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ORIGINAL ARTICLE

Genetic variability, character association and divergence studies in *Jatropha curcas* for improvement in oil yield

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Abstract

Key message **Variability in traits of 15, diverse 6-year-old candidate plus trees of *Jatropha curcas* was determined to identify the best gain heritable traits correlating with oil yield for *Jatropha* improvement.**

Abstract Study was carried out on 15 6-year-old candidate plus trees of *Jatropha curcas* adapted on semi-arid wasteland with an objective to assess variation in morphological, physiological and oil quality characters. Heritable and non-heritable components of the total variability of the characters were determined by genotypic (GCV) and phenotypic (PCV) co-efficient of variation, heritability and genetic advance (GA) and the best gain traits for *Jatropha* improvement through selection and breeding were assessed. Further, association among the traits were assessed and germplasm were separated into different clusters. Significant variation was found among the different genotypes for all the characters. The photosynthetic and transpiration rate correlated with oil content, seed and oil yield. The chlorophyll pigments correlated positively with the photosynthetic rate and oil content. The seed oil content varied considerably from 27.68 % (JCN01) to 37.49 % (JCN14) and had high heritability, but it had low PCV and GCV and moderate GA. The oil yield plant^{-1} had high genetic variability and varied significantly from 0.07 (JCN15) to 0.47 kg plant^{-1} (JCN09/IC 565733). Though the different fatty acids differed significantly with different germplasm and also had high heritability, they had low PCV, GCV and GA. Seed weight, fruit weight, seed weight fruit^{-1} and seed yield plant^{-1} strongly correlated with oil yield and had moderate to high GCV, PCV, coupled with high heritability and GA. Germplasm were separated into four distinct clusters with a maximum inter distance found between cluster II and IV, and minimum between cluster I and III. The study helped to identify the superior germplasm among diverse genotypes of *J. curcas* that can serve as parents with desirable characters like high oil yield, low stomatal conductance and high water use efficiency for further breeding purposes.

Keywords *Jatropha curcas* · Genetic variability · Correlation · Cluster analysis · Wasteland · Oil yield

Abbreviations

BSD	Basal stem diameter
NPB	Number of primary branches
DPB	Diameter of primary branches
NSB	Number of secondary branches
DSB	Diameter of secondary branches
PH	Plant height
VPC	Volume of plant canopy
M:F	Male-to-female flower ratio
FL	Fruit length

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FW	Fruit width
SFW	Single fruit weight
SSW	Single seed weight
SPF	Seeds fruit^{-1}
SW/F	Seed weight fruit^{-1}
SFCW	Single fruit-coat weight
SL	Seed length
SW	Seed width
SYPP	Seed yield plant^{-1}
A	Photosynthetic rate (net assimilation rate)
E	Transpiration rate
Gs	Stomatal conductance
Ci	Intercellular leaf CO_2 concentration
WUE	Water use efficiency
TChl	Total chlorophyll
Chl-*a*	Chlorophyll-*a*
Chl-*b*	Chlorophyll-*b*
CRT	Carotenoids
OC	Oil content
OYPP	Oil yield plant^{-1}
PA	Palmitic acid (hexadecanoic acid)
SA	Stearic acid (octadecanoic acid)
LA	Linoleic acid (9,12-octadecadienoic acid)
OA	Oleic acid (9-octadecenoic acid)
SFA	Saturated fatty acid (palmitic and stearic acid)
USFA	Unsaturated fatty acid (linoleic and oleic acid)

Introduction

Jatropha curcas L. is a potential plant for making biodiesel to cater to the growing energy needs (Ginwal et al. 2004; Ghosh et al. 2007). The *Jatropha* biodiesel has been proven to be superior compared to biodiesel made from other vegetable oils in terms of engine performance and emissions (Ghosh et al. 2007; Fairless 2007). In addition, it has the ability to reclaim eroded wastelands by improving soil quality (Ogunwole et al. 2008; Srivastava et al. 2011; Anand et al. 2015). *J. curcas*, being an oil bearing non-traditional crop grown on wastelands, does not interfere with arable lands for food production (Ghosh et al. 2007), and also has global warming mitigation potential (Francis et al. 2005; Mantri et al. 2014). Despite having been proved as a superior transport fuel including aviation fuel, there have been concerns over the availability of enough feedstock to cater to the enormous fuel needs (Ghosh et al. 2007; Ghosh 2014). Since *J. curcas* is an undomesticated plant, suitable agro-practices are essential for ensuring their growth and yield under varying agro-climatic conditions (Abhilash et al. 2011). Besides, the key impediment to wider acceptability and success of *Jatropha* plant as a biofuel crop is the lack of elite germplasm as it has not been subjected to intensive genetic improvement (Fairless 2007; Nietsche et al. 2015). For commercial success, large-scale plantations need to be established using elite germplasm with proven track records over a long period of time (Mantri et al. 2014). Moreover, a commercial plantation requires germplasm having combination of several desirable traits like high productivity and stress tolerant plant physiology (Sunil et al. 2013).

Therefore, there is a need to characterize different germplasms adapted to wastelands which have got desirable growth, physiological, reproductive, and biochemical characteristics at maturity that can be subsequently graded for breeding good varieties. For any breeding programme aimed at improving the yield and other characters, existing or induced variability is the pre-requisite. Thus, for greater success in transferring the desirable traits, it is pertinent to have information on both genotypic and phenotypic variation together with heritability and genetic advance for the possibility of direct selection as well as prediction of the inheritable nature of the traits. Many different workers have studied the growth, yield attributes, yield and quality parameters of *Jatropha* and have reported significant genetic differences for these traits among germplasm collected from different climatic zones (Ginwal et al. 2004; Rao et al. 2008; Das et al. 2010; Gairola et al. 2011; Srivastava et al. 2011; Wani et al. 2012; Biabani et al. 2012; Tripathi et al. 2013; Singh et al. 2013; Kaushik et al. 2007, 2014; Kumar and Singh 2014). Thus, there had been many meaningful efforts to characterize such variability in *Jatropha*, but most of them were carried out on juvenile plants. Very few researchers assessed near-mature or mature plants for characters like seed yield and its attributes (Mohapatra and Panda 2010). Being a perennial crop, the reproductive traits should ideally be assessed only after the plants are sufficiently mature (Rao et al. 2008). With this viewpoint, the present study was carried out on 15 6-year-old candidate plus trees (initially selected for various desirable traits) adapted on semi-arid rocky wasteland to assess the extent of variability in the characters and their association. The study helps to identify traits that have high variability and heritability. The study also helps to identify elite germplasm which had high photosynthetic rate and consequently high pigment content, seed and oil yield per plant. The diverse germplasm classified based on different desirable traits would be useful for parental selection in crop improvement programme.

Materials and methods

Based on phenotypic assessment of different desirable traits, cuttings were raised from 14 *J. curcas* plus trees growing in natural or cultivated stands at different locations of Gujarat, Odisha and Maharashtra states, while one genotype had its source outside India (Pamidimarri and Reddy 2014) and was raised through seedling (Table 1). Exotic germplasm was from Cape Verde that is supposed to be the point of distribution and spread of *J. curcas* to the tropical regions (Heller 1996), and such exotic germplasm might harbour useful and novel genes that can be beneficially used for widening the genetic base and inducing variability (Xu et al. 2013). Five-month-old saplings of these germplasm were subsequently transplanted in field during 2007 at an experimental site of CSIR-Central Salt and Marine Chemical Research Institute, Nesvad (21°30′29.71″N;72°02′11.54″E; 92 m), located in the Bhavnagar district of Gujarat state in India. The area receives about 550 mm of rainfall annually. The region has a mean maximum and minimum temperature of 35.3 and 18.7 °C, respectively. The experiment was laid out in a randomized complete block design (RCBD) with nine plants per selected plus tree in each of the three replication blocks. The planting density was 1111 plants ha^{-1} (3 m × 3 m planting distance). Normal agronomical practices were followed during the transplanting and establishment in field. The fertilizer was supplied annually through urea, single super phosphate and muriate of potash at the rate of 45:30:20 kg ha^{-1} N:P_2O_5:K_2O, respectively, for the initial 3 years following which the N dose was increased to 60 kg N ha^{-1}. The mineral fertilizers were applied in conjunction with 3 t *Jatropha* cake ha^{-1} for the

