Assessment of the genetic diversity of groundnut (Arachis hypogaea L.) genotypes for kernel yield, oil and fodder quantity and quality under drought conditions

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Assessment of the genetic diversity of groundnut (*Arachis hypogaea* L.) genotypes for kernel yield, oil and fodder quantity and quality under drought conditions

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Abstract

The objective of this study was to determine drought tolerance, kernel (KY) and fodder yield and quality amongst diverse groundnut genotypes for direct production or breeding. Hundred genotypes were evaluated at ICRISAT, India during 2018–2019 and 2019–2020 under drought-stressed (DS) and nonstressed (NS) conditions. Data were collected on KY; oil content (OC); oil yield (OY); protein content; palmitic, stearic, oleic, and linoleic acid contents; haulm yield (HY); and fodder quality parameters such as the contents of dry matter, ash, nitrogen (NC), neutral detergent fiber (NDFDM), acid detergent fiber (ADFDM), acid detergent lignin (ADLDM), in vitro digestibility, and metabolizable energy. Data were subjected to parametric and nonparametric statistical analyses. Combined analysis of variance revealed significant ($P < .05$) genotype differences for all assessed traits. Genotype × water regime interaction effects were significant for KY, OC, ash, NC, NDFDM, and ADLDM. Kernel yield positively and significantly ($P < .05$) correlated with OY ($r = .99$), LAC ($r = .13$), ash ($r = .32$), and NDFDM ($r = .54$) under DS condition. Haulm yield was positively and significantly ($P < .05$) correlated with OC ($r = .24$), NDFDM ($r = .19$), ADFDM ($r = .18$), and ADLDM ($r = .17$) under DS condition. The study identified four genotypes with high kernel and haulm yields, and six genotypes with high oleic acid content. Further, 10 genotypes were selected with relatively better drought tolerance. The selected genotypes are recommended for further breeding and variety release adapted to drought conditions.

1 | INTRODUCTION

Groundnut (*Arachis hypogaea* L.; 2n = 4x = 40) is an important oilseed crop with multiple uses in the food and feed sectors. It is cultivated in diverse agro-ecologies including the semi-arid tropics and subtropical regions globally. Groundnut is mainly cultivated as a source of vegetable oil for local, regional and international markets (Ojiewo et al., 2020).

Abbreviations: ADFDM, acid detergent fiber; ADLDM, acid detergent lignin; DM, dry matter; DS, drought-stressed; HY, haulm yield; KY, kernel yield; LAC, linoleic acid content; ME, metabolizable energy; NC, nitrogen content; NDFDM, neutral detergent fiber; NS, nonstressed; OAC, oleic acid content; OC, oil content; OY, oil yield; PAC, palmitic acid content; TPC, total protein content; SAC, stearic acid content; STI, stress tolerance index.

Further, groundnut kernels are eaten raw, roasted, boiled, or processed into groundnut butter (Janila et al., 2013). The oil content of groundnut kernels varies from 45 to 56% (Bishi et al., 2013; Sarvamangala et al., 2011; Yol et al., 2017). Groundnut oil is one of the premium cooking oils for its stability at high temperatures and higher smoke point conditions compared with soybean (*Glycine max*) and rapeseed (*Brassica napus*) oils (Che & Min, 2007). Groundnut kernels contain macro-and micronutrients such as calcium (920 mg kg^{-1}), magnesium (1,690 mg kg^{-1}), potassium (7,054 mg kg^{-1}), iron (46 mg kg^{-1}) and zinc (33 mg kg^{-1}; Nigam, 2014). The kernels are also rich in vitamins (e.g., vitamins E, K, and B) and protein (~25%; Janila et al., 2014; Sarvamangala et al., 2011). The main fatty acids present in groundnut are oleic acid (80%), linoleic acid (~40%) and palmitic acid (5–10%; Bishi et al., 2013). It also consists of minor fatty acids such as stearic, arachidic, eicosenoic, behenic, lignoceric, and gadoleic acids each accounting between 1 and 3% of the total fatty acid (Andersen et al., 1998). Groundnut genotypes with oleic acid content ≥78% are referred to as high oleic genotypes and possess oil with longer shelf life (Deshmukh et al., 2020; Janila, Radhakrishnan et al., 2018). The high auto-oxidative stability nature of oleic acid is a key factor attributing to the extended shelf life of the oil (Nawade et al., 2018). Groundnut oil with high linoleic acid content is prone to oxidation which result in unpleasant odor and taste, and reduced shelf-life (Shasidhar et al., 2020). Therefore, high oleic acid/linoleic acid ratio is a desired quality parameter to enhance the shelf-life of groundnut oil. Developing groundnut genotypes with high oleic acid is a key breeding objective for human health, product quality and to access the lucrative market opportunities (Nawade et al., 2018).

Groundnut haulm serves as an important feed source for livestock in fresh or dry forms. This is essential in the crop–livestock farming systems such as in Ethiopia and other arid and semi-arid regions where grazing lands are limited (Abady et al., 2019; Frimpong et al., 2017; Sabagh et al., 2019). Reportedly, the haulm contains protein ranging from 8 to 15%, lipid (1–3%), minerals (9–17%) and carbohydrates (38–45%; Janila et al., 2016). These attributes make groundnut haulm as a source of quality fodder to supplementing the diet of livestock. Key quality parameters of the haulm include the contents of nitrogen, in vitro organic matter digestibility, and metabolized energy (Joshi et al., 2019). In vitro organic matter digestibility is the proportion of organic matter that is digested in the ruminant digestive tract. Metabolizable energy is the net energy available for animal growth or reproduction after fecal and urinary energy loss (Samireddypalle et al., 2017). Conversely, carbohydrate components such as high neutral detergent fiber, acid detergent fiber, and acid detergent lignin have negative effects on haulm quality due to their indigestibility (Samireddypalle et al., 2017). Neutral detergent fiber includes all cell wall components and acid detergent fiber. Acid detergent fiber corresponds to cellulose and lignin contents (Mertens, 2000).

Core Ideas

- Diverse groundnut germplasm collections are available and can be evaluated for drought.
- Strong correlations observed among haulm quality traits under drought-stressed and optimum conditions.
- The study identified genotypes with high kernel and haulm yields and drought tolerance.

Due to its multiple uses and relatively higher drought tolerance, groundnut is grown in the mixed crop–livestock production systems in sub-Saharan Africa and Asia mainly by small-holder farmers. These agro-ecosystems are drought-prone where land, water, and natural pastures are becoming increasingly scarce (Abady et al., 2019). Drought stress caused by low precipitation is the leading cause of the decline of natural grazing lands resulting in high livestock mortality. For example, in Tanzania livestock mortality, herd value and income losses attributed to drought accounted for 5, 4, and 31%, respectively (Ahmed et al., 2019). Similarly, small-holder farmers in some parts of Ghana reported chronic water shortages for both human and livestock due to drought (Ngcamu & Chari, 2020). Drought stress occurring during the reproductive growth stage is the most devastating that can lead to a yield loss reaching up to 33% (Carvalho et al., 2017; Pereira et al., 2016). Therefore, it is an overriding consideration to develop and deploy dual-purpose groundnut cultivars with high kernel and haulm yields and associated quality parameters with drought tolerance. In the past there was no dedicated groundnut breeding program that aimed at breeding genotypes with high kernel and haulm yields with quality attributes under drought stress environments.

Groundnut exhibits extensive phenotypic and genotypic diversity (Pandey et al., 2012; Ren et al., 2014; Upadhyaya et al., 2005; Zheng et al., 2018). Moreover, marked variation for drought tolerance has been reported in groundnut germplasm collections (Falke et al., 2019; Frimpong et al., 2019; Hamidou et al., 2012). These present opportunities to develop fit-for-purpose genotypes for food and feed with drought tolerance. The International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) in India maintains the world's largest collection of groundnut germplasm which are essential sources of genetic variation with desirable attributes for breeding. The groundnut genetic resources at ICRISAT mainly comprise of the Spanish (subspecies *fastigiata*) and Virginia (subspecies *hypogaea*) market types. Many of these genotypes possess desirable agronomic traits which can be exploited for designing new groundnut cultivars (Singh & Nigam, 2016). Therefore, the diverse groundnut germplasm collections can be sourced and rigorously evaluated for drought tolerance and kernel and fodder yield and associated quality traits to select unique genotypes for breeding. In light of the above background, the objective of this study was to determine the response of diverse groundnut genotypes for drought tolerance, kernel and fodder yield, and quality for direct production or breeding.

2 | MATERIAL AND METHODS

2.1 | Plant materials, site description, and experiment design

Hundred groundnut genotypes acquired from ICRISAT in Patancheru, India were used for the study. The list of the genotypes with pedigree information are shown in Supplemental Table S1. Of these genotypes, 70 belonged to the subsp. *fastigiata* var. vulgaris and 30 to the subsp. *hypogaea* var. hypogaea. The genotypes were selected based on desirable traits including drought tolerance, resistance to foliar diseases such late leaf spot and rust, high oil and oleic acid contents, and being early-to-medium maturing. The genotypes were evaluated under drought-stressed (DS) and nonstressed (NS) conditions at ICRISAT (latitude, 17.51˚N, longitude, 78.27˚E and altitude 545 m) during the 2018–2019 and 2019–2020 postrainy cropping seasons using a 10-by-10 α-lattice design with two replications. Seed of each genotype were sown in four, 4-m-long rows with 30 cm between rows and 10 cm between plants. The field was maintained with regular irrigation until flowering for NS and DS treatments, after which irrigation was withdrawn for the DS treatment to induce moisture stress. For the NS treatment, sufficient irrigation was supplied until physiological maturity. Other agronomic practices were carried out following the standard guideline for groundnut production (Janila, Manohar et al., 2018).

