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Assessment of path analysis of various characteristics in fenugreek (*Trigonella foenum-graecum* L.) for improving biomass performance

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Abstract: As an annual herb, leaves, stems, and seeds of fenugreek is widely used for culinary, medicinal, and nutritional purposes, while evaluation of genetic variability for biomass yield improvement remains limited. The present study assessed 26 fenugreek landraces collected from various regions of Iran to investigate various traits and their contributions to biomass performance. Correlation analysis revealed strong positive associations among vegetative traits, particularly between plant height, stem height, and shoot biomass, while leaf dimensions and leaf area traits showed coordinated growth patterns. Chlorophyll exhibited correlation with carotenoids, while root and reproductive traits showed weak correlations with vegetative traits. Path coefficient analyses were performed to quantify direct and indirect coefficients on dry shoot biomass and other response variables while addressing multicollinearity. Fresh shoot biomass, pod length, and number of nodes were identified as major direct contributors to dry shoot biomass, collectively explaining 67% of the variation. Additional key predictors included plant height, middle leaf height, leaves per plant, lateral leaf area, and biochemical traits such as anthocyanins, carotenoids, phenol, and chlorophyll. Excessive root biomass was found to negatively impact above-ground yield. Bootstrap analysis confirmed the robustness of path coefficients, indicating minimal bias and reliable trait contributions. Breeders should focus on plant height, stem height, leaf area, internode length, and branching to boost biomass, while prioritizing pod number, pod length, and node number to enhance seed yield. Also, some physiological traits like chlorophyll, carotenoids, anthocyanins, and phenols can serve as useful indirect selection markers. Finally, genotypes with large root systems should be avoided to ensure resources are efficiently allocated to above-ground yield.

Keywords: bootstrapping, dry shoot biomass, genetic variability, leaf traits.

Introduction

As an annual herb, fenugreek (2n = 16), belonging to the Fabaceae family, valued both as a vegetable crop and a medicinal plant. It is widely beneficiated for culinary and therapeutic targets, and its seeds also serve as a carminative, making nearly all parts of the plant useful (Syed et al. 2020). The *Trigonella* comprises two main species as *T. foenum-graecum* or fenugreek, and *T. corniculata*. Although, fenugreek is a semi-erect, moderately branched herb producing bold yellow seeds, *T. corniculata* is bushy, with bright orange-yellow flowers and small, sickle-shaped pods (Shadab et al. 2024). Fenugreek is believed to have originated in Asia rather than Southern Europe, and this crop thrives under a wide range of climatic conditions (Seal et al. 2025). Low temperatures during early growth stages favor vegetative development, whereas dry and warmer conditions promote optimal seed ripening and yield. Fenugreek adapts to various soils, provided they are well-drained, and exhibits moderate salinity tolerance, performing even on black cotton soils, but its cultivation on highly saline or acidic soils is not recommended (Narayana et al. 2022).

Since fenugreek is primarily cultivated for its stems and leaves, maximizing biomass yield is a central objective in its improvement. Despite its economic importance, efforts to collect, evaluate, and utilize diverse genotypes for crop enhancement remain limited (Zandi et al. 2015). Assessing genetic variability and introducing high-yielding cultivars are therefore essential for increasing biomass production, particularly in native regions where local cultivars often perform sub-optimally. Understanding genetic variability is a prerequisite for effective crop improvement. In this context, path coefficient analysis serves as a valuable tool, as it decomposes correlations into direct and indirect effects of independent traits on target variables, providing detailed insights into yield-contributing factors (Islam et al. 2025). This approach quantifies the influence of individual traits through standardized partial regression coefficients and is especially useful when independent traits exhibit significant positive relationships with yield. Identifying traits with strong direct effects on biomass enables breeders to prioritize selection strategies and optimize resource allocation in breeding programs (Allier et al. 2020). Moreover, understanding these relationships supports the maintenance or enhancement of other agronomic traits that are critical for sustainable production. Overall, evaluating genetic variability and trait interrelationships provides a solid foundation for informed decision-making in breeding programs aimed at improving yield performance.

Previous studies have consistently highlighted key traits influencing fenugreek yield. Balai et al. (2006), reported that number of pods indicted the high direct impact on yield performance, as well as by pod length, number of seeds per pod, and 1000-seed weight, emphasizing their importance in selection. Sharma & Sastry (2011) further revealed that the number of seeds per pod, the number of pods per plant, and 1000-seed weight showed strong direct influences on yield, whereas plant height and maturity duration indicated negative direct coefficients. Associations confirmed significant correlations between yield and the pods per plant, and 1000-seed weight, seeds per pod, indicating these traits as prime targets for selection. Singh et al. (2019) similarly found that number of pods per plant, 1000-seed weight and number of seeds per pod, had significant correlations and direct effects on yield, whereas maturity duration showed a negative interrelationship. Meena et al. (2021) evaluated fenugreek genotypes and reported high genetic diversity for yield performance, and yield performance. Correlation and path coefficient analyses confirmed that pods per plant and seeds per pod had the high direct coefficients on yield, suggesting their prioritization in breeding programs. Although, the mentioned investigations underscored the importance of number of pods and seeds, as well as seed weight as most important traits to seed yield in fenugreek, while there is few information about biomass performance of fenugreek. The current investigation was undertaken to evaluate the magnitude of variability in fenugreek genotypes and to perform path analysis for biomass and its related traits.