Table 1 Selection criteria for 15 CPTs of *J. curcas*, their source location and geographical description

Genotype code	Criteria of selection	Accession number, if any	Location/source	Latitude	Longitude
JCN01	Size and shape of seed (long) and fruit (oblong) and difference in leaf morphology (exotic germplasm)	EU700455	Cape Verde	–	–
JCN02	High yield[a]	IC-565734	Banaskantha, Gujarat	24°17′53.23″N	72°44′44.65″E
JCN03	High yield[a]	IC-565730	Ranpur, Banaskantha, Gujarat	24°17′56.74″N	72°55′40.90″E
JCN04	Open canopy[c]	IC-565732	Chikhla, Banaskantha, Gujarat	24°19′33.71″N	72°53′31.69″E
JCN05	Visually more branching, profuse flowering in native stand and good adaptation to dry climate in cultivated condition	IC-565739	Zanjmer, Gopnath, Bhavnagar, Gujarat	21°11′36.36″N	72°3′46.37″E
JCN06	Visually high number of primary, secondary and tertiary branches	IC-565738	Akola, Maharashtra	20°42′31.92″N	77°2′57.92″E
JCN07	High yield[a] and open canopy[c]	IC-565731	Panchmahal, Gujarat	22°50′54.74″N	73°55′2.28″E
JCN08	High yield[a] and oil content[b]	–	Sardar Krushinagar Agriculture University, Dantiwada, Gujarat	24°19′28.61″N	72°19′37.60″E
JCN09	High yield[a], oil content[b] and open canopy[c], less affected by virus and fungus	IC-565733	Shyamlaji, Gujarat	23°41′38.65″N	73°22′42.28″E
JCN10	High yield[a]	–	Udaipur, Rajasthan	24°46′21.43″N	73°43′56.39″E
JCN11	High yield[a]	–	Udaipur, Rajasthan	24°45′17.06″N	73°43′12.19″E
JCN12	Oil content[b]	–	Ambaji—Khedbrahma area Banaskantha, Gujarat	24°18′41.11″N	72°57′58.64″E
JCN13	High yield[a] in native stand and visual insect resistance to leaf miner in cultivated stand	–	Bhiloda, Sabarkantha, Gujarat	23°48′29.42″N	73°16′50.24″E
JCN14	High yield in native stand and relatively high and consistent yield and oil content in cultivated conditions (CP-9) at Odisha (sub-humid climate) and Gujarat (semi-arid climate)[d]	IC-565735	Ganjam, Odisha	19°27′18.43″N	85° 2′3.09″E
JCN15	Open canopy[c]	–	Ambalimal, Banaskantha, Gujarat	24°21′57.88″N	72°49′30.65″E

[a] Selection of plus trees from native based on: high yield (>2.5 kg seed yield $plant^{-1}$)

[b] Seed oil content (>33 %)

[c] Open canopy (angle between main stem to primary and angle between primary to secondary branch >65°; angle of secondary to tertiary >50°

[d] Selection of IC-565735 was based on consistent high yield obtained among other cultivated germplasm at Odisha

initial 3 years, following which it was applied at the rate of 1 t ha^{-1} annually. The plants received very little irrigation (nearly 50 L water/plant/month for 5–6 months in a year).

Experimental soil

The land was shallow and rocky with concretion of 18 % up to 0–45 cm soil depth. The soil was calcareous and the texture was sandy loam. The physico-chemical properties of the undisturbed soil of this area were: 7.3 pH (soil/water, 1:2.5), 0.12 dS m^{-1} electrical conductivity (EC), 0.3 % organic carbon, 80 kg ha^{-1} available N, 2.9 kg ha^{-1} available P, and 176 kg ha^{-1} available K.

Recording of data

Data recorded on various traits have been broadly divided into four categories viz. growth characters, yield characters, physiological characters and seed oil quality characters. The observations pertained to growing season of 2013–2014 (July–March).

Plant growth characters

The growth data of the plants were recorded from all the nine plants in each of the three replications for the 15 genotypes. The growth characters studied were basal stem diameter, number of primary branches, diameter of primary branches, number of secondary branches, diameter of secondary branches, plant height and plant canopy volume. The plant canopy volume was calculated according prescribed formulae by Ghezehei et al. (2009).

Yield characters

The yield characters studied were fruit length, fruit width, single fruit weight, single seed weight, seed length, seed width, number of seed $fruit^{-1}$, seed weight $fruit^{-1}$, fruitcoat weight $fruit^{-1}$, male-to-female flower ratio, and seed yield $plant^{-1}$. The male-to-female ratio was calculated from 50 inflorescences. Hundred mature sundried fruits of the 15 germplasm were randomly drawn from each replication for measurements on fruits. Hundred seeds of each germplasm were randomly selected from each of the three replications for the measurement of seed characters. Seed yield was calculated for each plant separately and expressed as average seed yield $plant^{-1}$.

Physiological characters

Leaf gas exchange parameters were recorded from two leaves each from three randomly selected plants of each replication for all the germplasm. The gas exchange parameters were photosynthetic rate (A), transpiration rate (E), stomatal conductance (Gs), intercellular leaf CO_2 concentration (Ci) and water use efficiency (WUE = A/E) which were measured by using a portable Photosynthesis System (LICOR 6400-XT, USA) equipped with infrared gas analyser. The total chlorophyll, chlorophyll-*a*, chlorophyll-*b* and carotenoids were observed for leaf pigments analysis. The quantitative analysis of chlorophyll and carotenoids were done by colorimetric method (Arnon 1949) on Epoch BioTek spectrophotometer (USA) using 480, 510, 645, 652, and 663 nm wavelength.

Seed oil quality characters

The seed oil quality characters comprised seed oil content and its fatty acid analysis. Oil from seeds was extracted in a hexane solvent using a soxhlet apparatus (Akbar et al. 2009). Acid-catalysed esterification was used to reduce the free fatty acid present in the oil. The 5 % fresh acidic methanol and hexane was used for methyl esterification of *Jatropha* oil (Bojan and Durairaj 2012). The methyl esters were analysed for their fatty acids using GC–MS (Shimadzu, QP-2010).

Statistical analysis

Best gain traits for *Jatropha* oil yield improvement through selection and breeding were assessed based on genetic variability, heritability and correlation. Analysis of variance, phenotypic and genotypic variance, phenotypic coefficient of variation (PCV), genotypic coefficient of variation (GCV), heritability in broad sense and genetic advance as percentage of population mean (GAM%) (selection intensity at 5 % level) were estimated using standard procedure (Singh and Chaudhary 1979). The differences in mean were tested by Tukey's test using MSTAT statistical software (MSTAT-C 1991, Michigan State University, East Lansing, MI). Values of PCV and GCV for all the traits were divided into three categories viz., >20 % (high), 10–20 % (moderate) and <10 % (low) (Sivasubramanian and Madhavamenon 1973). Heritability in the broad sense was classified as low (<30 %), medium (30–60 %) and high (>60 %). The genetic advance was also classified as low (0–10 %), moderate (10–20 %) and high (>20 %) (Robinson et al. 1949; Johnson et al. 1955). The replicated data for correlation coefficient were analysed using the Windostat version 8.6 from Indostat service Hyderabad, India. Further, cluster analysis was performed to classify the germplasm to facilitate parental selection for breeding and genetic improvement of *J. curcas*. Divergence analysis (cluster analysis) was performed using Minitab 16 software by hierarchical single linkage method. The cluster distance was measured by Euclidean clustering method.

