1.32	1.43		2.28	1.96	
$CD_{0.05}$												
S		NS			NS			0.18			NS	
d		NS			NS			0.10			0.13	
S × d		NS			NS			0.26			NS	

Mean value ± standard error (SE); S: Seed sources; S1: Changer; S2: Kosariyan; S3: Samoh; S4: Hiranagar; S5: Jwalamukhi; S6: Sadwan; d: Date of sowing; d1: First date of sowing; d2: Second date of sowing; NS: Not Significant.

Table 7. Genetic parameters and repeatability coefficient for various characters

Phenotypic characters		GCV (%)	PCV (%)	Repeatability coefficient	Genetic advance	Genetic gain
Tree height		22.43	24.24	0.85	4.43	42.74
Tree diameter		14.12	17.66	0.63	3.38	23.26
Crown spread	N-S	4.53	10.42	0.18	0.13	4.06
	E-W	5.42	10.75	0.29	0.18	
Bole height		13.98	20.02	0.48	0.90	
Seed parameters						
Seed weight		14.6	15.2	0.92	2.89	28.9
Seed diameter		4.93	5.76	0.74	0.43	8.7

Table 8. Genetic estimates for nursery stage performance of progenies from different seed sources

Nursery parameters	GCV (%)	PCV (%)	Heritability	Genetic advance	Genetic gain
Seedling height	13.47	17.15	0.62	3.94	21.8
Collar diameter	9.39	13.07	0.52	0.41	13.9
Leaf length	5.37	8.271	0.42	0.43	7.18
Leaf width	7.82	12.08	0.42	0.22	10.43

heritability for fruit weight and plant height have been reported earlier (41). Traits with high heritability and genetic gain, such as seed weight and seedling height are ideal targets for selection (18).

Principal component analysis

The PCA biplot (Fig. 6) illustrates the relationships between samples and variables across two principal components, Dim1 and Dim2, which explain 41.8 % and 25.4 % of the data variance respectively (Cumulative value 67.2 %). Dim1 axis captures the most significant variation in the dataset. Samples with high positive or negative values along Dim1 are most influenced by variables strongly correlated with this component, whereas the Dim2 axis captures the second most significant variation. Samples with high positive or negative values along Dim2 are influenced by different sets of variables. The samples are categorized into six distinct groups or seed sources (S_1, S_2, S_3, S_4, S_5 and S_6), represented by different symbols and colours. S_1 (red circles) was clustered near the origin, suggesting moderate influence from multiple variables. S_2 (yellow triangles) was located towards the negative side of Dim1 and Dim2, indicating a distinct set of characteristics compared to other groups. S_3 (green squares) was positioned near the origin, similar to S_1, but with slightly different influences from the variables. S_4 (cyan crosses) was positioned below the origin along Dim2, indicating unique characteristics primarily influenced by specific variables. S_5 (blue squares) was spread out along the positive side of Dim1, indicating strong influence from variables pointing in this direction. S_6(pink stars) was positioned on the positive side of Dim2, indicating strong influence from variables in this direction. Furthermore, the vectors represent the variables that contribute to the principal components: SH, GE, LL, CD, IGP and TTFG have strong positive correlations with Dim1 and/or Dim2. However, TH, TD, CBH, GP, SW and SD have strong negative correlations with Dim1 and/or Dim2. Similar findings have been reported by various researchers who examined correlations among different seedling parameters (25, 27).

Conclusion

The study emphasizes the significant influence of provenance variation on the germination, survival and growth performance of *S. album* in the mid-hill zones of Himachal Pradesh. By evaluating different seed sources, the research provides valuable insights for selecting superior seed sources to conserve species diversity and improve the quality of planting stock. The findings reveal that seed sources Kosariyan (S_2), Samoh (S_3) and Changer (S_1) exhibited the best field germination parameters, while Jwalamukhi (S_5) excelled under *in vitro* germination. Furthermore, Jwalamukhi (S_5), followed by Samoh (S_3) and Changer (S_1) demonstrated the most promising seedling growth parameters compared to other sources. These findings highlight the critical importance of selecting appropriate seed sources to improve the productivity and establishment success of sandalwood plantations. This research holds significant implications for advancing tree breeding initiatives, enhancing plantation management practices and achieving greater productivity and sustainability in *S. album* cultivation.