Material and Methods

Twenty-six fenugreek landraces were collected from various regions across Iran (Tab. 1). A field trial was performed via a randomized block scheme with three replicates. Following standard tillage operations, including plowing and leveling in April, plots measuring 50 × 80 cm were prepared. Throughout the growing season, uniform irrigation and manual weed control were applied. Fertilization followed local recommendations, with 25 kg ha^{-1} nitrogen as starter, 60 kg ha^{-1} phosphorus, and 25 kg ha^{-1} potassium were applied. Plots were regularly monitored for pests and diseases, and protective measures were implemented as needed. At 50% flowering, seven plants were selected randomly for measuring of morphological and physiological traits, including plant height (PH), stem height (SH), root length (RL), fresh shoot biomass (FSB), fresh root biomass (FRB), dry shoot biomass (DSB), dry root biomass (DRB), number of internodes (NI), internode length (IL), number of nodes (NN), leaves per plant (LP), lateral branches (LB), middle leaf height (MLH), middle leaf width (MLW), middle leaf area (MLA), lateral leaf height (LLH), lateral leaf width (LLW), lateral leaf area (LLA), pods per plant (PP), pod length (PL), and seeds per pod (SP). Standard tools were used for measurements, including counting, a

Tab. 1 Name, elevation and coordinates of Iranian fenugreek genotypes.

#	Name	Elevation	Latitude	Longitude
1	Mashhad	995	36°19′N	59°32′E
2	Gorgan	155	36°50′N	54°26′E
3	Bushehr	18	28°55′N	50°51′E
4	Ardestan	1207	33°22′N	52°22′E
5	Rezvanshahr	5	37°32′N	49°08′E
6	Sarab	1650	37°56′N	47°32′E
7	Meshgin-A	1400	38°23′N	47°40′E
8	Tabriz-B	1351	38°04′N	46°17′E
9	Tehran-B	900	35°41′N	51°23′E
10	Urmia-A	1332	37°32′N	45°03′E
11	Isfahan	1574	32°39′N	51°40′E
12	Khansar	2215	33°13′N	50°18′E
13	Tabriz-A	1351	38°04′N	46°17′E
14	Kerman	1764	30°15′N	57°03′E
15	Kashmar	1063	35°14′N	58°27′E
16	Mughan-A	33	39°38′N	47°54′E
17	Jahrom	1050	28°30′N	53°34′E
18	Mughan-B	33	39°38′N	47°54′E
19	Ardabil	1351	38°15′N	48°17′E
20	Urmia-B	1332	37°32′N	45°03′E
21	Tabriz-C	1351	38°04′N	46°17′E
22	Tehran-A	900	35°41′N	51°23′E
23	Rafsanjan	1527	30°23′N	55°59′E
24	Meshgin-B	1400	38°23′N	47°40′E
25	Khalkhal	2243	37°36′N	48°31′E
26	Kiashahr	27	37°25′N	49°56′E

stainless-steel ruler (±1.0 mm), caliper (±0.1 mm), digital scale (±0.01 g), and a leaf area meter (AM-3000, ADC BioScientific Ltd). Chlorophyll a (Chl.a), chlorophyll b (Chl.b), and carotenoids (CAR) were quantified following the Arnon method, as described by Rostami et al. (2022). Anthocyanin (ANT) was assessed via spectrophotometric analysis by monitoring absorbance at 535 nm and standardized against cyanidin-3-glucoside (Guffanti et al. 2022). Total phenol content (PHE) was determined by mixing of centrifuged leaf sample with Folin–Ciocalteu reagent, and sodium carbonate, and absorbance recording at 750 nm (Singh, 2023).

The dataset was first assessed for normality using the Kolmogorov-Smirnov test. Phenotypic correlations among measured traits were calculated via Pearson's method, and these correlations were further decomposed into direct and indirect effects using path analysis. To determine the relative contributions of predictor variables to seed yield while minimizing multicollinearity, a linear stepwise regression model was applied in SPSS version 24.0. Predictor variables were organized into first-, second-, and third-order paths according to their influence on yield variation. Multicollinearity within each path was evaluated using tolerance values, which represent the proportion of variability in a predictor not explained by other predictors, and the tolerance, which indicate how much the variance of an independent variable is inflated due to correlations with other predictors. Tolerance values below 1.0 were considered indicative of high collinearity. Coefficients of determination for each predictor were derived from the path coefficients, analogous to conventional linear regression. To assess the reliability of the estimated path coefficients, standard errors were calculated using bootstrap analysis. Breeders are not only interested in point estimates of traits but also in evaluating their variability and constructing confidence intervals for true parameter values. Resampling methods, such as the bootstrap, allow estimation of standard errors, confidence intervals, and the empirical distribution of any statistic. In this study, the mean direct effects obtained from 1,600 bootstrap samples closely corresponded to the observed direct effects, confirming the robustness and reliability of the trait contributions.