2.2 | Data collection

Data were collected on kernel and haulm yields (KY and HY, respectively) from each plot and converted to tons per hectare (t ha^{-1}). Oil yield in t ha^{-1} (OY = oil content in % times kernel yield in t ha^{-1}), the contents of total oil (OC), total protein (TPC), palmitic acid (PAC), stearic acid (SAC), oleic acid (OAC), and linoleic acid (LAC) contents of the kernels were estimated using a Near Infrared Spectroscopy (NIRS; XDS monochromator, FOSS Analytical AB, Hillerød, Sweden; Deshmukh et al., 2020). Data on dry HY was collected and expressed in t ha^{-1}. Briefly, the haulm samples were collected at physiological maturity by cutting from aboveground at the soil surface followed by oven drying at 70 ˚C for 3 d. Subsequently, haulm weights were recorded, and the samples were ground into powder for NIRS analysis. Haulm fodder quality parameters including the contents of dry matter (DM), ash, neutral detergent fiber (NDFDM), acid detergent fiber (ADFDM), acid detergent lignin (ADLDM), and in vitro digestibility (IVOMD), and metabolizable energy (ME) were estimated using a NIRS using a FOSS Forage Analyzer 5000 with software package WinISI II (Kadim et al., 2005). Nitrogen was determined using the Kjeldahl method (Da Silva et al., 2016).

2.3 | Data analysis

Data was subjected to analysis of variance using SAS version 9.3 Software. Differences between treatment means were determined using the least significant difference (LSD) test at 5% significance level. Heritability in a broad sense (H^2) was calculated according to Hill et al. (2012) using the following formulae: $H^2 = V_g/[V_g + V_{ge}/e + V_e/re]$ where V_g is genetic variance, V_{ge} is genotype × environment interaction variance, V_e is error variance, e is number of environments, and r number of replications. Stress tolerance index (STI) was calculated to select high kernel and haulm yielding genotypes under DS and NS conditions using the following formula (Fernandez, 1992): $\mathrm{STI} = (Y_p Y_s)/(Y_{\bar{p}})^2$ where Y_s is yield of genotypes under DS condition; Y_p is yield of genotypes under NS condition, and $Y_{\bar{p}}$ is mean yield of test genotypes under NS condition. Pearson correlation coefficients was performed using SAS software to determine the level of association among the assessed traits. Principal component analysis was performed using JMP software. Principal component biplots were constructed to determine association among traits and groundnut genotypes to aid simultaneous selection of genotypes with multiple traits. Hierarchical cluster analysis based on Ward method was computed using JMP Trail 15 version software to determine genetic groupings of the test genotypes. For subspecies comparison, the mean values for the two subspecies were statistically compared using a t-test at 5% level of significance. Boxplots were constructed using the ggpubr package in R version 4.0 (R Core Team, 2020).

3 | RESULTS

3.1 | Effects of genotypes, water regimes, and seasons on KY, HY, OC, and haulm quality parameters

Combined analysis of variance revealed highly significant ($p < .05$) genotype differences for kernel yield, OC, and fatty acids contents (Table 1). Significant genotype by water regime interaction effect was recorded for kernel yield and OC.

TABLE 1 Mean squares and significant test among 100 groundnut genotypes evaluated for kernel yield (KY), oil content (OC), fatty acid compositions, and haulm yield (HY) and quality attributes across 2018–2019 and 2019–2020 postrainy seasons under drought-stressed and nonstressed conditions

		Kernel yield, oil content, and fatty acid compositions							
Source of variation	***df***	**KY**	**OC**	**OY**[a]	**TPC**	**PAC**	**SAC**	**OAC**	**LAC**
Year (Y)	1	74.55**	373.46**	14.20**	350.05**	0.041ns	85.02**	15.61ns	51.03ns
Water regime (WR)	1	186.61**	357.04**	46.48**	898.93**	11.06*	32.31**	1487.74**	2138.93**
Genotype (G)	99	0.58**	21.02**	0.14**	10.68**	20.11**	0.61**	774.97**	547.64**
Rep (Y)	2	2.01**	82.27**	0.69**	114.23**	5.61*	6.34**	60.65ns	266.49**
Block (Y × Rep)	36	0.15ns	3.91ns	0.03ns	4.23ns	0.73ns	0.077ns	37.708ns	22.25ns
G × WR	99	0.26*	6.78*	0.07*	3.17ns	0.81ns	0.15	35.13ns	24.22ns
G × Y	99	0.30**	5.85*	0.07**	6.06*	1.46*	0.16ns	51.41*	36.01*
G × WR × Y	100	0.44**	11.36**	0.17**	8.10**	0.95ns	0.30**	47.25*	37.31*
Error	362	0.15	4.52	0.039	3.81	0.95	0.15	35.68	25.45

		Haulm yield and quality parameters								
Source of Variation	***df***	**HY**	**DM**	**Ash**	**NC**	**NDFDM**	**ADFDM**	**ADLDM**	**IVOMD**	**ME**
Year (Y)	1	174.03**	722.36**	208.75**	13.02**	3600.71**	56.56**	31.04**	708.05**	16.96**
Water regime (WR)	1	678.03**	4.08**	519.04**	6.04**	62.94**	112.34**	5.94**	282.77**	18.57**
Genotype (G)	99	6.11**	0.14*	2.93**	0.06**	7.00*	5.49*	0.32*	3.33**	0.09**
Rep (Y)	2	47.99**	0.79*	8.07*	0.10*	7.14ns	30.78*	1.01*	19.33**	0.65**
Block (Y × Rep)	36	2.62*	0.05ns	2.03ns	0.03ns	5.01ns	5.09ns	0.28ns	2.23*	0.06*
G × WR	99	1.62ns	0.08ns	2.50*	0.04*	6.69*	4.53ns	0.27*	1.85ns	0.05ns
G × Y	99	1.68ns	0.10ns	2.13*	0.03ns	5.42*	4.07ns	0.29*	1.86ns	0.05ns
G × WR × Y	100	5.17**	0.10ns	2.68**	0.02ns	4.33ns	4.92*	0.50**	2.17*	0.06*
Error	362	1.52	0.09	1.54	0.02	4	3.54	0.2	1.52	0.2

[a]OY, oil yield; TPC, total protein content; PAC, palmitic acid content; SAC, stearic acid content; OAC, oleic acid content; LAC, linoleic acid content; HY, haulm yield; DM, dry matter; NDFDM, Neutral detergent fiber; ADFDM, acid detergent fiber; ADLDM, acid detergent lignin; IVOMD, in vitro organic matter digestibility; ME, metabolizable energy.
*Significant at the .05 probability level;
**Significant at the .01 probability level; ns, nonsignificant.

Genotype × year interaction effect was significant for all traits except SAC, whereas genotype × water regime × year interaction effect was significant for all traits except PAC. Analysis of variance revealed highly significant ($p < .05$) genotype differences for HY and quality parameters. Also, significant genotype × water regime interaction effect was noted for nitrogen, NDFDM, and ADLDM. Genotype × year interaction effect was significant for ash, NDFDM, and ADLDM, whereas genotype × water regime × year interaction effect was significant for HY, ash, ADLDM, IVODM, and ME.

3.2 | Performance of groundnut genotypes for KY, OC, and fatty acids composition under NS and DS conditions

Mean performance of the assessed groundnut genotypes for (KY, OC, and fatty acid composition under DS and NS conditions in the 2018–2019 and 2019–2020 postrainy seasons are presented in Table 2 and Supplemental Table S2. Highly significant ($p < .001$) genotype differences were recorded for KY under NS and DS conditions. Under DS condition, the highest KY was recorded for ICGV 06040 (1.2 t ha^{-1}), ICGV 7222 (1.17 t ha^{-1}), ICGV 01260 (1.14 t ha^{-1}), ICGV 10178 (1.11 t ha^{-1}), ICGV 06175 (1.1 t ha^{-1}), and ICGV 10373 (1.07 tha^{-1}). Genotypes ICGV 10143, ICGV 7222, ICGV 03042, ICGV 06039, ICGV 98412, ICGV 14001, and ICGV 06040 were high-yielding (>2 t ha^{-1}) under NS condition.

For OC, highly significant ($p < .001$) differences were recorded among the test genotypes under both conditions. Under DS condition, the highest OC was recorded for ICGV 10379 (53.9%), ICGV 00064 (52.8%), ICGV 86699 (52.07%), ICGV 95111 (51.97%), and ICGV 96266 (51.14%). Genotypes ICGV 98385, ICGV O1279, GPBD 4, and ICGV 00246 recorded high OC of >50% under NS condition. Highly significant ($p < .001$) genotype differences were recorded for OY under both conditions. Under DS condition, the highest OY was recorded for ICGV 6040 (0.58 t ha^{-1}), ICGV 10178 (0.54 t ha^{-1}), ICGV 01260 (0.54 t ha^{-1}), ICGV 7222 (0.53 t ha^{-1}), ICGV 10373 (0.52 t ha^{-1}), and ICGV 06175

TABLE 2 Mean values for kernel yield (KY), total protein content (TPC), and fatty acid compositions of 100 groundnut genotypes and the top 15 best and bottom five performing genotypes when evaluated under drought-stressed (DS) and nonstressed (NS) conditions in 2018–2019 and 2019–2020 postrainy seasons, ranked based on KY under DS conditions