Results

There was a wide range of variability in all the characters with a broad spectrum of ranges in the genotypes studied. The mean, minimum and maximum values and coefficient of variation of these characters have been tabulated accordingly. The analysis of variance (ANOVA) revealed that there was significant variation among the 15 candidate plus trees (CPTs) for all the characters related to growth, physiology, yield characters, yield and seed oil parameters of *J. curcas*.

Variation in growth, yield, physiological and seed oil quality characters

Significant trait differences were observed in the growth characters among the selected CPTs, and the mean, range and CV values for the growth characters observed are presented in Table 2. The highest numbers of primary as well as secondary branches plant^{-1} were recorded in the exotic germplasm (JCN01) while the lowest were recorded in JCN02, which also recorded the lowest average diameter of secondary branches. JCN14 recorded the maximum diameter of primary as well as secondary branches. The mean plant height was 233.4 cm and this trait exhibited the least coefficient of variation (1.49 %). The highest plant height, significantly superior to other germplasm, was recorded for JCN09 which also had significantly thickest basal stem diameter, while significantly short height plants were recorded for JCN08. JCN08 also recorded the lowest diameter of primary branches and volume of plant canopy. The maximum volume of plant canopy was recorded in JCN03.

The mean, range and CV values for yield characters are presented in Table 3. Seed yield plant^{-1} exhibited a wide range from 0.22 to 1.28 kg plant^{-1} with a mean value of 0.85 kg. The highest seed yield was obtained from JCN02, which also recorded the lowest coat weight fruit^{-1}. However, JCN02 was at par with JCN-09, -11, -14 and -03 with respect to seed yield plant^{-1}. Even though highest fruit length and seed length was obtained in JCN14, all the other germplasm except JCN-04, -05 and -06 were statistically at par to it for these two characters. JCN04 recorded the highest number of seeds fruit^{-1} which was superior to other germplasm, but exhibited the lowest fruit length. JCN08 manifested the significantly highest single seed weight and seed weight fruit^{-1} (capsule) when compared to other germplasm and also recorded maximum fruit width which was, however, at par with all others except JCN06. JCN13 exhibited the highest male-to-female flower ratio and was closely followed by JCN05. JCN13 recorded significantly highest fruit weight which was at par with JCN-07, -08, -10 and JCN-11. JCN13, closely followed by JCN11, also had the lowest number of seeds fruit^{-1}. The significantly lowest male-to-female flower ratio was found in JCN12.

Values for mean, range and CV obtained for physiological parameters in the present investigation are presented in Table 4. JCN-14, -12 and -08 were statistically equivalent for all the pigments studied with the highest chlorophyll a, carotenoid and total chlorophyll content in JCN14, whereas chlorophyll b was highest in JCN08. JCN14 also recorded the highest photosynthetic rate but was at par with several others. The exotic germplasm (JCN01) recorded the highest stomatal conductance and intercellular leaf CO_2 concentration, but was at par to most of the others. Variation observed in photosynthetic rate and stomatal conductance in the candidate plus trees have been presented in Fig. 1. The highest water use efficiency was recorded in JCN15, closely followed by JCN05 which was at par with others.

Results of ANOVA on all the oil traits indicated highly significant variation ($p \leq 0.001$) among all the genotypes (Table 5). The seed oil content varied from 27.68 % (JCN01) to 37.49 % (JCN14) with a mean of 33.79 %. While JCN01 had the significantly lowest oil content than others, JCN14 was found at par with JCN09 and JCN08. The oil yield plant^{-1} ranged from 0.07 to 0.47 kg and the maximum was recorded in JCN09, closely followed by JCN14. The mean content of saturated fatty acid was 25.08 % (16.44 and 8.64 % of palmitic acid and stearic acid, respectively), while that of unsaturated fatty acid was 74.92 % (32.95 and 41.95 % of linoleic acid and oleic acid, respectively). The highest saturated fatty acid content was observed in JCN01 which was closely followed by JCN-09, -08, -14, -02 and -05. Palmitic acid was found to be the maximum in JCN08, whereas it was the minimum in JCN13. Stearic acid was highest in JCN01 and lowest in JCN11. On the other hand, JCN13 recorded the maximum (72.23 %) unsaturated fatty acid content. Linoleic (35.60 %) and oleic acid (42.26 %) content was recorded the maximum in genotype JCN11 and JCN14, respectively.

Genetic analysis

The estimation of genotypic variance (σ^2g), phenotypic variance (σ^2p), genotypic (GCV%) and phenotypic (PCV%) coefficient of variation, broad sense heritability (h^2B) and genetic advance as percentage of mean (GAM%) of 15 *Jatropha* accessions are presented in Table 6.

PCV and GCV

Among the growth characters, the highest PCV (26.63 %) and GCV (24.82 %) were observed for the volume of plant

Table 2 Mean values for various plant growth characters of 15 *J. curcas* germplasm

Genotype code	BSD (mm)	NPB	DPB (mm)	NSB	DSB (mm)	PH (cm)	VPC (m^3)
JCN01	146.94^{cd}	4.22^{a}	63.85^{fg}	10.11^{a}	35.35^{g}	227.8^{c}	8.69^{cde}
JCN02	145.17^{de}	2.22^{d}	91.44^{abc}	6.67^{b}	48.33^{de}	250.0^{b}	10.48^{cde}
JCN03	153.94^{bc}	3.33^{ab}	84.28^{d}	8.44^{ab}	43.03^{f}	250.6^{b}	14.27^{a}
JCN04	157.28^{b}	2.67^{bcd}	92.39^{ab}	8.11^{ab}	46.04^{ef}	242.2^{b}	13.56^{ab}
JCN05	126.56^{h}	3.11^{bcd}	68.50^{f}	7.78^{ab}	42.73^{f}	183.9^{d}	7.63^{e}
JCN06	135.50^{fg}	3.00^{bcd}	74.81^{e}	8.44^{ab}	45.37^{ef}	225.0^{c}	11.38^{abc}
JCN07	149.39^{bcd}	2.78^{bcd}	75.87^{e}	7.44^{b}	44.05^{f}	227.0^{c}	10.70^{bcd}
JCN08	137.61^{efg}	3.11^{bcd}	61.46^{g}	7.33^{b}	38.15^{g}	152.8^{e}	4.23^{f}
JCN09	166.33^{a}	3.22^{bc}	92.28^{ab}	7.89^{ab}	53.99^{abc}	268.9^{a}	9.96^{cde}
JCN10	134.89^{fg}	2.67^{bcd}	92.77^{ab}	8.22^{ab}	54.85a^{b}	252.0^{b}	9.70^{cde}
JCN11	132.61^{gh}	2.67^{bcd}	87.80^{bcd}	7.22^{b}	53.08^{abc}	252.2^{b}	10.72^{bcd}
JCN12	142.83^{def}	2.89^{bcd}	85.63^{cd}	7.56^{ab}	50.62^{cd}	229.3^{c}	9.18^{cde}
JCN13	133.76^{gh}	3.22^{bc}	83.83^{d}	8.78^{ab}	48.53^{de}	248.3^{b}	8.96^{cde}
JCN14	147.44^{cd}	2.67^{bcd}	95.93^{a}	7.67^{ab}	55.63^{a}	245.6^{b}	7.98^{de}
JCN15	142.78^{def}	2.33^{cd}	89.02^{bcd}	7.78^{ab}	50.86^{bcd}	245.6^{b}	7.59e
Mean	143.54	2.94	82.66	7.96	47.37	233.4	9.67
Min	126.56	2.22	61.46	6.67	35.35	152.8	4.23
Max	166.33	4.22	95.93	10.11	55.63	268.9	14.27
CV (%)	1.87	10.31	2.33	10.53	2.88	1.49	9.82
CPTs (M.S.)	334.179***	0.693***	371.471***	1.941*	109.777***	2622.14***	18.185***
Error (M.S.)	7.178	0.092	3.703	0.703	1.867	12.139	0.9

Mean values denoted with different alphabets in a particular column are significantly different at 95 % confidence level ($p \leq 0.05$; Tukey's test)