Results

Correlation analysis (Tab. 2) revealed positive correlations among several plant growth and biomass traits, whereas plant height (PH) and stem height (SH) were highly correlated, while fresh shoot biomass (FSB) exhibited strong associations with dry shoot biomass and lateral branches. Leaf dimensions also displayed strong internal correlations, with middle leaf width (MLW) and lateral leaf width (LLW) showing a high association, and middle leaf height (MLH) positively correlated with MLW. Similarly, leaf area measurements were closely linked, including MLH with middle leaf area and lateral leaf height (LLH) with lateral leaf width (Tab. 2). Chlorophyll content was another trait with high internal correlation, as chlorophyll a (Chl.a) and chlorophyll b (Chl.b) were strongly associated. Also, positive correlations were evident among other traits as; taller plants tended to have higher shoot biomass, and lateral branching was moderately associated with larger leaves (Tab. 2). Dry shoot biomass closely followed fresh shoot biomass, and carotenoid content (CAR) showed moderate correlations with both chlorophyll a and b (Tab. 2). The study showed that growth, biomass, leaf traits, and pigment contents in the plants were strongly interconnected, reflecting coordinated development among these traits Similar patterns have been reported by Ma et al. (2025), who observed a strong positive association between fresh and dry biomass, supporting current finding that fresh shoot biomass closely reflects dry shoot biomass. Strong positive associations among photosynthetic pigments have also been documented, with Saadati et al. (2022) reporting high correlations between chlorophyll a and chlorophyll b, alongside moderate associations between carotenoids and both chlorophyll forms.

In contrast, root traits such as root length (RL) and fresh root biomass (FRB) generally exhibited weak correlations with shoot traits (Tab. 2), indicating that

Tab. 2 The pairwise correlation coefficients among traits of 26 fenugreek (*Trigonella foenum-graecum* L.) landraces.

	SH	RL	FSB	FRB	DSB	DRB	NI	IL	NN	LP	LB	MLH	MLW	MLA	LLH	LLW	LLA	PP	PL	SP	Chl.a	Chl.b	CAR	PHE	ANT
PH	0.98	0.18	0.66	0.17	0.64	-0.02	0.31	0.24	0.21	0.13	0.20	0.23	0.41	0.44	0.33	0.17	0.34	0.27	0.46	-0.11	0.35	0.44	0.39	0.11	0.24
SH		0.02	0.65	0.16	0.62	-0.07	0.25	0.23	0.23	0.11	0.17	0.22	0.47	0.45	0.34	0.24	0.39	0.30	0.48	-0.08	0.29	0.40	0.33	0.10	0.20
RL			0.09	0.04	0.17	0.36	0.49	-0.11	-0.08	0.05	0.10	0.15	-0.23	0.12	0.05	-0.36	-0.14	-0.29	-0.09	-0.37	0.27	0.22	0.23	-0.05	0.21
FSB				0.44	0.71	0.20	0.42	0.01	0.11	0.43	0.37	0.62	0.46	0.44	0.41	0.27	0.35	0.35	0.27	-0.03	0.49	0.52	0.52	0.28	0.39
FRB					0.04	0.23	0.18	-0.16	-0.01	0.14	0.22	0.39	0.20	0.22	0.37	0.17	0.24	0.08	-0.19	-0.20	0.27	0.25	0.26	0.19	-0.08
DSB						0.35	0.35	0.25	-0.05	0.32	0.26	0.57	0.54	0.52	0.42	0.23	0.43	0.20	0.53	0.04	0.37	0.43	0.40	0.07	0.25
DRB							0.21	-0.17	-0.40	0.05	0.18	0.48	0.01	0.41	0.45	0.02	0.01	-0.39	-0.01	-0.11	0.33	0.39	0.34	0.04	0.14
NI								-0.14	0.24	0.36	0.23	0.10	0.07	-0.03	0.14	0.13	0.14	0.10	0.25	0.02	0.31	0.15	0.28	-0.18	-0.10
IL									0.14	-0.20	0.11	-0.04	0.52	0.15	0.26	0.29	0.42	0.14	0.34	0.19	-0.16	-0.17	-0.18	-0.25	-0.02
NN										-0.20	0.18	-0.04	0.29	0.07	-0.08	0.27	0.35	0.56	0.39	0.23	0.15	0.10	0.13	0.04	0.08
LP											0.52	0.23	0.26	0.08	0.17	0.39	0.25	0.36	0.09	0.08	0.32	0.24	0.35	0.24	0.16
LB												0.41	0.48	0.53	0.57	0.63	0.54	0.38	0.23	0.04	0.31	0.34	0.33	0.06	0.26
MLH													0.51	0.70	0.50	0.22	0.41	0.11	0.04	-0.07	0.45	0.53	0.48	0.34	0.45
MLW														0.65	0.59	0.70	0.89	0.57	0.40	0.19	0.15	0.18	0.17	0.12	0.18
MLA															0.59	0.32	0.60	0.28	0.29	0.09	0.24	0.38	0.28	0.09	0.45
LLH																0.54	0.67	0.22	0.03	-0.17	0.18	0.22	0.17	0.00	-0.05
LLW																	0.78	0.52	0.42	0.12	0.11	0.12	0.14	0.16	-0.03
LLA																		0.59	0.41	0.12	0.01	0.01	0.02	0.01	0.04
PP																			0.34	0.44	0.26	0.18	0.27	0.27	0.11
PL																				0.36	0.21	0.21	0.23	-0.15	0.08
SP																					0.00	-0.12	0.00	-0.27	0.11
Chl.a																						0.94	0.99	0.50	0.23
Chl.b																							0.96	0.54	0.35
CAR																								0.53	0.29
PHE																									0.40

Significant correlations with degrees of freedom (DF) = 24, at 0.05 and 0.01 probability levels were 0.39 and 0.50.