	KY		OC		OY[a]		TPC		PAC		SAC		OAC		LAC	
Genotypes	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
	$t\ ha^{-1}$		%		$t\ ha^{-1}$		%									
Top 15 genotypes																
ICGV 6040	1.20	2.36	48.63	51.99	0.58	1.23	27.80	26.87	13.31	13.33	2.99	2.76	40.61	37.68	35.52	38.87
ICGV 7222	1.17	2.64	45.50	49.1	0.53	1.30	30.28	27.05	12.49	13.05	2.71	2.41	44.78	37.85	32.25	39.19
ICGV 01260	1.14	1.72	47.31	47.12	0.54	0.81	27.75	26.46	12.39	12.72	3.04	2.81	44.61	42.35	32.58	35.16
ICGV 10178	1.11	1.46	48.62	47.09	0.54	0.69	25.76	24.47	13.2	13.45	2.96	2.70	38.97	36.43	37.01	39.04
ICGV 06175	1.10	2.09	46.87	50.45	0.52	1.05	28.34	24.27	12.56	12.95	2.47	2.22	45.25	38.23	32.41	39.17
ICGV 10373	1.07	1.65	48.53	50.19	0.52	0.83	27.57	25.96	12.67	12.13	2.63	2.17	43.69	50.61	33.77	28.71
ICGV 10143	1.00	2.89	45.41	49.19	0.45	1.42	30.16	28.27	12.22	12.99	2.89	2.45	44.53	37.65	32.11	39.28
ICGV 171046	0.99	1.40	46.25	51.01	0.46	0.71	30.44	26.60	8.61	8.39	2.89	2.86	67.91	64.82	12.38	16.65
ICGV 14421	0.96	2.19	45.65	50.87	0.44	1.11	28.06	25.98	11.77	12.61	2.18	2.39	43.94	39.64	34.00	39.05
ICGV 03042	0.94	2.52	47.79	49.59	0.45	1.25	25.96	24.45	12.65	13.33	2.66	2.18	42.39	35.77	34.85	41.12
ICGV 13200	0.94	1.55	47.74	49.80	0.45	0.77	27.16	27.55	11.53	11.37	2.79	2.60	46.37	45.20	31.79	34.20
ICGV 11380	0.91	2.16	47.22	51.42	0.43	1.11	31.87	26.34	12.31	12.08	3.01	2.66	46.36	42.20	31.43	37.03
ICGV 99241	0.91	1.76	48.99	51.59	0.45	0.91	24.43	23.01	12.78	12.82	2.93	2.59	40.51	36.52	36.08	41.10
ICGV 181017	0.90	1.49	47.6	47.72	0.43	0.71	29.65	28.22	8.20	8.00	2.58	2.01	70.65	72.12	10.20	8.72
ICGV 92121	0.89	1.58	44.91	48.58	0.40	0.77	28.98	28.09	11.88	12.57	2.90	2.44	46.93	38.75	30.06	38.05
Bottom five genotypes																
ICGV 11396	0.37	2.10	49.93	49.42	0.18	1.04	27.34	25.02	12.99	12.64	3.05	2.21	41.4	38.01	34.00	39.04
ICGV 97150	0.32	0.76	48.58	49.5	0.16	0.38	26.34	25.13	12.30	12.93	2.41	2.10	53.04	49.59	25.93	30.40
ICGV 7220	0.30	2.00	46.65	48.85	0.14	0.98	29.61	27.01	12.95	12.76	2.97	2.59	42.07	38.84	33.73	37.84
ICGV 98385	0.29	1.07	50.11	52.83	0.15	0.57	26.04	23.88	12.53	12.76	2.56	2.34	53.56	49.95	25.95	31.44
ICGV 11422	0.26	1.24	48.35	49.4	0.13	0.61	25.90	24.16	13.24	12.98	2.89	2.11	38.46	38.34	37.06	38.73
Mean	0.68	1.65	47.75	49.09	0.33	0.81	27.9	25.78	11.62	11.86	2.84	2.43	49.57	46.84	28.39	3.66
H^2, %	91.03	67.31	32.03	16.64	80.26	76.76	35.37	16.55	64.77	52.37	76.94	72.23	5.08	2.77	7.37	3.82
P-value	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001
SED	0.23	0.5	1.93	2.13	0.11	0.24	1.74	2.01	0.98	0.97	0.31	0.46	6.02	5.96	4.93	5.13
$LSD_{.05}$	0.32	0.69	2.68	2.96	0.15	0.33	2.43	2.8	1.36	1.35	0.43	0.63	8.4	8.31	6.87	7.15
CV, %	33	30	4.03	4.33	34.82	29.76	6.25	7.8	8.41	8.16	11.07	18.76	12.15	12.73	17.36	16.19

[a]OY , oil yield; PAC, palmitic acid content; SAC, stearic acid content; OAC, oleic acid content; LAC, linoleic acid content; H^2, heritability in the broad-sense; SED, standard error of the mean differences; LSD, least significant difference; CV, coefficient of variation.

(0.52 t ha^{-1}). Genotypes ICGV 10143, ICGV 06039, ICGV 7222, ICGV 03042, ICGV 14001, and ICGV 06040 recorded high OY (>1.2 t ha^{-1}) under NS condition. Significantly higher TPC (>30%) was recorded in genotypes ICGV 11380, ICGV 171007, ICGV 181490, and ICGV 171046 under DS condition, whereas genotypes ICGV 06146, ICGV 13219, ICGV 14030, and ICGV 10143 recorded high TPC (>28%) under NS condition.

Palmitic acid content differed significantly among the assessed groundnut genotypes under both conditions. Under DS condition, the highest PAC was recorded for ICGV 00187 (13.76%), ICGV 13254 (13.54%), ICGV 00213 (13.39%), ICGV 06040 (13.31%), and ICGV 96165 (13.29%). Under NS condition, genotypes ICGV 00187, ICGV 96165, and ICGV 94118 had the highest PAC (>14%). For SAC, the highest value was recorded for ICGV 00213 (3.66%), ICGV 98412 (3.58%), ICGV 96174 (3.54%), and ICGV 00187 (3.5%) under DS condition, whereas genotypes ICGV 94118, ICGV 98412, GG 20, and ICGV 13254 recorded high concentrations (>3%) under NS condition. Highly significant (p < .001) genotype differences were observed for OAC under both conditions. The highest OAC was recorded for ICGV 181026 (71.64%), ICGV 15019 (71.16%), ICGV 181017 (70.65%), ICGV 181063 (69.68%), and ICGV 16667 (68.89%) under DS condition, whereas ICGV 181026, ICGV 181017, ICGV 171027, ICGV 16688, and ICGV 15074 recorded high OAC (>69%) under NS condition. Highly significant (p < .001) genotype differences were observed for linoleic acid. Under DS condition, genotypes ICGV 181026, ICGV 181017, ICGV 15019, ICGV 181063, ICGV 16667, ICGV 171046, and ICGV 171026 expressed low LAC (<13%) under NS condition. High H^2 values (>70%) were recorded for KY, OY, and SAC under both water conditions. Low to medium H^2 values were observed for OAC, LAC, OC, TPC, and PAC under both moisture conditions (Table 2).

3.3 | Performance of groundnut genotypes for HY and quality parameters

Mean performance of groundnut genotypes for HY and quality parameters under DS and NS conditions are presented in Table 3 and Supplemental Table S3. Significant genotype differences were observed among the test genotypes for HY under both conditions. Under DS condition, the highest HY was recorded for ICGV 01260 (7.79 t ha^{-1}), ICGV 96165 (7.29 t ha^{-1}), ICGV 171027(6.88 t ha^{-1}), ICGV 96266 (6.71 t ha^{-1}), and ICGV 14232 (6.51 t ha^{-1}), whereas genotypes ICGV 01491, ICGV 181006, ICGV 00211, and ICGV 97115 recorded high HY (>8.5 t ha^{-1}) under NS condition.

Higher H^2 value (>60%) was recorded for HY and ME under DS condition and nitrogen content (NC) under NS condition, whereas lower H^2 value was recorded for ash content, DM, ADFDM, and ADLDM under DS condition. Under NS condition, higher NCs were recorded for genotypes ICGV 93162 (2.94%), ICGV 171007 (2.91%), and ICGV 99019 (2.84%), whereas genotypes ICGV 01491, ICGV 171007, ICGV 171039, and ICGV 05057 recorded high NC of >3% under DS condition. Significantly (p < .001) higher ash contents were recorded for ICGV 86015 (18.36%), ICGV 96165 (17.18%), ICGV 14232 (17.15%), ICGV 14421 (16.27%), and ICGV 7220 (15.95%) under DS condition. Highly significant (p < .001) differences were recorded among groundnut genotypes for NDFDM under DS condition. Under DS condition, the lowest NDFDM was recoded for genotypes ICGV 86015 (32.03%), ICGV 96165 (34.29%), ICGV 14232 (37.04%), and ICGV 00187 (37.23%). Significant (p < .05) genotype differences were observed for ADFDM and ADLDM under DS condition. The highest ADFDM was noted for ICGV 03043 (31.93%), ICGV 00211 (31.4%), ICGV 171013 (31.3%), and ICGV 16667 (31.24%), whereas genotypes ICGV 171039, ICGV 181033, ICGV 13200, ICGV 14030, and ICGV 13219 recorded low ADFDM of <27% under DS. High ADLDM were recorded for ICGV 181489 (5.56%), ICGV 16667 (5.54%), ICGV 00211 (5.46%), ICGV 03043 (5.43%), and ICGV 171013 (5.43%), whereas genotypes ICGV 171039 (4.21%), ICGV 14030 (4.24%), ICGV 181033 (4.36%), ICGV 171046 (4.38%) and ICGV 13219 (4.39%) recorded low ADLDM of <5% under DS condition. Groundnut genotypes differed significantly (P < .05) for IVODM under DS condition. The highest IVODM was recorded for GG 20 (63.52%), ICGV 171007 (63.43%), ICGV 14030 (63.41%), ICGV 86031 (63.23%), and ICGV 13219 (63.07%) under DS condition. Significant genotype differences were observed among the genotypes for ME under both conditions. Under DS condition, high ME values were recorded for GG 20 (63.52%), ICGV 171007 (63.43%), ICGV 14030 (63.41%), CGV 86031(63.23%), and CGV 13219 (63.07%).