MS mean square, *CV* coefficient of variation

*, ** and *** significantly different at $p \leq 0.05$; $p \leq 0.01$ and $p \leq 0.001$, respectively

canopy while moderate PCV (12.72–18.38 %) and GCV (12.64–15.21 %) were obtained for the number of primary branches, diameter of primary branches, diameter of secondary branches and plant height. Number of secondary branches exhibited moderate PCV but low GCV. The lowest values of PCV and GCV among the growth characters were recorded for basal stem diameter. Seed yield plant^{-1} exhibited the highest and also similar values for PCV (40.79 %) and GCV (40.48 %) among the yield and yield attributing characters. Single fruit weight, single seed weight, seed weight fruit^{-1}, single fruit-coat weight and male-to-female flower ratio showed moderate PCV with range from 11.89 to 16.34 % and GCV with range from 11.86 to 16.18 %. Lower PCV and GCV were recorded in fruit length and width, seeds fruit^{-1}, seed length and width. Among the physiological traits, the pigment content showed either high or moderate PCV and GCV values. Highest PCV (24.00 %) with moderate GCV was observed in Chlorophyll-*b*. High PCV and GCV values were also recorded for total chlorophyll, chlorophyll a and carotenoids. Among the gas exchange parameters, high PCV with moderate GCV was observed in stomatal conductance, while the other traits had low to moderate values. The oil yield plant^{-1} exhibited maximum and similar PCV (44.44 %) and GCV (44.12 %) while all other traits, viz., oil content and different fatty acids had low values.

Heritability and genetic advance

Heritability among growth characters was recorded high for all the traits except the number of secondary branches which was moderate. Among all growth traits, plant height had maximum heritability (98.62 %) followed by diameter of primary branches, diameter of secondary branches and basal stem diameter. The value for genetic advance was high or moderate for all the growth characters studied, and the highest genetic advance was observed in the volume of plant canopy. High heritability and genetic advance values were recorded in all the growth traits except basal stem diameter and the number of secondary branches.

Among the seed yield and yield attributing parameters, all the traits had high heritability except fruit and seed width that had moderate values. Single seed weight exhibited the highest broad sense heritability (99.65 %) followed by single fruit weight, seed yield plant^{-1} and seed weight fruit^{-1}. GAM% was recorded low or high that varied from 3.23 % (fruit width) to 82.76 % (seed yield plant^{-1}) in yield attributing traits. High heritability and

Table 3 Mean values for male-to-female ratio, seed yield characters and seed yield of 15 *J. curcas* germplasm

Genotype code	M:F	FL (mm)	FW (mm)	SL (mm)	SW (mm)	SFW (g)	SSW (g)	SW/F (g)	SPF	SFCW (g)	SYPP (kg plant^{-1})
JCN01	16.13^{bcd}	28.51^{ab}	21.27^{a}	18.55^{ab}	8.91^{ab}	2.31^{d}	0.50^{j}	1.34^{h}	2.69^{ef}	0.96^{fgh}	0.33^{g}
JCN02	14.40^{ef}	25.95^{bcde}	20.79^{ab}	18.56^{ab}	9.04^{a}	2.36^{d}	0.56^{g}	1.52^{f}	2.69^{ef}	0.84^{i}	1.28^{a}
JCN03	15.17^{de}	26.90^{abcd}	21.25^{a}	18.34^{ab}	8.83^{ab}	2.69^{c}	0.64^{d}	1.76^{cd}	2.76^{cd}	0.93^{ghi}	1.16^{ab}
JCN04	13.20^{fg}	23.90^{e}	20.28^{ab}	17.48^{bcd}	8.50^{bc}	2.38^{d}	0.52^{i}	1.49^{f}	2.89^{a}	0.89^{hi}	0.53^{f}
JCN05	17.30^{ab}	24.92^{de}	20.38^{ab}	16.96^{d}	8.70^{abc}	2.11^{e}	0.47^{k}	1.25^{i}	2.65^{fg}	0.87^{hi}	0.62^{ef}
JCN06	12.83^{g}	25.60^{cde}	19.56^{b}	17.08^{cd}	8.16^{c}	2.32^{d}	0.54^{h}	1.43^{g}	2.64^{fg}	0.89^{hi}	0.60^{f}
JCN07	13.53^{fg}	27.77^{abc}	21.26^{a}	18.81^{a}	8.91^{ab}	3.00^{ab}	0.64^{d}	1.78^{cd}	2.76^{cd}	1.23^{bc}	1.07^{b}
JCN08	13.50^{fg}	27.89^{abc}	21.76^{a}	18.46^{ab}	8.74^{ab}	3.00^{ab}	0.73^{a}	1.98^{a}	2.73^{de}	1.02^{efg}	0.85^{cd}
JCN09	13.59^{fg}	28.59^{ab}	21.42^{a}	18.51^{ab}	8.62^{abc}	2.73^{c}	0.66^{c}	1.80^{bc}	2.72^{de}	0.92^{ghi}	1.26^{a}
JCN10	15.23^{cde}	27.15^{abcd}	20.94^{ab}	18.14^{abc}	8.85^{ab}	2.98^{ab}	0.60^{f}	1.69^{e}	2.80^{bc}	1.29^{ab}	0.88^{c}
JCN11	13.34^{fg}	27.92^{abc}	20.89^{ab}	18.28^{ab}	8.94^{ab}	2.98^{ab}	0.65^{d}	1.68^{e}	2.60^{gh}	1.29^{ab}	1.23^{a}
JCN12	11.23^{h}	28.05^{abc}	20.93^{ab}	17.74^{abcd}	8.63^{abc}	2.93^{b}	0.64^{d}	1.76^{cd}	2.73^{de}	1.17^{cd}	0.78^{cd}
JCN13	18.07^{a}	27.40^{abcd}	20.89^{ab}	18.55^{ab}	8.96^{ab}	3.06^{a}	0.68^{b}	1.73^{de}	2.55^{h}	1.33^{a}	0.74^{de}
JCN14	13.40^{fg}	28.77^{a}	21.38^{a}	18.67^{a}	8.96^{ab}	2.76^{c}	0.62^{e}	1.70^{e}	2.76^{cd}	1.05^{ef}	1.20^{ab}
JCN15	16.58^{bc}	27.37^{abcd}	21.36^{a}	18.12^{abc}	8.66^{abc}	2.95^{b}	0.65^{d}	1.84^{b}	2.83^{b}	1.11^{de}	0.22^{g}
Mean	14.50	27.11	20.96	18.15	8.76	2.70	0.61	1.65	2.72	1.05	0.85
Min	11.23	23.90	19.56	16.96	8.16	2.11	0.47	1.25	2.55	0.84	0.22
Max	18.07	28.77	21.76	18.67	9.04	3.06	0.73	1.98	2.89	1.33	1.28
CV (%)	3.15	3.22	2.34	2.00	1.99	0.86	0.72	1.14	0.68	2.25	5.00
CPTs (M.S.)	10.51***	6.098***	0.913**	0.999***	0.157***	0.309***	0.016***	0.122***	0.023***	0.087***	0.359***
Error (M.S.)	0.209	0.762	0.240	0.132	0.031	0.001	0.000	0.000	0.0003	0.001	0.002

Mean values denoted with different alphabets in a particular column are significantly different at 95 % confidence level ($p \leq 0.05$; Tukey's test)

MS mean square, *CV* coefficient of variation

*, ** and *** significantly different at $p \leq 0.05$; $p \leq 0.01$ and $p \leq 0.001$, respectively

genetic advance were observed in single fruit and seed weight, seed weight fruit^{-1}, single fruit-coat weight, seed yield plant^{-1} and the male-to-female flower ratio.

Among physiological parameters, high heritability was recorded in all the traits exhibiting maximum (98.99 %) for total chlorophyll and minimum (67.88 %) for stomatal conductance. The genetic advance percentage was found to be moderate to high for all the physiological traits. High heritability and genetic advance were recorded for transpiration rate and all the pigments including total chlorophyll content.