Traits are plant height (PH), stem height (SH), root length (RL), fresh shoot biomass (FSB), fresh root biomass (FRB), dry shoot biomass (DSB), dry root biomass (DRB), number of internodes (NI), internode length (IL), number of nodes (NN), leaves per plant (LP), lateral branches (LB), middle leaf height (MLH), middle leaf width (MLW), middle leaf area (MLA), lateral leaf height (LLH), lateral leaf width (LLW), lateral leaf area (LLA), pods per plant (PP), pod length (PL), seeds per pod (SP), chlorophyll-a (Chl.a), chlorophyll-b (Chl.b), carotenoids (CAR), anthocyanin (ANT), and phenol (PHE).

above- and below-ground traits are largely independent. Similarly, reproductive traits such as seeds per pod (SP) had weak associations with most vegetative traits, suggesting separate genetic control for reproductive and growth characteristics. Some traits also displayed weak negative correlations; for instance, dry root biomass (DRB) was slightly negatively associated with internode length, RL was negatively correlated with lateral leaf height, and SP showed a minor negative correlation with LLW (Tab. 2). These results indicate that plant height, stem height, and shoot biomass are closely associated, while leaf dimensions exhibit coordinated growth. Chlorophyll content is strongly correlated internally and moderately associated with carotenoids. In contrast, root and reproductive traits show weak associations with vegetative traits, suggesting independent genetic control. These findings highlight biomass and branching traits as promising targets for selection in breeding programs aimed at developing high-yielding fenugreek landraces. Comparative analyses across species and within legumes have shown weak or inconsistent correlations between root traits (root length and root biomass) and above-ground growth, suggesting a decoupling of resource allocation between below- and above-ground organs. (Palacio et al. 2007). Also, it found in fenugreek that reproductive characters (such as seeds per pod) load onto components separate from many vegetative growth traits, implying partly distinct genetic control of reproductive versus vegetative traits (Roba & Mohammed 2024). Hernández-Ochoa (2024) has also reported weak negative trade-offs between specific root or reproductive measures and particular shoot traits (negative relationships between certain root-system metrics and internode-related traits or between some reproductive and leaf-dimension variables), consistent with the minor negative correlations of current study.

To assess the contributions of different traits to dry shoot biomass (DSB), a linear regression model was fitted while controlling for multicollinearity (Tab. 3). All traits were initially included as first-order predictors, with DSB serving as the response variable. Relatively high multicollinearity was observed among most traits, except for fresh shoot biomass (FSB), fresh root biomass (FRB), number of nodes (NN), and pod length (PL). To address this, standardized coefficients were estimated using a stepwise multiple regression model, allowing the identification of the most influential traits while minimizing the effects of multicollinearity. The path analysis indicated that for dry shoot biomass (DSB), the model explained 67% of the variation, while fresh shoot biomass, pod length, and number of nodes were identified as significant predictors, with acceptable multicollinearity levels (Tab. 4). In second step, for FSB, plant height, middle leaf height, and leaves per plant were significant contributors, accounting for 69% of the variation. Also, PL was influenced by stem height and seeds per pod, explaining 33% of the variation. Finally, in the second step, the NN was predicted by pods per plant, leaves per plant, and number of internodes, with R2 = 0.57 (Tab. 4). Digrado et al. (2022) showed in cowpea that plant height, node number, and leaf dimensions collectively have strong direct and indirect effects on above-ground biomass. In pea, non-destructive performance trait phenotyping similarly identified height and leaf-area-related traits as major contributors to

Tab. 3 Regression slope, standard error (SE) and Tolerance collinearity index for traits of fenugreek genotypes for predicting of the response variable (PDB, plant dry biomass).

X	Slope	SD	Tolerance
SH	-0.08	0.06	0.002
RL	-0.38	0.23	0.007
FSB	0.36	0.19	0.155
FRB	-2.85	1.01	0.245
DRB	-3.19	2.88	0.003
NI	1.00	0.60	0.003
IL	0.18	0.11	0.022
NN	-0.36	0.15	0.109
LP	0.00	0.01	0.047
LB	-0.30	0.33	0.008
MLH	-0.26	0.20	0.003
MLW	-0.43	0.30	0.003
MLA	0.01	0.01	0.003
LLH	0.03	0.12	0.014
LLW	-0.16	0.07	0.014
LLA	0.03	0.01	0.001
PP	-0.03	0.03	0.004
PL	0.01	0.05	0.126
SP	0.06	0.07	0.045
Chl.a	-0.01	0.19	0.004
Chl.b	3.67	2.16	0.001
CAR	-2.67	1.88	0.001
PHE	0.44	0.31	0.030
ANT	0.04	0.05	0.066

Traits are plant height (PH), stem height (SH), root length (RL), fresh shoot biomass (FSB), fresh root biomass (FRB), dry shoot biomass (DSB), dry root biomass (DRB), number of internodes (NI), internode length (IL), number of nodes (NN), leaves per plant (LP), lateral branches (LB), middle leaf height (MLH), middle leaf width (MLW), middle leaf area (MLA), lateral leaf height (LLH), lateral leaf width (LLW), lateral leaf area (LLA), pods per plant (PP), pod length (PL), seeds per pod (SP), chlorophyll-a (Chl.a), chlorophyll-b (Chl.b), carotenoids (CAR), anthocyanin (ANT), and phenol (PHE).

biomass variation (Quirós Vargas et al. 2019). Those combined findings supported the assertion that FSB, PL, and NN are biologically meaningful predictors for DSB, just as current path analysis. Breeders should prioritize genotypes with taller plant stature, larger and well-distributed foliage, longer pods, and greater node number, as these traits collectively maximize fresh and dry biomass accumulation.