3.4 | Comparison of groundnut subspecies for KY, HY, and quality parameters

Comparison of groundnut subspecies (i.e., *fastigiata and hypogaea*) for KY and HY and kernel and fodder quality under DS and NS conditions are presented in Figure 1 and Supplemental Figure S1. Significant (p < .05) difference was recorded between the two subspecies for KY with *fastigiata* recoding higher KY. Under both conditions, significant differences were observed between the two subspecies for OC. Subspecies *hypogaea* recorded high mean OC of 48.87% and 49.75% under DS and NS conditions compared to subspecies *fastigiata.* There were nonsignificant differences between the two subspecies for TPC, PAC, SAC, OAC, and LAC under both conditions. Significantly (p < .001) higher HY was recorded for subspecies *hypogaea*

TABLE 3 Mean values for haulm yield (HY) and fodder quality parameters of 100 groundnut genotypes and the top 15 best and bottom five performing genotypes when evaluated under drought-stressed (DS) and nonstressed (NS) conditions in 2018–2019 and 2019–2020 postrainy seasons, ranked based on HY under DS conditions

Genotypes	HY		DM[a]		Ash		NC		NDFDM		ADFDM		ADLDM		IVOMD		ME	
	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
	t ha^{-1}		%															
Top 15 genotypes																		
ICGV 01260	7.79	7.66	91.74	91.55	12.5	12.26	2.57	2.62	38.8	35.49	30.24	27.08	5.19	4.74	60.26	62.65	8.46	8.81
ICGV 96165	7.29	6.88	92.06	91.55	17.18	13.23	2.77	2.72	32.86	34.29	29.68	27.03	4.76	4.83	60.48	62.66	8.29	8.8
ICGV 171027	6.88	7.36	91.6	91.49	13.84	11.49	2.78	2.52	35.91	39.12	28.33	29.27	4.6	5.26	61.59	61.49	8.52	8.68
ICGV 96266	6.71	7.65	91.91	91.63	15.33	11.56	2.75	2.68	34.68	36.46	29.74	28	4.81	5.05	61.36	63.45	8.47	8.98
ICGV 14232	6.51	6.66	91.87	91.33	17.15	12.75	2.64	2.67	33.18	37.04	30.81	28.7	4.93	4.95	59.9	61.83	8.21	8.69
ICGV 93162	6.47	7.38	91.97	91.46	13.16	11.81	2.73	2.94	38.51	36.29	30.85	26.34	5.34	4.64	61.1	63.58	8.5	8.92
ICGV 99241	6.35	8.28	91.58	91.27	12.47	12.19	2.78	2.57	35.63	36.58	26.78	28.6	4.39	5.27	62.88	63.07	8.78	8.99
ICGV 00064	6.3	7.75	91.79	91.68	15.22	12.92	2.84	2.72	34.86	35.57	28.99	28.22	4.82	5.14	61.23	62.35	8.42	8.73
ICGV 10178	6.28	7.41	91.52	91.55	13.18	12.31	2.51	2.59	39.41	36.62	31.09	28.43	5.2	5.07	60.38	62.7	8.46	8.85
ICGV 92121	6.26	7.27	91.32	91.63	12.89	11.94	2.83	2.72	36.85	35.71	28.05	26.58	4.59	4.8	62.7	63.55	8.78	8.93
ICGV 98077	6.14	7.6	91.84	91.65	15.02	12.31	2.96	2.72	36.33	36.03	29.41	27.83	5.03	4.87	59.98	62.76	8.18	8.81
ICGV 98184	6.11	6.49	92.05	91.11	15.73	12.35	2.65	2.51	35.2	38.55	30.7	29.56	4.93	5.24	61.04	61.24	8.44	8.69
ICGV 181489	6.06	7.92	91.59	91.47	13.57	12.53	2.7	2.65	37.45	36.97	30.86	28.7	5.56	5.17	61.19	62.66	8.5	8.82
GG 20	6.02	7.43	91.82	91.53	12.24	12.14	2.87	2.75	35.52	35.1	27.25	26.95	4.5	4.92	63.52	63.76	8.88	8.99
ICGV 11422	6	8.23	91.69	91.53	14.39	12.77	2.77	2.6	35.39	36.35	29.07	27.95	4.97	4.83	61.65	62.14	8.53	8.71
Bottom five genotypes																		
ICGV 11380	3.54	5.55	91.39	91.35	13.07	12.01	2.79	2.63	36.05	37.12	28.32	28.58	4.62	5.03	61.79	62.39	8.64	8.85
GPBD 4	3.47	6.15	91.51	91.43	14.43	11.99	2.83	2.55	34.4	37.49	27.45	28.04	4.44	4.92	62.3	62.55	8.6	8.85
ICGV 13189	3.4	5.32	91.22	91.26	12.7	12.09	2.69	2.46	37.54	35.24	29.42	26.6	5.15	4.59	62.52	64.14	8.84	9.11
ICGV 93260	3.09	6.51	91.43	91.42	15.45	12.26	2.91	2.6	34.31	37.15	28.5	28.5	4.56	5.02	61.14	62.72	8.42	8.89
ICGV 13207	2.66	3.54	91.44	91.35	14.16	13.49	2.58	2.52	35.32	35.9	29.45	28.66	4.99	5.06	60.94	61.9	8.6	8.76
Mean	5.08	6.92	91.57	91.42	13.89	12.28	2.78	2.6	36.04	36.5	28.99	28.24	4.86	5.03	61.37	62.56	8.53	8.84
H^2, %	60.70	29.11	32.68	15.23	40.57	19.91	39.76	67.82	27.07	15.02	24.56	15.48	47.62	37.31	42.02	33.18	67.82	56.18
P-value	<.001	<.001	.06	.29	<.001	.19	<.001	<.001	<.001	.11	.003	.16	.012	.06	.002	.008	<.001	.001
SED	1.09	1.49	0.34	0.25	1.44	0.93	0.16	0.15	2.16	1.88	2.11	1.67	0.47	0.42	1.41	1.16	0.22	0.18
$LSD_{.05}$	1.53	2.08	0.48	0.35	2.09	1.3	0.22	0.2	3.01	2.62	2.94	2.33	0.67	0.59	1.96	1.62	0.3	0.24
CV, %	21.62	21.58	0.37	0.28	10.42	7.61	5.93	5.62	5.99	5.13	7.27	5.93	9.84	8.45	2.29	1.85	2.59	2.06

[a]DM, dry matter; NC, nitrogen content; NDFDM, neutral detergent fiber; ADFDM, acid detergent fiber; ADLDM, acid detergent lignin; IVOMD, in vitro organic matter digestibility; ME, metabolizable energy; H^2, heritability in the broad sense; SED, standard error of the mean differences; LSD, least significant difference; CV, coefficient of variation.

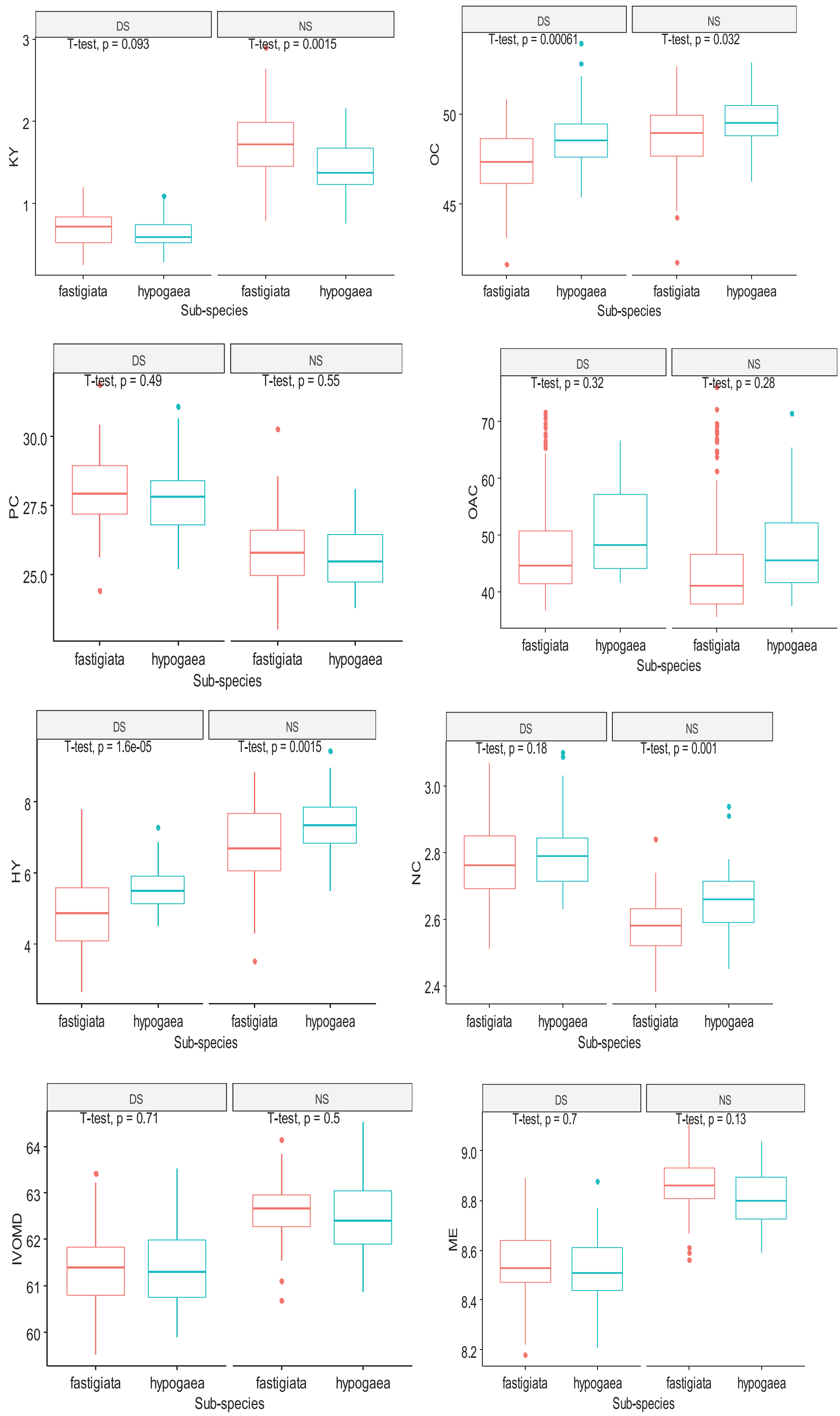

FIGURE 1 Mean response of groundnut subspecies for kernel and haulm yields, and kernel and fodder quality parameters under drought-stressed (DS) and nonstressed (NS) conditions evaluated during 2018–2019 and 2019–2020 postrainy seasons at the International Crops Research Institute for the Semi-Arid Tropics, India. KY, kernel yield; OC, oil content; PC, protein content; OAC, oleic acid content; HY, haulm yield; NC, nitrogen content; IVOMD, in vitro organic matter digestibility; ME, metabolizable energy