For oil characters and fatty acid profile, high heritability was recorded for all the traits. Highest heritability was observed for oil yield plant^{-1} (98.59 %) followed by oil content (98.21 %). Oil yield plant^{-1} also recorded a high genetic advance.

Correlation

Estimates of genotypic and phenotypic correlation coefficients between each pair of characters are presented in Table 7. Significant genotypic and phenotypic correlations were observed between several traits and the magnitudes of genotypic correlation coefficients (rg) were higher than their corresponding phenotypic correlation coefficient (rp) indicating that a genetic association existed between these characters. Among the growth characters, the number of primary and secondary branches correlated ($p < 0.001$) negatively to their diameters, respectively. The diameters of basal stem, primary and secondary branches correlated positively with plant height and plant canopy. The volume of plant canopy correlated negatively to all the leaf pigment contents and net photosynthetic rate. The basal stem diameter, diameter of primary as well as the secondary branches had positive and significant genotypic correlation with oil yield plant^{-1}, while the number of secondary branches correlated negatively.

Except for the number of seeds fruit^{-1} and fruit-coat weight, all the fruit and seed characters had significant positive correlation with oil yield. However, male-to-female flower ratio correlated negatively. In our study, there was significantly high and positive correlation of oil yield plant^{-1} with seed yield plant^{-1} and seed oil content (rg = 0.99 and 0.72, respectively). Fruit length, fruit width,

Table 4 Mean values for various physiological characters of 15 *J. curcas* germplasm

Genotype code	TChl (mg g^{-1})	Chl-*a* (mg g^{-1})	Chl-*b* (mg g^{-1})	CRT (mg g^{-1})	*A* (µmol CO_2 m^{-2} s^{-1})	*E* (mmol H_2O $m^{-2}s^{-1}$)	Gs (mol H_2O $m^{-2}s^{-1}$)	Ci (µmol CO_2 mol air^{-1})	WUE (*A*/*E*)
JCN01	2.09^{abc}	1.43^{abc}	0.64^{abcd}	0.69^{bcd}	17.50^{bcdef}	3.57^{ab}	0.29^{a}	233.71^{a}	4.92^{b}
JCN02	1.43^{c}	0.82^{f}	0.58^{abcd}	0.54^{efg}	15.95^{ef}	2.70^{bcd}	0.16^{b}	172.91^{bcd}	5.92^{ab}
JCN03	1.45^{c}	0.93^{def}	0.50^{bcd}	0.44^{g}	17.03^{cdef}	3.45^{ab}	0.24^{ab}	216.92^{ab}	4.94^{b}
JCN04	1.44^{c}	0.90^{ef}	0.52^{bcd}	0.48^{fg}	15.12^{f}	2.45^{cd}	0.19^{ab}	193.49^{abcd}	6.16^{ab}
JCN05	1.57^{bc}	1.11^{de}	0.45^{d}	0.49^{efg}	16.98^{cdef}	2.76^{bcd}	0.16^{b}	156.35^{d}	6.34^{ab}
JCN06	1.62^{abc}	1.11^{de}	0.48^{cd}	0.47^{g}	18.80^{abcde}	3.68^{a}	0.27^{a}	213.17^{abc}	5.11^{b}
JCN07	1.77^{abc}	1.16^{cde}	0.59^{abcd}	0.54^{efg}	19.67^{abc}	3.76^{a}	0.26^{ab}	188.90^{abcd}	5.23^{b}
JCN08	2.48^{a}	1.61^{a}	0.84^{a}	0.70^{abc}	19.59^{abc}	3.53^{ab}	0.24^{ab}	180.00^{abcd}	5.55^{ab}
JCN09	2.26^{abc}	1.43^{ab}	0.78^{abc}	0.62^{cdef}	20.14^{ab}	3.24^{abc}	0.23^{ab}	173.08^{bcd}	6.27^{ab}
JCN10	1.85^{abc}	1.17^{bcd}	0.66^{abcd}	0.63^{cde}	19.89^{abc}	3.24^{abc}	0.20^{ab}	157.95^{cd}	6.20^{ab}
JCN11	1.69^{abc}	1.06^{def}	0.59^{abcd}	0.43^{g}	17.41^{bcdef}	3.57^{ab}	0.25^{ab}	217.06^{ab}	4.91^{b}
JCN12	2.46^{ab}	1.61^{a}	0.81^{ab}	0.78^{ab}	20.75^{a}	3.43^{ab}	0.23^{ab}	173.50^{bcd}	6.10^{ab}
JCN13	1.78^{abc}	1.19^{bcd}	0.58^{abcd}	0.57^{cdefg}	19.28^{abcd}	3.47^{ab}	0.24^{ab}	180.79^{abcd}	5.58^{ab}
JCN14	2.49^{a}	1.67^{a}	0.79^{abc}	0.84^{a}	20.92^{a}	3.57^{ab}	0.28^{a}	191.06^{abcd}	5.87^{ab}
JCN15	1.72^{abc}	1.06^{def}	0.63^{abcd}	0.56^{defg}	16.43^{def}	2.30^{ab}	0.21^{ab}	199.53^{abcd}	7.19^{a}
Mean	1.87	1.22	0.63	0.58	18.37	3.25	0.23	189.89	5.75
Min	1.43	0.82	0.45	0.43	15.12	2.30	0.16	156.35	4.91
Max	2.49	1.67	0.84	0.84	20.92	3.76	0.29	233.71	7.19
CV (%)	2.94	7.34	16.65	8.25	5.34	8.96	14.97	9.51	10.25
CPTs (M.S.)	0.447***	0.219***	0.046***	0.045***	10.168***	0.649***	0.004**	1543.858***	1.295***
Error (M.S.)	0.087	0.008	0.011	0.002	0.963	0.085	0.001	326.467	0.348

Mean values denoted with different alphabets in a particular column are significantly different at 95 % confidence level ($p \leq 0.05$; Tukey's test)

MS mean square, *CV* coefficient of variation

*, ** and *** significantly different at $p \leq 0.05$; $p \leq 0.01$ and $p \leq 0.001$, respectively

seed length, single fruit weight, single seed weight and seed weight $fruit^{-1}$ had high genotypic correlation (<0.001) among each other, whereas the number of seeds $fruit^{-1}$ had no correlation with any of these characters. The fruit length and width, seed length, unit weight of fruit and seed were apparently found positively correlated to total chlorophyll, net photosynthetic rate and stomatal conductance. The length and weight of fruits and seeds, total chlorophyll and net photosynthetic rate were found correlated ($p < 0.001$) positively with seed oil content, whereas the number of secondary branches was associated negatively. The number of seeds $plant^{-1}$ apparently had low association with most of the characters including seed and oil productivity.

The net photosynthetic rate, transpiration rate and stomatal conductance were significantly associated with all the photosynthetic pigments positively and also among each other. Oil yield correlated significantly and positively with photosynthetic and transpiration rate. Consequently, most of the characters showed a similar genotypic association pattern with seed yield $plant^{-1}$ as with oil yield $plant^{-1}$.