In the third step, PH was moderately associated with chlorophyll-b content, while MLH was significantly influenced by middle leaf area and chlorophyll-a, explaining 54% of its variation. Pods per plant (PP) was significantly predicted by lateral leaf area, dry root biomass, and carotenoid content, collectively explaining 63% of the variation (Tab. 4). Number of internodes (NI) was primarily influenced by root length, accounting for 21% of the variation. Leaves per plant (LP) was predicted by lateral

Tab. 4 Response traits (Y), coefficient of determination (R2), predictor traits (X), standard coefficients (β, and tolerance collinearity index (Tol) for fenugreek genotypes in predicting of the response traits in stepwise regression model.

Y	R^2	X	β	Tol.	Y	R^2	X	β	Tol.
DSB	0.67	FSB	0.62	0.93	PP	0.63	LLA	0.57	1.00
		PL	0.48	0.79			DRB	-0.55	0.88
		NN	-0.30	0.85			CAR	0.44	0.88
FSB	0.69	PH	0.52	0.94	NI	0.21	RL	0.49	1.00
		MLH	0.43	0.91					
		LP	0.27	0.94	Chl.b	0.26	PHE	0.54	1.00
PL	0.33	SH	0.51	0.99	MLA	0.55	LLH	0.62	1.00
		SP	0.40	0.99			ANT	0.49	1.00
NN	0.57	PP	0.73	0.87	Chl.a	0.22	PHE	0.50	1.00
		LP	-0.60	0.76					
		NI	0.39	0.87	LB	0.37	LLW	0.63	1.00
PH	0.36	Chl.b	0.44	1.00	MLW	0.45	LLH	0.49	0.93
							IL	0.39	0.93
MLH	0.54	MLA	0.63	0.94					
		Chl.a	0.30	0.94	LLA	0.67	LLW	0.59	0.71
							LLH	0.36	0.71
LP	0.24	LB	0.52	1.00					
					DRB	0.16	LLH	0.45	1.00
SH	0.19	MLW	0.47	1.00					
					CAR	0.25	PHE	0.53	1.00

Traits are plant height (PH), stem height (SH), root length (RL), fresh shoot biomass (FSB), fresh root biomass (FRB), dry shoot biomass (DSB), dry root biomass (DRB), number of internodes (NI), internode length (IL), number of nodes (NN), leaves per plant (LP), lateral branches (LB), middle leaf height (MLH), middle leaf width (MLW), middle leaf area (MLA), lateral leaf height (LLH), lateral leaf width (LLW), lateral leaf area (LLA), pods per plant (PP), pod length (PL), seeds per pod (SP), chlorophyll-a (Chl.a), chlorophyll-b (Chl.b), carotenoids (CAR), anthocyanin (ANT), and phenol (PHE).

branches, while stem height (SH) was influenced by middle leaf width. These results indicate that specific vegetative traits, such as leaf area, branching, and leaf dimensions, play a key role in determining reproductive and growth traits in fenugreek, with low multicollinearity among predictors ensuring reliable estimation of their contributions. In the fourth step, path analysis also highlighted the contributions of vegetative and biochemical traits to several physiological and growth-related response variables in fenugreek, whereas Chlorophyll b (Chl.b) was positively influenced by phenol content, while chlorophyll a (Chl.a) was similarly affected by PHE (Tab. 4). Middle leaf area (MLA) was primarily predicted by lateral leaf height (LLH) and anthocyanin content, together explaining 55% of its variation. Lateral branching (LB) was strongly influenced by lateral leaf width (LLW), while

Tab. 5 The identified indirect coefficients of path analysis as shown in outside of diagonal.

		FSB	PL	NN
DSB	FSB		0.13	-0.03
	PL	0.17		-0.12
	NN	0.07	0.19	

		PH	MLH	LP
FSB	PH		0.10	0.03
	MLH	0.12		0.06
	LP	0.07	0.10	

		PP	LP	NI
NN	PP		-0.22	0.04
	LP	0.26		0.14
	NI	0.07	-0.22	

		LLA	DRB	CAR
PP	LLA		0.01	0.01
	DRB	0.01		0.15
	CAR	0.01	-0.19	

		SH	SP
PL	SH		-0.03
	SP	-0.04	

		MLA	Chl.a
MLH	MLA		0.07
	Chl.a	0.15	

		LLH	ANT
MLA	LLH		-0.02
	ANT	-0.03	

		LLH	IL
MLW	LLH		0.10
	IL	0.13	

		LLW	LLH
LLA	LLW		0.19
	LLH	0.32	

Traits are plant height (PH), stem height (SH), root length (RL), fresh shoot biomass (FSB), fresh root biomass (FRB), dry shoot biomass (DSB), dry root biomass (DRB), number of internodes (NI), internode length (IL), number of nodes (NN), leaves per plant (LP), lateral branches (LB), middle leaf height (MLH), middle leaf width (MLW), middle leaf area (MLA), lateral leaf height (LLH), lateral leaf width (LLW), lateral leaf area (LLA), pods per plant (PP), pod length (PL), seeds per pod (SP), chlorophyll-a (Chl.a), chlorophyll-b (Chl.b), carotenoids (CAR), anthocyanin (ANT), and phenol (PHE).