under DS (mean = 5.64 t ha^{-1}) and NS (mean = 7.44 t ha^{-1}) compared to subspecies *fastigiata*. Subspecies *hypogaea* recorded significantly higher DM content of 91.77% than subspecies *fastigiata* under DS condition. Ash content showed nonsignificant differences between the two *Arachis* subspecies under both conditions. Under NS condition, significant ($p < .05$) differences were recorded between the two subspecies for NC with subspecies *hypogaea* recording higher mean NC of 2.80%. For NDFDM and ADFDM, nonsignificant subspecies differences in mean values were observed under both water conditions. Subspecies *hypogaea* had high mean value for ADLDM (5.12%) compared to lower value of 4.99% for subspecies *fastigiata* under NS condition. For IVODM and ME, nonsignificant differences were detected between the two subspecies under both water conditions. Except for OAC and PAC, significant ($p < .05$) difference was recorded between DS and NS treatments (Supplemental Figure S2). Higher mean values were recorded for TPC, SAC, DM, ash, and NC under DS than NS condition.

3.5 | Drought stress tolerance

Stress tolerance index (STI) of the assessed groundnut genotypes is presented in Table 4. The STI was used to identify genotypes that can provide high yields under both stressed and nonstressed conditions (Fernandez, 1992). Higher STI values for KY were recorded for ICGV 7222 (STI = 1.14), ICGV 10143 (1.06), ICGV 6040 (1.04), ICGV 03042 (0.87), and ICGV 06175 (0.85). For HY, groundnut genotypes such as ICGV 01260, ICGV 99241, ICGV 96266, ICGV 171027, and ICGV 01491 recorded higher STI values of >1 indicating the stable performance of the genotypes under both conditions. Genotypes ICGV 7222, ICGV 10143, ICGV 01260, and ICGV 99241 are drought tolerant and ICGV 6040 is early maturing genotypes developed by ICRISAT in India (Table S1).

3.6 | Relationships between KY and HY and oil and haulm quality parameters under NS and DS conditions

Pearson correlation coefficients showing relationships among KY and HY and kernel and haulm quality parameters among the 100 groundnut genotypes evaluated under DS and NS conditions are presented in Tables 5. Under DS condition, KY was positively correlated ($p < .001$) with OY ($r = .99$) and negatively and significantly correlated ($P < .05$) with SAC ($r = .63$). Oil content exhibited positive and significant correlation with OY ($r = .12$) and OAC ($r = .12$). Kernel yield was poorly and positively correlated with HY ($r = .14$), but negatively correlated with DM (.76), NC (.53), IVODM (.37), and ME (.33). Contrastingly, KY positively and significantly correlated with ash content ($r = .32$), NDFDM ($r = .54$), ADFDM ($r = .18$), and ADLDM ($r = .46$). Haulm yield was positively correlated with OY ($r = .15$) and negatively correlated with NC ($r = .20$), IVODM ($r = .13$), and ME (0.12), and positive correlation with NDFDM ($r = 0.19$), ADFDM ($r = .18$), and ADLDM ($r = .17$).

Under NS condition, KY exhibited positive correlations with OY ($r = .98$), protein content ($r = .11$) and LAC ($r = .15$). Oil content exhibited low and positive correlation with OY ($r = .14$), SAC (.19) and LAC (.18). Haulm yield exhibited positive correlation with OC (.31), DM ($r = .54$), ash content ($r = .4$), NC ($r = .4$), ME ($r = .4$), and IVODM ($r = .43$). Positive correlations were recorded between NC and IVODM (.67), NC and ME (.51), and IVODM and ME (.94). Positive correlations were observed between NC and IVODM (.72), NC and ME (.56), and IVODM and ME (.95). Positive correlations were recoded between neutral detergent fiber and ADFDM ($r = .62$), NDFDM and ADLDM ($r = .84$), and ADFDM and ADLDM ($r = .79$). Positive correlations were observed between NDFDM and ADFDM ($r = .5$), NDFDM and ADLDM ($r = .5$), and ADFDM and ADLDM ($r = .85$).

3.7 | Principal component and biplot analyses

Principal component analysis for the assessed traits among 100 groundnut genotypes revealed five and six principal components (PCs) with Eigenvalues greater than one under DS and NS condition, respectively. The principal component accounted for 79.35% and 82.54% of the total phenotypic variation under DS and NS conditions, respectively (Table 6). Under DS condition, PC1 positively correlated with ADFDM, ADLDM, and NDFDM and negatively correlated with IVODM and ME which accounted for 25.71% of total variation. Oleic acid content positively correlated with PC2, whereas PAC, LAC, and SAC negatively correlated with PC2 which accounted for 17.36% of total variation. Kernel yield, OY, and PC positively correlated with PC3 which accounted for 14.08% of total variation. Oil content and HY positively correlated with PC4 which accounted for 12% of total variation. Kernel yield and OY positively correlated with PC5 which accounted for 10.22% of total variation.

Under NS condition, NDFDM, ADFDM, and ADLDM positively correlated with PC1 whereas NC negatively correlated with PC1 which accounted for 24.38% of total variation. Kernel yield, OY, PAC, SAC, and LAC positively correlated with PC2, whereas OAC negatively correlated with PC2 which accounted for 21.68% of total variation. PC3 positively correlated with HY and negatively correlated with PC and ash content and both traits accounted for 13.02% of total variation. PC4 positively correlated with ME which

TABLE 4 Stress tolerance index (STI) of 100 groundnut genotypes based on kernel yield (KY) and haulm yield (HY) evaluated under drought-stressed and nonstressed conditions in 2018–2019 and 2019–2020 postrainy seasons

Number	Genotypes	STI KY	STI HY	Number	Genotypes	STI KY	STI HY
1	ICGV 16667	0.27	0.91	51	ICGV 00350	0.53	0.68
2	ICGV 93128	0.24	0.70	52	ICGV 86590	0.42	0.80
3	ICGV 95066	0.41	0.77	53	ICGV 02266	0.54	0.55
4	ICGV 96174	0.19	0.77	54	ICGV 13189	0.58	0.38
5	ICGV 97087	0.32	1.01	55	ICGV 13207	0.36	0.20
6	ICGV 98077	0.18	0.97	56	ICGV 14421	0.77	0.49
7	ICGV 01279	0.33	0.83	57	ICGV 13219	0.25	0.34
8	ICGV 03042	0.87	0.68	58	GPBD 4	0.23	0.45
9	ICGV 06039	0.78	0.45	59	ICGV 86031	0.27	0.45
10	ICGV 6040	1.04	0.73	60	ICGV 16686	0.39	0.90
11	ICGV 07010	0.48	0.75	61	ICGV 16005	0.30	0.68
12	ICGV 10143	1.06	0.60	62	ICGV 171013	0.50	0.45
13	ICGV 11422	0.12	1.03	63	ICGV 171026	0.35	0.81
14	ICGV 11396	0.29	0.86	64	ICGV 171039	0.53	0.56
15	ICGV 11418	0.23	0.96	65	ICGV 171046	0.51	0.54
16	ICGV 91223	0.23	0.53	66	ICGV 181017	0.49	0.98
17	ICGV 94118	0.48	0.63	67	ICGV 181063	0.15	0.88
18	ICGV 99019	0.55	0.92	68	ICGV 98412	0.61	0.82
19	ICGV 00162	0.24	0.68	69	ICGV 181489	0.15	1.00
20	ICGV 00211	0.46	0.84	70	ICGV 181490	0.56	0.52
21	ICGV 00187	0.32	0.59	71	ICGV 92054	0.22	0.85
22	ICGV 00213	0.37	0.64	72	ICGV 93162	0.27	1.00
23	ICGV 06146	0.46	0.39	73	ICGV 95111	0.32	0.96
24	ICGV 07120	0.41	0.75	74	ICGV 96165	0.28	1.05
25	ICGV 10178	0.60	0.97	75	ICGV 97115	0.25	0.90
26	ICGV 11380	0.72	0.41	76	ICGV 98184	0.32	0.83
27	ICGV 14001	0.71	0.61	77	ICGV 01491	0.21	1.06
28	ICGV 14030	0.41	0.43	78	ICGV 03287	0.34	0.72
29	ICGV 86015	0.40	0.45	79	ICGV 05057	0.27	0.70
30	ICGV 93260	0.48	0.42	80	ICGV 06175	0.85	0.74
31	ICGV93261	0.49	0.41	81	ICGV 00064	0.39	1.02
32	ICGV 92121	0.52	0.95	82	ICGV 00246	0.31	0.75
33	ICGV 99241	0.59	1.10	83	ICGV 97150	0.09	0.91
34	ICGV 00351	0.36	0.65	84	ICGV 98385	0.11	0.94
35	ICGV 01260	0.72	1.25	85	ICGV 96266	0.16	1.07
36	ICGV 01265	0.45	0.63	86	ICGV 14224	0.52	0.88
37	ICGV 13200	0.54	0.37	87	ICGV 14232	0.48	0.91
38	ICGV 7220	0.22	0.40	88	ICGV 7262	0.35	0.65
39	ICGV 7222	1.14	0.53	89	ICGV 7247	0.43	0.69
40	ICGV 13317	0.65	0.64	90	ICGV 10371	0.33	0.69
41	ICGV 13254	0.40	0.80	91	ICGV 10373	0.65	0.87
42	ICGV 181026	0.34	0.70	92	ICGV 10379	0.54	0.96
43	ICGV 15073	0.36	0.77	93	ICGV 15094	0.18	0.86
44	ICGV 15074	0.49	0.64	94	ICGV 87846	0.46	0.89