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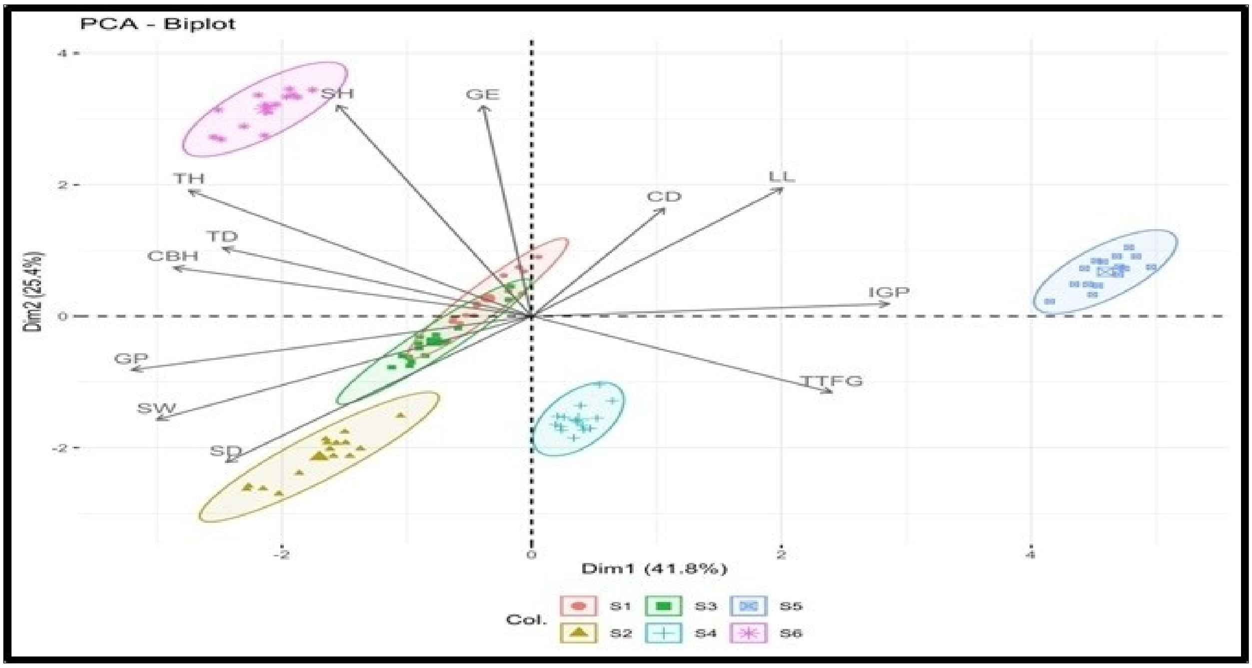

Fig. 6. Principal component analysis.

SH: Seedling height; CD: Collar diameter; LL: Leaf length; GP: Germination percentage; IGP: *In vitro* germination percentage; TTFG: Time taken for germination; TH: Tree height; TD: Tree diameter; CBH: Clear bole height; SD: Seed diameter; SW: Seed weight.

Authors' contributions

RT contributed to conceptualization, methodology, investigation, formal analysis, visualization and writing (original draft and review & editing); TG to conceptualization, visualization and methodology; RKG to methodology and data analysis; AK, DKS, DK and ST to review and editing (with DK also contributing to interpretation); MT to the methodology of *in vitro* germination. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflicts of interest to declare.

Ethical issues: None

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