middle leaf width (MLW) was determined by LLH and internode length. Lateral leaf area (LLA) was shaped by both LLW and LLH, whereas dry root biomass (DRB) and carotenoid content (CAR) were affected by LLH and phenol content (PHE), respectively (Tab. 4). These results highlight that key vegetative traits; including leaf area, lateral branching, pod length, and fresh shoot biomass, serve as major determinants of both biomass accumulation and reproductive performance in fenugreek. Dry shoot biomass can be effectively increased by selecting genotypes with higher fresh biomass, more nodes, and longer pods, while pods per plant and leaves per plant are strongly influenced by leaf size and branching patterns. Also, leaf morphology and biochemical traits, such as chlorophyll, carotenoids, anthocyanins, and phenol content, play important roles in physiological performance and potentially enhance stress tolerance and nutritional quality. Root traits, although indirectly related, contribute to overall plant vigor and yield. Sagbhor et al. (2019), found that the number of leaves had the high direct influences on average plant weight, as well as plant height, leaf area, and biological yield. Also, they found that the number of root nodules and total chlorophyll content also exhibited positive indirect effects on plant weight. However, total chlorophyll content had a negative direct effect on average plant weight, suggesting a complex interplay between

Tab. 6 Bootstrapping of path coeffects for target traits (Y) and predictor traits (X) in fenugreek genotypes based on stepwise regression model.

Y	X	Mean	Std. Error	Lower	Upper
DSB	FSB	0.619	0.175	0.297	1.045
	PL	0.476	0.173	0.049	0.734
	NN	-0.303	0.153	-0.597	0.008
FSB	PH	0.521	0.109	0.338	0.772
	MLH	0.433	0.144	0.171	0.734
	LP	0.270	0.127	0.056	0.559
PL	SH	0.507	0.249	0.096	1.044
	SP	0.400	0.161	-0.018	0.640
NN	PP	0.732	0.166	0.516	1.139
	LP	-0.604	0.196	-1.074	-0.247
	NI	0.390	0.177	0.132	0.821
PH	Chl.b	0.444	0.166	0.052	0.743
MLH	MLA	0.625	0.173	0.240	0.920
	Chl.a	0.305	0.137	0.044	0.582
LP	LB	0.521	0.182	0.142	0.871
SH	MLW	0.468	0.248	0.031	0.996
PP	LLA	0.571	0.162	0.272	0.864
	DRB	-0.551	0.141	-0.901	-0.318
	CAR	0.444	0.111	0.267	0.697
NI	RL	0.489	0.174	0.176	0.840
Chl.b	PHE	0.541	0.176	0.158	0.858
MLA	LLH	0.616	0.109	0.375	0.805
	ANT	0.485	0.132	0.225	0.739
Chl.a	PHE	0.496	0.183	0.071	0.798
LB	LLW	0.628	0.132	0.335	0.849
MLW	LLH	0.487	0.194	0.156	0.908
	IL	0.392	0.147	0.135	0.730
LLA	LLW	0.588	0.326	0.145	1.163
	LLH	0.356	0.156	0.130	0.738
DRB	LLH	0.448	0.231	0.010	0.926
CAR	PHE	0.529	0.181	0.131	0.856

Traits are plant height (PH), stem height (SH), root length (RL), fresh shoot biomass (FSB), fresh root biomass (FRB), dry shoot biomass (DSB), dry root biomass (DRB), number of internodes (NI), internode length (IL), number of nodes (NN), leaves per plant (LP), lateral branches (LB), middle leaf height (MLH), middle leaf width (MLW), middle leaf area (MLA), lateral leaf height (LLH), lateral leaf width (LLW), lateral leaf area (LLA), pods per plant (PP), pod length (PL), seeds per pod (SP), chlorophyll-a (Chl.a), chlorophyll-b (Chl.b), carotenoids (CAR), anthocyanin (ANT), and phenol (PHE).

photosynthetic capacity and growth parameters. In terms of biochemical traits, Kadam et al. (2017), reported seasonal variations in chlorophyll a, chlorophyll b, and carotenoid content in fenugreek leaves, indicating that pigment levels can fluctuate with environmental conditions and developmental stages.

Path analysis revealed not only the direct effects but also the indirect contributions of various traits on key response variables in fenugreek. For DSB trait, FSB, PL, and NN exerted notable indirect effects, with FSB contributing positively through PL and NN, while NN had a slight negative indirect influence via other traits (Tab. 5). PH, MLH, and LP indirectly affected FSB, with PH showing the strongest positive indirect effect. Pods per plant (PP) was influenced indirectly by LP and NI, whereas LLA, DRB, and CAR, also contributed indirectly to PP through multiple pathways. For physiological traits, MLA was strongly affected by lateral leaf height LLH and ANT content, while Chl.a and Chl.b were influenced indirectly by MLA and PHE (Tab. 5). Leaf morphology traits, including LLW and LLH, showed significant indirect effects on LLA and leaf area-related traits. These results revealed a complex network of direct and indirect relationships among vegetative, reproductive, and biochemical traits, offering valuable insight into how growth and physiological attributes collectively shape fenugreek performance. Mahanti et al. (2022) found that the number of leaves, plant height, and leaf area had the highest association on biomass, followed by the number of root nodules and chlorophyll content. These findings align with your results, where vegetative traits such as leaf area, branching, and leaf dimensions play a pivotal role in determining reproductive and growth traits in fenugreek.