(Continues)

TABLE 4 (Continued)

Number	Genotypes	STI KY	STI HY	Number	Genotypes	STI KY	STI HY
45	ICGV 15083	0.67	0.82	95	ICGV 86699	0.26	0.82
46	ICGV 15019	0.51	0.71	96	GG 20	0.44	0.93
47	ICGV 6420	0.52	0.84	97	ICGV 171007	0.20	0.70
48	ICGV 5155	0.40	0.63	98	ICGV 171027	0.28	1.06
49	ICGV 16688	0.48	0.92	99	ICGV 181006	0.21	0.97
50	ICGV 03043	0.50	0.71	100	ICGV 181033	0.68	0.91

accounted for 9.74% of total variation. PC5 positively correlated with DM which accounted for 7.64% of total variation. PC6 positively correlated with DM and negatively correlated with OC which accounted for 6.09% of total variation.

The relationship between groundnut genotypes and assessed traits based on principal component biplots under DS and NS conditions are presented in Figure 2. Smaller angles between dimension vectors in the same direction indicated high correlation of the variables in terms of discriminating genotypes. Genotypes that are good in a particular trait were plotted closer and furthest to the vector line. Under DS condition, genotypes ICGV 93162, ICGV 10373, ICGV 01260, ICGV 10379, ICGV 10178, ICGV 05155, ICGV 03042, and ICGV 96174 were grouped together based on high NDFDM, ADFDM, ADLDM, and DM, HY, OY, and KY Figure (2a). Genotypes ICGV 181017, ICGV 01491, ICGV 15019, ICGV 181026, ICGV 16005, and ICGV 181063 excelled with high OAC. Genotypes ICGV 171007, ICGV 181063, ICGV 171039, ICGV 181039, ICGV 93261, GPBD 4, and ICGV 13219 were grouped together and possessed high ME, IVODM, NC, and TPC.

Under NS condition, genotypes ICGV 7220, ICGV 06039, ICGV 05155, ICGV 03287, ICGV 06175, ICGV 14001, ICGV 00211 and ICGV 11396 were grouped together recording high KY, OY and OC (Figure 2b). Genotypes ICGV 181017, ICGV 181026, ICGV 181063, ICGV 181489, ICGV 181006, ICGV 16005 and ICGV 15083 were grouped together based on high dry matter content, HY, and OAC. Genotypes ICGV 171007, ICGV 13189, ICGV 99019, ICGV 86031, ICGV 86590, and ICGV 86699 were excelling in NC, ME, IVODM, and PC.

3.8 | Cluster analysis among groundnut genotypes based on KY, HY, and kernel and fodder quality parameters

Cluster analysis showing the grouping of 100 groundnut genotypes based on KY and HY, and kernel and fodder quality traits are summarized in Table 7 and Figure 3. The test genotypes were allocated into 12 genetic groups. Cluster 11 and 12 comprised of high kernel- and oil-yielding genotypes with mean of 1.72 t ha^{-1} and 0.84 t ha^{-1}. Genotypes with high OC (>49.5%) were grouped in Clusters 8 and 12. Clusters 1 and 2 comprised of high OAC groundnut genotypes with mean values of 65.57 and 66%, respectively. Conversely, Clusters 1 and 2 consisted of genotypes with lower LACs of <16%. Genotypes with high NC, IVODM, and ME were grouped in Clusters 4 and 5. Genotypes with higher HY possessing good haulm fodder qualities were grouped in Cluster 6. In this cluster, genotypes ICGV 01490, ICGV 96266, ICGV 93162, ICGV 98077, ICGV 11422, and ICGV 11418 recorded the highest mean HY (≥6.5 t ha^{-1}), NC (≥2.75%), IVODM (≥62%), and ME (≥8.5%).

4 | DISCUSSION

Groundnut is a key legume crop for food and feed in crop–livestock farming systems. It is the main source of cash for small-holder farmers in arid and semi-arid parts of sub-Saharan Africa and Asia. Despite the multiple uses of groundnut breeding for drought tolerance, high KY and HY, and quality traits have been largely ignored in groundnut improvement programs. As a result, genotypic variation of groundnut germplasm for KY and HY and kernel and haulm quality parameters remains largely unknown, thus limiting selection and development of dual-purpose groundnut cultivars for kernel and haulm production in smallholder crop–livestock systems.

The present study found significant variations in KY and HY, kernel and fodder quality parameters, and drought tolerance among genetically distinctive groundnut genotypes (Table 1). The significant genotype differences observed among the studied groundnut genotypes for KY and HY, and quality traits allowed selection of suitable dual-purpose genotypes (Table 1). Also, genotype × water regime × year interaction effect was significant for KY and HY, indicating that the performance of the assessed genotypes varied across seasons and water conditions (Table 1). Groundnut genotypes ICGV 7222, ICGV 10143, ICVG 06040, ICGV 03042, and ICGV 06175 were selected with marked drought tolerance and

TABLE 5 Pearson correlation coefficients among kernel (KY), haulm yields (HY), and kernel and fodder quality parameters in 100 groundnut genotypes evaluated under drought-stressed (upper diagonal) and nonstressed (lower diagonal) conditions in 2018–2019 and 2019–2020 postrainy seasons

Traits	KY	OC[a]	OY	TPC	PAC	SAC	OAC	LAC	HY	DM	Ash	NC	NDFDM	ADFDM	ADLDM	IVOMD	ME
KY		.04ns	.99**	.03ns	−.02ns	−.63**	−.05ns	.13*	.14*	−.76**	.32**	−.53**	.54**	.18*	.46**	−.37**	−.32**
OC	−.03ns		.12*	−.48**	−.03ns	−.04ns	.12*	−.05ns	.24**	−.02ns	.07ns	−.14*	.10*	.13*	.13*	−.08ns	−.09ns
OY	.98**	.14*		−.01ns	−.03ns	−.62**	−.04ns	.13*	.15*	−.76**	.33**	−.54**	.54**	.19*	.46**	−.37**	−.33**
TPC	.11*	−.62**	.01		−.07ns	.11*	.07ns	−.10*	−.21**	.01ns	−.02ns	.06ns	−.05ns	−.06ns	−.11*	.05ns	.04ns
PAC	.08ns	.06ns	.09	−.08ns		.13*	−.89**	.87**	.02ns	.03ns	.08ns	−.04ns	−.02ns	.06ns	.04*	−.14*	−.13*
SAC	−.04ns	.19*	−.01	.04ns	.28**		−.13*	.02ns	−.08ns	.68**	−.30**	.44**	−4.08	−.22**	−.49**	.31**	.28**
OAC	−.15*	−.11*	−.17	.16*	−.89**	−.32**		−.98**	.02ns	.04ns	−.04ns	.10ns	−.07ns	−.07ns	−.09ns	.18*	.15*
LAC	.15*	.18*	.18	−.21**	.86**	.24**	−.99**		−.01ns	−.12*	.08ns	−.16*	.13*	.10*	.15*	−.22**	−.18*
HY	−.02ns	.33**	.04	−.44**	−.07ns	.03ns	.05ns	−.04ns		.01ns	.03ns	−.20**	.19*	.18*	.17*	−.13*	−.12*
DM	−.23**	.46**	−.15	−.49**	−.04ns	.30**	−.04ns	.05ns	.54**		−.40**	.53**	−.58**	−.16*	−.45**	.40**	.39**
Ash	.03ns	−.17*	.0002	.18**	.05ns	−.07ns	−.01ns	.01ns	−.19**	−.26**		−.33**	−.08ns	.33**	.13*	−.53**	−.71**
NC	−.23**	.24**	−.18	−.27**	.04ns	.23**	−.03ns	.02ns	.40**	.56**	−.09ns		−.70**	−.72**	−.73**	.67**	.51**
NDFDM	.17*	−.31**	.11	.34**	−.05ns	−.26**	.09ns	−.08ns	−.40**	−.69**	−.15**	−.76**		.62**	.84**	−.57**	−.39**
ADFDM	−.07ns	.01ns	−.07	.04ns	−.06ns	.04ns	.07ns	−.07ns	−.04ns	.06ns	−.05ns	−.49**	.50**		.79**	−.74**	−.63**
ADLDM	−.03ns	−.01ns	−.03	.06ns	−.04ns	.001ns	.06ns	−.05ns	−.01ns	.03ns	−.28**	−.46**	.50**	.85**		−.66**	−.49**
IVOMD	−.2*	.3**	−.13	−.4**	−.03ns	.2**	−.004ns	−.003ns	.43**	.63**	−.26**	.72**	−.78**	−.41**	−.39**		.94**
ME	−.15**	.30**	−.09	−.35**	−.03ns	.25**	−.02ns	.01ns	.40**	.63**	−.40**	.56**	−.67**	−.27**	−.20**	.95**	

[a]OC, oil content; OY, oil yield; TPC, total protein content; PAC, palmitic acid content; SAC, stearic acid content; OAC, oleic acid content; LAC, linoleic acid content; DM, dry matter; NC, nitrogen; NDFDM, neutral detergent fiber; ADFDM, acid detergent fiber; ADLDM, acid detergent lignin; IVOMD, in vitro organic matter digestibility; ME, metabolizable energy.