Cluster analysis

Fifteen genotypes were grouped into four clusters based on their pattern of character variation (Fig. 2). Major numbers of genotypes were grouped together in Clusters II and III. The cluster II consisted of seven genotypes and cluster III consisted of six genotypes. The remaining genotypes were grouped under cluster I and IV. The cluster means of characters indicated significant variation among clusters (Table 8). Highest mean for number of primary and secondary branches, fruit length, seed length and width, stomatal conductance, internal leaf CO_2 level, transpiration rate, total chlorophyll, chlorophyll-*a*, carotenoids, palmitic acid, stearic acid and total saturated fatty acid were observed in cluster I. Cluster II had the highest mean values for basal stem diameter, seed yield $plant^{-1}$, oil content %, oil yield $plant^{-1}$, photosynthesis rate and

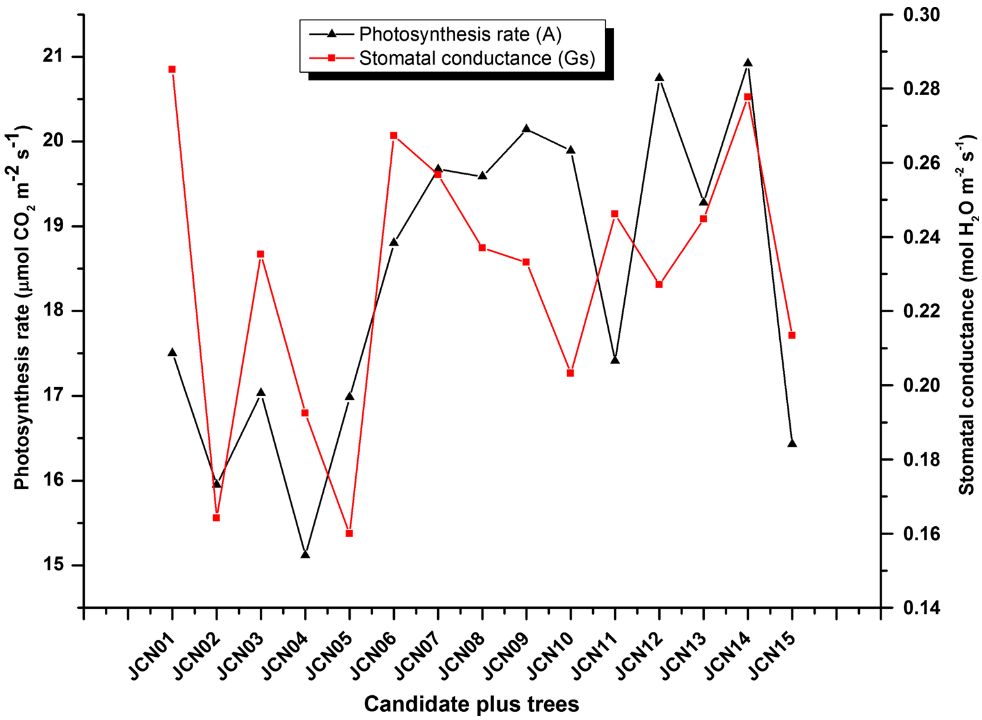

Fig. 1 Variation observed in photosynthesis rate and stomatal conductance in different candidate plus trees of *J. curcas*

Table 5 Mean values for seed oil characters of 15 *J. curcas* germplasm

Genotype code	OC (%)	OYPP (kg)	PA (%)	SA (%)	LA (%)	OA (%)	SFA (%)	USFA (%)
JCN01	27.68^{f}	0.09^{h}	16.94^{abcd}	10.26^{a}	30.95^{cde}	41.85^{abcd}	27.20^{a}	72.80^{d}
JCN02	33.33^{c}	0.43^{bc}	16.51^{abcde}	9.22^{abc}	33.02^{abcd}	41.25^{cd}	25.73^{abc}	74.27^{bcd}
JCN03	34.13^{c}	0.40^{cd}	16.74^{abcde}	8.33^{cdef}	33.98^{ab}	40.94^{cd}	25.08^{bc}	74.92^{bc}
JCN04	30.31^{e}	0.16^{g}	16.32^{abcde}	8.89^{bcd}	35.03^{a}	39.76^{d}	25.21^{bc}	74.79^{bc}
JCN05	31.50^{d}	0.19^{g}	17.12^{abc}	8.40^{cdef}	30.25^{de}	44.23^{ab}	25.52^{abc}	74.48^{bcd}
JCN06	33.04^{c}	0.20^{g}	16.72^{abcde}	8.33^{cdef}	33.23^{abc}	41.73^{abcd}	25.04^{bc}	74.96^{bc}
JCN07	35.85^{b}	0.38^{d}	15.77^{cde}	8.50^{cde}	34.84^{a}	40.89^{cd}	24.27^{cd}	75.73^{ab}
JCN08	37.13^{a}	0.32^{e}	17.73^{a}	8.86^{bcd}	31.29^{bcde}	42.12^{abcd}	26.58^{ab}	73.42^{cd}
JCN09	37.34^{a}	0.47^{a}	17.42^{ab}	9.38^{abc}	31.82^{bcde}	41.39^{cd}	26.79^{ab}	73.21^{cd}
JCN10	33.26^{c}	0.29^{e}	15.46^{de}	8.68^{bcde}	33.05^{abcd}	42.81^{abc}	24.14^{cd}	75.86^{ab}
JCN11	33.59^{c}	0.41^{bcd}	15.65^{cde}	7.22^{f}	35.60^{a}	41.54^{cd}	22.86^{d}	77.14^{a}
JCN12	35.43^{b}	0.28^{ef}	16.28^{abcde}	8.22^{cdef}	33.73^{abc}	41.77^{abcd}	24.50^{cd}	75.50^{ab}
JCN13	33.45^{c}	0.25^{f}	15.26^{e}	7.50^{ef}	34.12^{ab}	43.11^{abc}	22.77^{d}	77.23^{a}
JCN14	37.49^{a}	0.45^{ab}	15.91^{bcde}	9.86^{ab}	29.62^{e}	44.26^{a}	25.77^{abc}	74.23^{bcd}
JCN15	33.26^{c}	0.07^{h}	16.76^{abcde}	7.96^{def}	33.72^{abc}	41.56^{bcd}	24.72^{c}	75.28^{b}
Mean	33.79	0.29	16.44	8.64	32.95	41.95	25.08	74.92
Min	27.68	0.07	15.26	7.22	29.62	39.76	22.77	72.80
Max	37.49	0.47	17.73	10.26	35.60	44.26	27.20	77.23
CV (%)	1.07	5.28	3.06	4.57	2.84	2.09	2.34	0.78
CPTs (M.S.)	21.563***	0.0504***	1.571***	1.994***	9.643***	4.453***	4.939***	4.939***
Error (M.S.)	0.13	0.0002	0.252	0.156	0.877	0.767	0.343	0.343

Mean values denoted with different alphabets in a particular column are significantly different at 95 % confidence level ($p \leq 0.05$; Tukey's test)

MS mean square, *CV* coefficient of variation

*, ** and *** significantly different at $p \leq 0.05$; $p \leq 0.01$ and $p \leq 0.001$, respectively

Table 6 Estimation of mean, variance, coefficient of variation, heritability and genetic advance in *J. curcas*

Traits	Grand mean	δ^2p	δ^2g	PCV%	GCV%	h^{2}B%	GAM%
Growth characters							
BSD	143.54	116.18	109.00	7.51	7.27	93.82	14.51
NPB	2.94	0.29	0.20	18.38	15.21	68.54	25.95
DPB	82.66	126.29	122.58	13.60	13.39	97.07	27.19
NSB	7.96	1.11	0.41	13.26	8.07	37.00	10.11
DSB	47.37	37.84	35.97	12.98	12.66	95.06	25.43
PH	233.41	882.15	870.01	12.72	12.64	98.62	25.85
VPC	9.67	6.66	5.76	26.69	24.82	86.46	47.54
Seed yield characters							
M:F	14.50	3.64	3.43	13.16	12.78	97.09	25.56
FL	27.11	2.54	1.78	5.88	4.92	69.99	8.48
FW	20.96	0.46	0.22	3.25	2.26	48.15	3.23
SL	18.15	0.42	0.29	3.58	2.96	68.63	5.06
SW	8.76	0.07	0.04	3.07	2.33	57.86	3.66
SFW	2.70	0.10	0.10	11.89	11.86	99.48	24.36
SSW	0.61	0.01	0.01	12.04	12.02	99.65	24.72
SW/F	1.65	0.04	0.04	12.29	12.23	99.14	25.09
SPF	2.72	0.01	0.01	3.27	3.19	95.64	6.44
SFCW	1.05	0.03	0.03	16.34	16.18	98.11	33.02
SYPP	0.85	0.12	0.12	40.79	40.48	99.24	82.76
Physiological characters							
TChl	1.87	0.15	0.15	20.74	20.53	98.99	41.87
Chl-*a*	1.22	0.08	0.07	23.02	21.82	94.78	42.60
Chl-*b*	0.63	0.02	0.01	24.00	17.28	72.03	25.65
CRT	0.58	0.02	0.01	22.01	20.41	92.72	38.98
A	18.37	4.03	3.07	10.93	9.53	87.23	17.13
E	3.25	0.27	0.19	16.08	13.36	83.06	22.86
Gs	0.23	0.002	0.00	20.39	13.84	67.88	19.36
Ci	189.89	732.23	405.78	14.25	10.61	74.44	16.27
WUE	5.75	0.66	0.32	14.16	9.77	69.03	13.90
Seed oil characters							
OC	33.79	7.27	7.14	7.98	7.91	98.21	16.15
OYPP	0.29	0.02	0.02	44.44	44.12	98.59	90.25
PA	16.44	0.69	0.44	5.06	4.03	63.52	6.62
SA	8.64	0.77	0.61	10.15	9.06	79.74	16.67
LA	32.95	3.80	2.92	5.92	5.19	76.91	9.37
OA	41.95	2.00	1.23	3.37	2.64	61.55	4.27
SFA/USFA	25.08/74.92	1.88	1.53	5.46	4.94	81.71	9.19