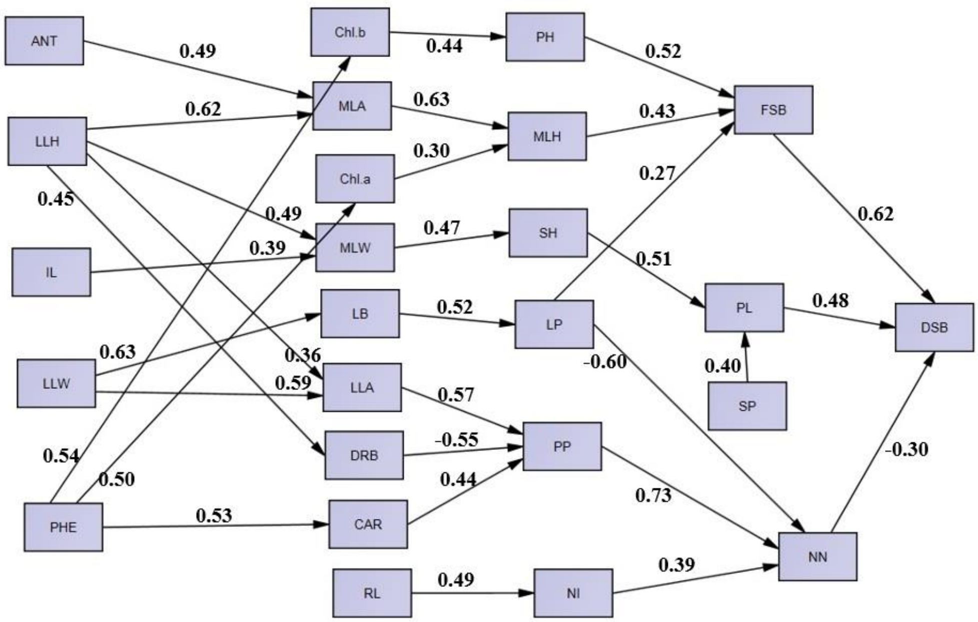

Fig. 1 Diagram of path analysis in for dry plant biomass in fenugreek. Traits are plant height (PH), stem height (SH), root length (RL), fresh shoot biomass (FSB), fresh root biomass (FRB), dry shoot biomass (DSB), dry root biomass (DRB), number of internodes (NI), internode length (IL), number of nodes (NN), leaves per plant (LP), lateral branches (LB), middle leaf height (MLH), middle leaf width (MLW), middle leaf area (MLA), lateral leaf height (LLH), lateral leaf width (LLW), lateral leaf area (LLA), pods per plant (PP), pod length (PL), seeds per pod (SP), chlorophyll-a (Chl.a), chlorophyll-b (Chl.b), carotenoids (CAR), anthocyanin (ANT), and phenol (PHE).

Path analysis was conducted to identify the most efficient routes influencing DSB in fenugreek. The paths ANT → MLA → MLH → FSB → DSB following to IL → MLW → SH → PL → DSB and PHE → CAR → PP → NN → DSB were found to be the most efficient, both associated with high biomass performance (Fig. 1). This indicates that increasing ANT, CAR, FSB, IL, MLA, MLH, MLW, NN, PHE, PL, PP, and SH can effectively enhance fenugreek biomass. Also, the other four other paths were identified as significant contributors: IL → MLW → SH → PH → DSB, LLH → LLA → PP → NN → DSB, RL → NI → NN → DSB and PHE → Chl.a → MLH → FSB → DSB (Fig. 1), suggesting that, in addition to the traits mentioned above, Chl.a, LLA, LLH, NI, PH, and RL also play key roles in improving biomass yield. In contrast, the path LLH → DRB → PP → NN → DSB was less favorable way, exhibiting a negative effect on yield and markedly reducing biomass performance, indicating that root biomass is the least desirable trait for biomass improvement. Breeders can utilize these findings to efficiently improve fenugreek biomass by focusing on the most influential vegetative, reproductive, and biochemical traits. Breeders can improve fenugreek biomass by selecting genotypes with enhanced above-ground traits like fresh shoot biomass, pod length, node number, plant height, and leaf area, with biochemical markers like anthocyanins, carotenoids, phenols, and chlorophyll a. Excessive root biomass should be avoided, as it can reduce yield. Focusing on these traits and their efficient pathways allows rapid development of high-biomass, high-yielding fenugreek genotypes. Key vegetative traits, including middle leaf properties (height, width and area), lateral leaf properties (height and area), internode length, and stem height, can be targeted to enhance shoot biomass, while reproductive traits such as pod properties (number and length), and number of nodes contribute significantly to both vegetative and seed yield. Biochemical traits, including anthocyanins, carotenoids, phenol content, and chlorophyll-a, indirectly enhanced biomass accumulation and may contributed to improved stress tolerance and nutritional quality. In contrast, excessive dry root biomass negatively affected shoot yield, indicating that selection for higher above-ground biomass should avoid genotypes with disproportionate root allocation (Singh & Singh 2022), conducted path coefficient analysis on fenugreek genotypes and revealed that the number of leaves had the high direct coefficients on yield, regarding to plant height and number of seeds per pod. Also, they observed that chlorophyll content had a significant positive indirect effect on seed yield through plant height and number of leaves. These results underscore the importance of selecting genotypes with optimal leaf number and chlorophyll content to enhance biomass and seed yield in fenugreek breeding programs.

Bootstrap analysis with 1600 resamples (Tab. 6) revealed consistently low standard errors and negligible biases for all direct effects, highlighting the reliability and stability of the path analysis outcomes. These results indicate that the applied methodology effectively addresses multicollinearity, even among closely interrelated traits. The use of a stepwise multivariate regression approach further minimized multicollinearity by maintaining the relative independence of predictor variables at each stage of modeling. Structuring predictors into primary, secondary, tertiary, and quaternary categories to manage multicollinearity has been successfully employed in previous research on crops such as *Carthamus tinctorius* (Shekari et al. 2025) and *Nigella sativa* (Sabaghnia et al. 2025), demonstrating the effectiveness of this strategy for analyzing complex trait interactions.