*Significant at the .05 probability level;

**Significant at the .01 probability level; ns, nonsignificant.

TABLE 6 Principal component scores, Eigenvalues, variances of kernel yield (KY), oil and haulm fodder quality parameters among 100 groundnut genotypes evaluated under drought-stressed and nonstressed conditions in the 2018–2019 and 2019–2020 postrainy seasons

	Drought-stressed					Nonstressed					
Traits	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**
KY	.11	.16	**.75**	.02	**.62**	.07	**.63**	−.35	.52	.43	.06
OC	.22	.13	−.44	**.55**	.31	.24	.23	.36	−.10	.30	**−.52**
OY	.14	.17	**.70**	.10	**.67**	.11	**.65**	−.29	.49	.47	−.02
TPC	−.37	.05	**.49**	−.40	−.18	−.14	−.05	**−.49**	.29	−.43	.45
PAC	.48	**−.80**	.09	.19	.01	−.41	**.72**	.41	−.19	−.11	.14
SAC	.00	**−.48**	.10	.17	−.09	−.37	**.42**	.25	.25	−.26	.01
OAC	−.48	**.81**	−.20	−.18	.09	.42	**−.80**	−.34	.07	.11	−.10
LAC	.49	**−.79**	.19	.20	−.06	−.39	**.81**	.35	−.09	−.10	.07
HY	.32	.24	−.35	**.45**	.36	.15	−.40	**.58**	−.05	.34	.15
DM	.24	.13	−.47	.37	.29	.19	−.29	.39	.10	**.43**	**.59**
Ash	.22	−.24	−.47	**−.67**	.38	−.13	.27	**−.58**	−.54	.18	.08
NC	**−.66**	−.34	−.24	.02	.13	**−.63**	−.36	.29	−.16	.23	.18
NDFDM	**.54**	.44	.38	.36	−.39	**.86**	.10	.26	.12	−.22	−.10
ADFDM	**.85**	.35	−.07	−.15	−.21	**.89**	.20	.14	.05	−.15	.05
ADLDM	**.78**	.38	.04	.07	−.35	**.78**	.09	.33	.26	−.18	.17
IVOMD	**−.83**	−.04	−.01	.45	−.10	**−.73**	−.45	.16	.39	.03	−.12
ME	**−.70**	.07	.22	.54	−.23	−.54	−.35	.18	**.61**	−.16	−.22
Eigenvalue	4.37	2.95	2.39	2.04	1.74	4.14	3.69	2.21	1.66	1.30	1.03
Proportion variance, %	25.71	17.36	14.08	12.00	10.22	24.38	21.68	13.02	9.74	7.64	6.09
Cumulative variance, %	25.71	43.06	57.14	69.13	79.35	24.38	46.06	59.07	68.81	76.45	82.54

OC, oil content; OY, oil yield; TPC, total protein content; PAC, palmitic acid content; SAC, stearic acid content; OAC, oleic acid content; LAC, linoleic acid content; HY, haulm yield; DM, dry matter; NC, nitrogen content; NDFDM, neutral detergent fiber; ADFDM, acid detergent fiber; ADLDM, acid detergent lignin; IVOMD, in vitro organic matter digestibility; ME, metabolizable energy.

possessing high STI values for KY (Table 4). Also, genotypes ICGV 01260, ICGV 99241, ICGV 96266, ICGV 171027, and ICGV 01491 recorded high STI values for HY. The stable yield performance of these genotypes in the two environments suggests that these genotypes can be used in groundnut breeding to exploit their drought tolerance and yield potentials.

Agronomic traits such as KY and HY are key attributes for selection and development of dual-purpose groundnut cultivars (Pande et al., 2005). In the present study, genotypes ICGV 10143, ICGV 7222, ICGV 6040, ICGV 03042, and ICGV 06039 were high kernel and oil yielders (Table 3; Supplemental Table S2). Also, genotypes ICGV 01490, ICGV 96266, ICGV 93162, ICGV 98077, ICGV 11422, and ICGV 11418 were the highest haulm yielders and possessed better fodder quality traits such as NC, IVODM, and ME (Table 4; Supplemental Table S3). Moreover, genotypes such as ICGV 10178, ICGV 01260, ICGV 06175, and ICGV 10379 produced both high KY and HY and therefore making them ideal candidates for production in mixed crop–livestock farming systems (Tables 3, 4). In addition, kernel and haulm quality traits such as high OAC, TPC, and OAC, reduced NDFDM, ADFDM, and ADLDM, and higher NC, IVODM, and ME are distinguished traits for selection of groundnut genotypes for production (Nigam, 2014; Samireddypalle et al., 2017). Genotypes ICGV 06146, ICGV 11380, ICGV 14030, ICGV 13189, and ICGV 7222 recorded high protein contents (Table 3; Supplemental Table S2). Genotypes ICGV 1279, ICGV 6420, ICGV 5155, ICGV 97087, and ICGV 99241 were best performers with high OC, whereas CGV 181017, ICGV 01491, ICGV 15019, ICGV 181026, ICGV 16005, and ICGV 181063 were identified as high OAC genotypes (Supplemental Table S2). All the test genotypes that recorded higher OAC under both conditions showed lower LAC (<13%). Low oleic/linoleic ratio enhances the stability and shelf-life of groundnut oil and other groundnut derived products (Achola et al., 2017). Genotypes ICGV 92121, ICGV 86590, ICGV 93161, ICGV GG 20, and ICGV 171007 had high NC, IVODM, and ME, and the lowest mean NDFDM, ADFDM, and ADLDM under both DS and NS conditions. The present study identified divergent parental lines for groundnut breeding for enhanced KY and HY, and kernel and fodder quality. Genotypes ICGV 7222, ICGV 10143, ICGV 6040, ICGV 03042, ICGV 06175, ICGV 01260, ICGV 99241, ICGV 96266, ICGV 171027, and ICGV 01491 possessing drought tolerance are recommended for cultivar development under DS environments (Table 4).

TABLE 7 Grouping of 100 groundnut genotypes evaluated under drought-stressed and nonstressed conditions across 2018–2019 and 2019–2020 postrainy seasons

Cluster	Number of genotypes	Traits	Name of genotypes
1	14	OAC	ICGV 16667, ICGV 181026, ICGV 15073, ICGV 15074, ICGV 15083, ICGV 16688 ICGV 16686, ICGV 16005, ICGV 181017, ICGV 181063, ICGV 181489, ICGV 15094 ICGV 171027, ICGV 181006
2	3	OAC and LAC	ICGV 15019, ICGV 171013, ICGV 181490
3	4	NC	ICGV 171026, ICGV 171039, ICGV 171046, ICGV 181033
4	13	NC	ICGV 93128, ICGV 95066, ICGV 99019, ICGV 00187, ICGV 00213, ICGV 93260 ICGV93261, ICGV 92121, ICGV 01265, ICGV 13200, ICGV 86590, ICGV 86031, GG 20
5	1	IVOMD, NC, and TPC	ICGV 171007
6	12	HY	ICGV 98077, ICGV 11422, ICGV 11418, ICGV 92054, ICGV 93162, ICGV 95111 ICGV 97115, ICGV 01491, ICGV 97150, ICGV 98385, ICGV 96266, ICGV 86699
7	12	ME	ICGV 07010, ICGV 07120, ICGV 99241, ICGV 13254, ICGV 6420, ICGV 00350 ICGV 02266, GPBD 4, ICGV 05057, ICGV 00246, ICGV 7247, ICGV 87846
8	5	DM and Ash content	ICGV 01279, ICGV 86015, ICGV 96165, ICGV 00064, ICGV 14232
9	8	SAC	ICGV 96174, ICGV 91223, ICGV 94118, ICGV 00162, ICGV 7220, ICGV 13207 ICGV 98412, ICGV 7262
10	5	ME	ICGV 06146, ICGV 11380, ICGV 14030, ICGV 13189, ICGV 13219
11	7	KY and OY	ICGV 06039, ICGV 6040, ICGV 10143, ICGV 14001, ICGV 7222, ICGV 13317 ICGV 14421
12	16	KY and OC	ICGV 97087, ICGV 03042, ICGV 11396, ICGV 00211, ICGV 10178, ICGV 00351 ICGV 01260, ICGV 5155, ICGV 03043, ICGV 98184, ICGV 03287, ICGV 06175 ICGV 14224, ICGV 10371, ICGV 10373, ICGV 10379

OAC, oleic acid content; LAC, linoleic acid content; NC, nitrogen content; IVOMD, in vitro organic matter digestibility; TPC, total protein content; HY, haulm yield; ME, metabolizable energy; DM, dry matter; SAC, stearic acid content; KY, Kernel yield; OY, oil yield; OC, Oil content.

Comparison across subspecies for KY and HY, and quality traits revealed the Virginia bunch (subspecies *hypogaea*) recorded slightly higher values for several traits including OC, OAC, HY, DM, NC, ADFDM, and ADLDM (Figure 1). These allowed identification of genotypes with desirable kernel quality, HY, and fodder quality. The Spanish bunch groundnuts have higher OC than other types of groundnuts including Virginia groundnut (Nigam, 2014). The highest mean OC recorded for Virginia subspecies (Figure 1) is probably due to the long intercrosses between the two subspecies. Therefore, groundnut genotypes belonging to the Virginia are useful genetic resources for the development of high oil groundnut cultivars. Also, Virginia groundnuts are late maturing than Spanish bunch groundnuts (Krapovickas & Gregory, 1994). The high HY recorded by the Virginia subspecies may offer opportunity to improve biomass production. Despite a lack of statistical significance difference, Virginia subspecies comprised of genotypes with high OAC content, but low LAC compared to the Spanish subspecies. These imply that the variability within the Virginia subspecies for majority of the assessed traits can be exploited through selection for developing high oleic groundnut cultivars.