$\delta^2 p$ phenotypic variance, $\delta^2 g$ genotypic variance, *PCV* phenotypic coefficient of variation, *GCV* genotypic coefficient of variation, h^2B heritability in broad sense, *GAM%* genetic advance as percent of mean

chlorophyll-*b*. Thus this cluster possessed high mean values of several desirable traits having high heritability for realizing high oil productivity. Cluster III had highest mean values for plant canopy volume, oleic acid and unsaturated fatty acid. The highest mean for diameter of primary and secondary branches, plant height, fruit width, single seed and fruit weight, seed weight fruit^{-1}, number of seeds fruit^{-1}, fruit-coat weight, male-to-female flower ratio, water use efficiency and linoleic acid percentage were observed in cluster IV. The lowest mean value for diameter of primary and secondary branches, plant height, single seed and fruit weight, seed weight fruit^{-1}, number of seeds fruit^{-1}, fruit-coat weight, water-use efficiency, oil content, linoleic acid and unsaturated fatty acid were observed in cluster I. The cluster II genotypes had lowest mean values for number of secondary branches and male-to-female

Table 7 Genotypic and phenotypic correlation among characters measured on 15 CPTs of *J. curcas*

	BSD	NPB	DPB	NSB	DSB	PH	VPC	M:F	FL	FW
BSD	1.00	0.10	0.37*	0.11	0.08	0.46**	0.44**	−0.35*	0.17	0.38**
NPB	0.08	1.00	−0.67***	1.00***	−0.66***	−0.23	−0.07	0.27	0.32*	0.09
DPB	0.35*	−0.55***	1.00	−0.44**	0.89***	0.82***	0.44**	−0.19	−0.01	−0.04
NSB	0.02	0.60***	−0.22	1.00	−0.50***	0.13	0.13	0.54***	0.02	−0.30*
DSB	0.07	−0.56***	0.85***	−0.34*	1.00	0.66***	0.13	−0.21	0.21	0.02
PH	0.44**	−0.19	0.81***	0.06	0.64***	1.00	0.63***	−0.01	0.16	−0.03
VPC	0.41**	−0.07	0.41**	0.12	0.11	0.59***	1.00	−0.21	−0.45**	−0.54***
M:F	−0.30*	0.23	−0.20	0.30*	−0.21	−0.01	−0.18	1.00	−0.11	0.09
FL	0.14	0.20	0.01	0.15	0.17	0.14	−0.34*	−0.12	1.00	0.93***
FW	0.24	0.19	0.02	0.09	−0.03	−0.04	−0.33*	0.06	0.57***	1.00
SL	0.32*	0.04	0.15	0.07	0.05	0.25	−0.12	0.03	0.60***	0.61***
SW	−0.04	−0.06	0.10	−0.039	0.05	0.14	−0.14	0.26	0.35*	0.35*
SFW	−0.03	−0.21	0.24	−0.19	0.39**	0.14	−0.22	−0.11	0.55***	0.47**
SSW	0.10	−0.16	0.15	−0.26	0.28	0.04	−0.27	−0.18	0.55***	0.53***
SW/F	0.23	−0.22	0.22	−0.28	0.30*	0.05	−0.23	−0.24	0.51***	0.57***
SPF	0.52***	−0.27	0.33*	−0.07	0.10	0.11	0.18	−0.26	−0.13	0.18
FCV/F	−0.34*	−0.13	0.19	−0.02	0.39**	0.21	−0.14	0.08	0.43**	0.20
TChl	0.11	0.22	−0.12	−0.01	0.12	−0.24	−0.61***	−0.35*	0.64***	0.45**
Chl-*a*	0.05	0.32*	−0.21	0.14	0.03	−0.30*	−0.57***	−0.29	0.64***	0.42**
Chl-*b*	0.16	−0.01	0.05	−0.25	0.23	−0.09	−0.50***	−0.34*	0.44**	0.37*
CRT	0.10	0.13	0.02	0.10	0.14	−0.13	−0.53***	−0.22	0.56***	0.46**
A	−0.03	0.09	−0.01	−0.05	0.27	−0.06	−0.33*	−0.30*	0.59***	0.20
E	−0.07	0.41**	−0.31*	0.10	−0.11	−0.10	−0.08	−0.25	0.48***	0.05
Gs	0.19	0.35*	−0.18	0.26	−0.07	0.05	−0.07	−0.17	0.50***	0.10
Ci	0.13	0.35*	−0.16	0.32*	−0.27	0.13	0.24	−0.05	0.15	−0.04
WUE	0.03	−0.43**	0.33*	−0.14	0.33*	0.06	−0.18	0.11	−0.11	0.08
OC	0.19	−0.32*	0.26	−0.44**	0.44**	−0.02	−0.23	−0.43**	0.43**	0.36*
SYPP	0.24	−0.21	0.40**	−0.40**	0.41**	0.30*	0.21	−0.37*	0.26	0.22
OYPP	0.28	−0.21	0.39**	−0.41**	0.43**	0.27	0.15	−0.40**	0.33*	0.28

	SL	SW	SFW	SSW	SW/P	SPF	SFCW
BSD	0.39**	−0.06	−0.04	0.11	0.24	0.55***	−0.36**
NPB	0.07	−0.01	−0.26	−0.19	−0.28	−0.35*	−0.17
DPB	0.16	0.14	0.24	0.15	0.23	0.34*	0.19
NSB	−0.16	−0.22	−0.31*	−0.43**	−0.45**	−0.13	−0.04
DSB	0.12	0.10	0.40**	0.29	0.30*	0.10	0.40**

Table 7 continued

	SL	SW	SFW	SSW	SW/P	SPF	SFCW
PH	0.32*	0.19	0.14	0.04	0.05	0.11	0.21
VPC	−0.16	−0.19	−0.25	−0.29	−0.25	0.18	−0.17
M:F	0.06	0.38*	−0.12	−0.19	−0.25	−0.27	0.07
FL	0.82***	0.52***	0.65***	0.66***	0.61***	−0.17	0.51***
FW	0.96***	0.84***	0.68***	0.74***	0.80***	0.24	0.33*
SL	1.00	0.77***	0.59***	0.62***	0.60***	0.00	0.40**
SW	0.75***	1.00	0.36*	0.26	0.20	−0.19	0.44**
SFW	0.48***	0.27	1.00	0.90***	0.88***	0.04	0.83***
SSW	0.52***	0.20	0.89***	1.00	0.97***	−0.04	0.55***
SW/F	0.50***	0.16	0.88***	0.96***	1.00	0.22	0.48***
SPF	0.00	−0.13	0.05	−0.04	0.23	1.00	−0.18
FCV/F	0.31*	0.31*	0.83***	0.53***	0.47**	−0.17	1.00
TChl	0.30*	0.07	0.39**	0.45**	0.45**	0.03	0.19
Chl-*a*	0.24	0.03	0.31*	0.34*	0.33*	−0.03	0.18
Chl-*b*	0.32*	0.14	0.43**	0.49***	0.52***	0.13	0.19
CRT	0.29	0.12	0.26	0.24	0.28	0.17	0.15
A	0.22	0.02	0.49***	0.46**	0.42**	−0.14	0.42**
E	0.23	0.09	0.28	0.29	0.18	−0.41**	0.31*
Gs	0.25	−0.03	0.23	0.23	0.18	−0.18	0.22
Ci	0.04	−0.13	−0.10	−0.08	−0.10	−0.08	−0.07
WUE	−0.13	−0.11	0.04	−0.01	0.10	0.40**	−0.04
OC	0.33*	0.07	0.59***	0.76***	0.76***	0.04	0.22
SYPP	0.42**	0.37*	0.25	0.39**	0.33*	−0.17	0.07
OYPP	0.44**	0.35*	0.30*	0.45**	0.41**	−0.13	0.08