Discussion

Correlation analysis highlighted strong positive associations among vegetative traits, particularly between plant height, stem height, and shoot biomass. Taller plants with longer stems tended to produce higher shoot biomass, consistent with observations in legume crops (Pinto et al. 2021). This strong interrelationship suggests coordinated growth mechanisms, likely influenced by common genetic and hormonal pathways regulating cell elongation and division. Leaf dimensions and leaf area traits were also highly correlated, with middle and lateral leaf widths positively associated with leaf heights and areas. These results indicate that leaf expansion occurs in a coordinated manner and contributes substantially to photosynthetic capacity, which underpins biomass accumulation. Such associations align with previous studies reporting that leaf size and architecture are critical determinants of light interception and vegetative productivity in legumes and other vegetable crops (Ayaz et al. 2004; Mattera et al. 2013). Root traits and certain pod traits exhibited weak correlations with vegetative traits, indicating largely independent genetic control of above- and below-ground growth. This separation may reflect evolutionary trade-offs between resource allocation to shoots versus roots or reproductive versus vegetative growth, a phenomenon reported in other leguminous species (Tuller et al. 2018; Marcellus et al. 2024).

Path coefficient analyses provided detailed insights into the relative importance of individual traits for dry shoot biomass and other key response variables. Fresh shoot biomass, pod length, and number of nodes emerged as primary direct contributors to dry shoot biomass, which confirms that above-ground vegetative traits, particularly those reflecting shoot vigor and branching, are critical determinants of biomass accumulation. The positive contribution of pod length suggests a link between reproductive organ development and vegetative growth, possibly mediated by source-sink dynamics, where well-developed pods enhance assimilate partitioning and stimulate shoot growth (Ali et al. 2022; Yang et al. 2025). Also, plant height, middle leaf height, and leaves per plant were significant contributors to fresh shoot biomass, while lateral leaf area, stem height, and number of internodes also influenced reproductive traits such as pods per plant and pod length. These results emphasize the interconnected nature of vegetative and reproductive growth, suggesting that selecting for robust vegetative architecture can indirectly improve yield components. Breeders should focus on above-ground traits like fresh shoot biomass, plant height, leaf area, branching, and pod length, to maximize fenugreek biomass. Similar findings have been reported in fenugreek and other legumes, where leaf area and branching patterns were positively associated with both biomass and seed yield (Singh et al. 2006; Meena et al. 2021). Although, root traits contributed indirectly to dry root biomass through effects on internode number and leaf development, dry root biomass displayed a negative association with shoot yield. This implies that excessive root allocation may reduce above-ground biomass, reflecting a classic allocation trade-off between roots and shoots. Breeding strategies focusing on optimal root-to-shoot ratios could therefore enhance shoot productivity without compromising plant stability or resource uptake.

Chlorophylls (types a and b) were influenced by phenol content, while anthocyanins positively affected middle leaf area and indirectly contributed to fresh shoot biomass. These compounds likely enhance photosynthetic efficiency and provide antioxidant protection, supporting sustained growth under environmental stress. The integration of biochemical traits into selection criteria is particularly valuable for improving stress tolerance and nutritional quality. Carotenoids, for instance, contribute to light harvesting and photoprotection, while phenolic compounds and anthocyanins mitigate oxidative damage, suggesting that genotypes with higher levels of these metabolites may perform better under abiotic stress conditions, such as drought or high light intensity (Rostami et al. 2022). Reproductive traits, including pods per plant, were influenced by lateral leaf area, number of nodes, and biochemical traits through multiple pathways. Likewise, leaf area and leaf morphology traits affected physiological attributes such as middle leaf area and chlorophyll content. These findings highlight that breeding programs must consider both direct and indirect trait contributions, as selecting for one key trait may simultaneously enhance several interrelated traits. Such integrated selection strategies have been recommended, where complex trait networks determine yield potential (Allier et al. 2020; Shekari et al. 2025).

The identified efficient paths indicated that, stem height, middle leaf area, carotenoids, pods per plant, fresh shoot biomass, internode length, middle leaf height, number of nodes, middle leaf width, phenol content, pod length, and anthocyanin were associated with high biomass performance of fenugreek. The research identified key selection targets for fenugreek improvement, whereas vegetative traits such as leaf area, leaf dimensions, internode length, and stem height significantly contribute to biomass and indirectly to reproductive traits. Reproductive traits, including pods per plant, pod length, and number of nodes, directly influence seed yield. Biochemical traits, particularly anthocyanins, carotenoids, phenol content, and chlorophyll-a, enhance physiological performance and may improve stress tolerance and nutritional quality. By integrating these traits into a combined selection strategy, breeders can efficiently develop high-yielding genotypes with optimized vegetative architecture, reproductive potential, and biochemical composition. Also, the research underscores the importance of considering both direct and indirect trait effects to maximize breeding efficiency, which provide a foundation for future fenugreek breeding programs aimed at developing high-yielding cultivars.

Conclusion

The research revealed high genetic variability among fenugreek landraces, with key vegetative, reproductive, and biochemical traits significantly influencing biomass yield. Path coefficient analysis identified fresh shoot biomass, leaf area, pod number, and biochemical traits such as anthocyanins, carotenoids, and phenol as primary contributors. The other identified traits in efficient paths were stem height, internode length, middle leaf height, number of nodes, middle leaf width, and pod length. These findings provide clear targets for breeding programs, enabling the development of high-yielding fenugreek genotypes with optimized shoot production.

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