Associations of KY and HY and quality is key to design breeding strategies for development of dual-purpose groundnut genotypes. Under DS condition, OC exhibited low and positive correlation with OY and OAC, suggesting selection for higher OC result in improved OY and OAC. Haulm yield exhibited positive and significant correlation with OY and OC under DS and NS conditions, suggesting that these traits can be simultaneously improved via selection. Haulm quality traits such as NC, IVODM, and ME exhibited negative relationships with HY under DS condition (Table 5). Contrastingly, these traits showed positive correlations with HY under NS condition, underlying the causal role of water deficit contributing for the trade-off between haulm quality traits and HY (Table 5). This limits simultaneous selection and improvement of the of HY and quality traits under DS condition. Drought stress affects the symbiotic nitrogen fixation capacity of the crop, and consequently leads to reduced NC and haulm digestibility which results in low ME (Blümmel et al., 2012).

In the present study, positive and significant correlations were exhibited between NC and IVODM, NC and ME, and IVODM and ME under both water conditions (Table 5). Further, these traits influence haulm quality. Negative and significant correlation were detected with the indigestible haulm quality traits such as NDFDM, ADFDM, and ADLDM under both conditions. This suggests that NC, IVODM, and ME can be simultaneously improved through selection. Nitrogen

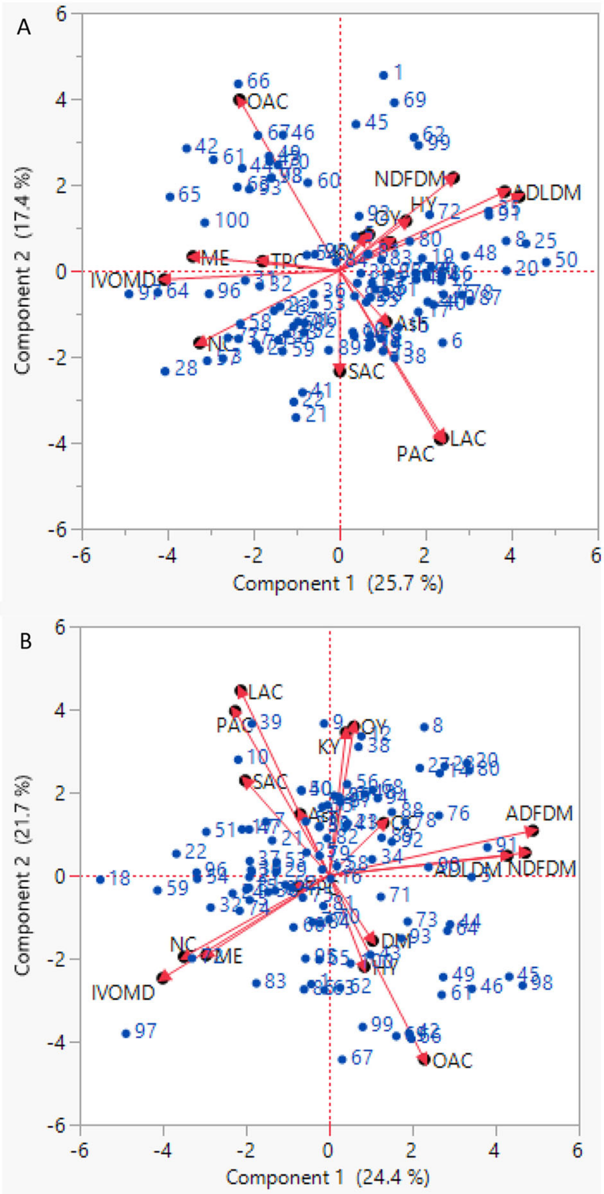

FIGURE 2 Principal components biplot showing the relationship between assessed traits among 100 groundnut genotypes under drought-stressed (a) and nonstressed (b) conditions evaluated across the 2018–2019 and 2019–2020 postrainy seasons at the International Crops Research Institute for the Semi-Arid Tropics, India. KY, Kernel yield; OC, Oil content; OY, oil yield; TPC, total protein content; PAC, palmitic acid content; SAC, stearic acid content; OAC, oleic acid content; LAC, linoleic acid content; HY, haulm yield; NC, nitrogen content; IVOMD, in vitro organic matter digestibility; ME, metabolizable energy. See code of genotypes in Supplemental Table S1

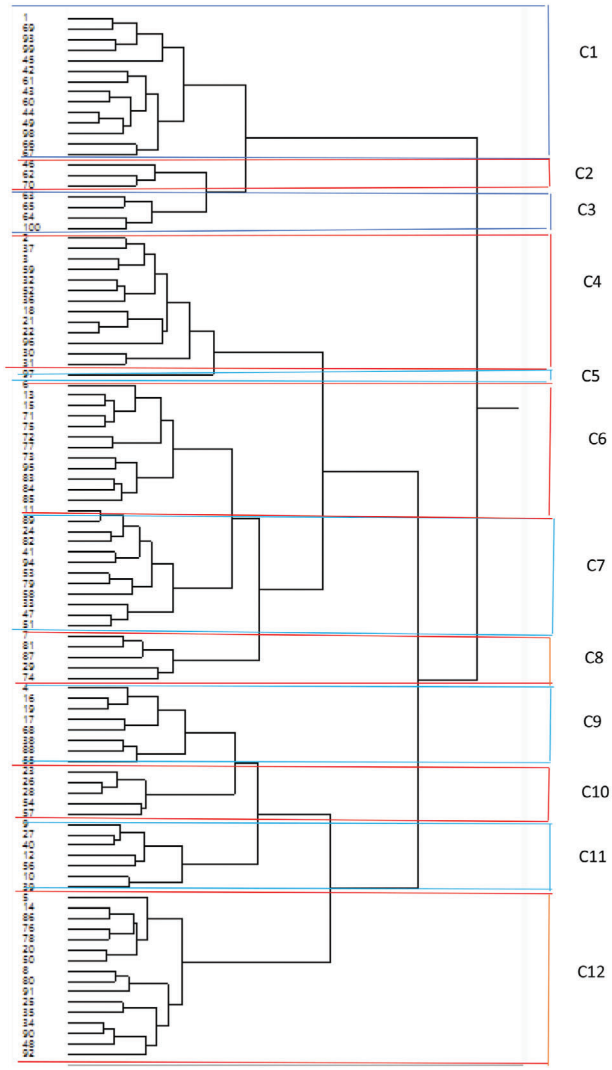

FIGURE 3 Hierarchical clustering using Ward's method showing groupings of 100 groundnut genotypes assessed based on kernel and haulm yields, and kernel and fodder quality parameters under drought-stressed and non-stressed conditions when genotypes were assessed in the 2018–2019 and 2019–2020 postrainy seasons at the International Crops Research Institute for the Semi-Arid Tropics, India. See code of genotypes in Supplemental Table S1

content is an important haulm quality trait and influence KY due remobilization of nitrogen resources to pods (Blümmel et al., 2012). Under DS condition, negative correlations displayed between NC with KY and HY suggested the effect of drought on groundnut biomass and KY production with consequences on the source–sink relationship for nitrogen.

Selecting genotypes based on multiple traits enables to enhance the genetic gains of target traits. Under DS condition, the principal component analysis indicated high contribution and strong association of NDFDM, ADFDM, ADLDM, and HY to the first principal component (Table 6; Figure 2). Oleic acid content and ME correlated with the second principal component, suggesting these traits have much influence during selection and can be simultaneously selected and improved. Under NS condition, NDFDM, ADFDM, ADLDM, OC, KY, AND OAC were main contributors in the first principal component (Table 6; Figure 2). These traits can also be simultaneously selected for breeding.

5 | CONCLUSIONS

A well-characterized groundnut germplasm collection is essential to select unique genotypes with drought-tolerance and high kernel, oil, and HY and quality. The study revealed the presence of marked genetic variability among the tested groundnut genotypes for the measured traits which can be exploited in groundnut breeding. Kernel yield and HY were not inversely related. Low correlation between KY and HY under DS and NS, suggests independent selection and improvement of the two traits. Strong correlations among the haulm quality traits in both moisture conditions provides an opportunity for breeding of these traits in parallel and developing high haulm fodder quality under DS and optimum conditions. The following genotypes: ICGV 10178, ICGV 01260, ICGV 06175 and ICGV 10379 expressed high KY and HY, and CGV 181017, ICGV 01491, ICGV 15019, ICGV 181026, ICGV 16005, and ICGV 181063 had higher OAC. Further, genotypes ICGV 7222, ICGV 10143, ICGV 6040, ICGV 03042, ICGV 06175, ICGV 01260, ICGV 99241, ICGV 96266, ICGV 171027, and ICGV 01491 were relatively drought tolerant. The above genotypes are recommended for production or breeding drought-stress tolerant groundnut varieties with high kernel and fodder yields and quality attributes.

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AUTHOR CONTRIBUTIONS

Seltene Abady: Conceptualization; Data curation; Formal analysis; Methodology; Writing-original draft. Hussein Shimelis: Conceptualization; Methodology; Project administration; Resources; Validation; Writing-original draft. Janila Pasupuleti: Conceptualization; Methodology; Project administration; Supervision; Resources. Jacob Mashilo: Conceptualization; Formal analysis; Resources; Validation. Sunil Chaudhari: Resources. Surendra S. Manohar: Resources

CONFLICT OF INTEREST

The authors report no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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