Table 7 continued

	TChl	Chl-*a*	Chl-*b*	CRT	*A*	*E*	Gs	Ci	WUE	OC	SYPP	OYPP
BSD	0.12	0.04	0.29	0.12	−0.02	−0.11	0.30*	0.21	0.09	0.19	0.26	0.30*
NPB	0.26	0.37*	0.04	0.16	0.17	0.51***	0.61***	0.44**	−0.57***	−0.37*	−0.28	−0.27
DPB	−0.13	−0.24	0.11	0.00	0.01	−0.34*	−0.24	−0.23	0.47**	0.26	0.40**	0.39**
NSB	0.01	0.09	−0.11	0.03	0.00	0.36*	0.72***	0.68***	−0.49***	−0.77***	−0.69***	−0.70***
DSB	0.11	0.04	0.28	0.14	0.34*	−0.14	−0.14	−0.41**	0.52***	0.46**	0.42**	0.43**
PH	−0.25	−0.32*	−0.10	−0.15	−0.06	−0.10	0.11	0.20	0.08	−0.02	0.30*	0.27
VPC	−0.65***	−0.68***	−0.65***	−0.62***	−0.41**	−0.02	−0.05	0.40**	−0.41**	−0.27	0.23	0.16
M:F	−0.36*	−0.31*	−0.48**	−0.25	−0.34*	−0.33*	−0.25	−0.07	0.22	−0.45**	−0.37*	−0.40**
FL	0.80***	0.74***	1.00***	0.66***	0.73***	0.65***	0.79***	0.18	−0.24	0.51***	0.31*	0.39**
FW	0.66***	0.53***	0.98***	0.54***	0.42**	0.25	0.40**	0.01	0.06	0.52***	0.29	0.37*
SL	0.35*	0.25	0.62***	0.39**	0.34*	0.42**	0.54***	0.22	−0.32*	0.40**	0.51***	0.54***
SW	0.08	0.03	0.23	0.27	0.06	0.17	0.04	−0.03	−0.22	0.09	0.49***	0.46**
SFW	0.39**	0.32*	0.61***	0.27	0.55***	0.34*	0.36*	−0.12	0.04	0.60***	0.25	0.30*
SSW	0.45**	0.36*	0.68***	0.25	0.53***	0.35*	0.34*	−0.11	−0.01	0.77***	0.39**	0.46**
SW/F	0.45**	0.35*	0.72***	0.29	0.48***	0.22	0.27	−0.13	0.13	0.77***	0.34*	0.41**
SPF	0.02	−0.05	0.20	0.16	−0.17	−0.48***	−0.21	−0.07	0.53***	0.04	−0.18	−0.14
SFCW	0.21	0.19	0.30*	0.16	0.47**	0.38**	0.35*	−0.08	−0.09	0.21	0.08	0.08
TChl	1.00	1.00***	1.00***	0.93***	0.83***	0.47**	0.55***	−0.18	0.19	0.54***	0.09	0.20
Chl-*a*	0.94***	1.00	1.00***	0.90***	0.85***	0.55***	0.63***	−0.12	−0.02	0.47**	0.02	0.12
Chl-*b*	0.80***	0.55***	1.00	1.00***	0.85***	0.33*	0.44**	−0.31*	0.30*	0.71***	0.24	0.36*
CRT	0.85***	0.86***	0.58***	1.00	0.73***	0.31*	0.40**	−0.26	0.20	0.37*	0.00	0.09
A	0.70***	0.71***	0.48***	0.59***	1.00	0.75***	0.59***	−0.32*	−0.18	0.71***	0.33*	0.42**
E	0.38*	0.41**	0.21	0.20	0.59***	1.00	0.86***	0.27	−0.72***	0.36*	0.40**	0.43**
Gs	0.38*	0.42**	0.21	0.30*	0.42**	0.69***	1.00	0.59***	−0.72***	0.19	−0.23	0.07
Ci	−0.11	−0.09	−0.11	−0.15	−0.25	0.34*	0.70***	1.00	−0.67***	−0.41**	−0.23	−0.25
WUE	0.14	0.04	0.08	0.18	0.04	−0.47**	−0.47**	−0.56***	1.00	0.12	−0.35*	−0.31*
OC	0.52**	0.44**	0.49***	0.35*	0.62***	0.28	0.14	−0.31*	0.11	1.00	0.64***	0.72***
SYPP	0.10	0.02	0.19	0.01	0.28	0.31*	−0.17	−0.17	−0.23	0.63***	1.00	0.99***
OYPP	0.20	0.12	0.26	0.09	0.36*	0.33*	0.05	−0.18	−0.19	0.72***	0.99***	1.00

Genotypic correlation coefficient (rg) above the diagonal and phenotypic correlation coefficient (rp) below the diagonal

*, ** and *** significantly different at $p \leq 0.05$; $p \leq 0.01$ and $p \leq 0.001$, respectively

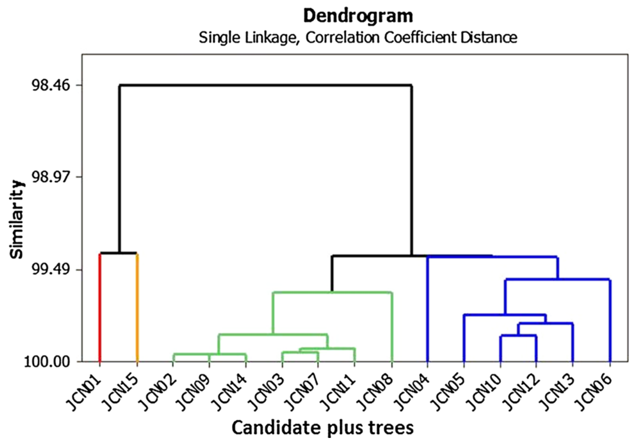

Fig. 2 Dendrogram showing similarity between various genotypes on the basis of single linkage correlation distance using hierarchical agglomerative approach (*different colours* represent different clusters) (color figure online)

flower ratio. The genotype in cluster IV had the lowest mean values for characters like number of primary branches, plant canopy volume, seed and oil yield plant^{-1}, photosynthesis rate, transpiration rate, total Chl, Chl-*a*, carotenoids, stearic and oleic acid.

The maximum distances from centroid for clusters were 0.00, 3.68, 1.42 and 0.00 for clusters I, II, III, and IV, respectively. The inter cluster distances are depicted in Table 9. The maximum distance (14.98) was observed between cluster II and IV, while minimum (3.93) was between cluster I and III.

Discussion

Enhancing the oil yield is the ultimate goal of any *Jatropha* improvement programme. However, being poly-genetically controlled trait, selection based on yield alone is not effective. Genetic variation in traits of *J. curcas* can be gainfully exploited in a crop improvement program, particularly for selection of elite germplasm having more oil content, seed and oil yield. Correlation among the traits is a vital statistical tool that measures the degree and magnitude of association and is useful in designing an effective breeding program as it indicates whether the choice of one trait confirms the appearance or disappearance of other (Kumar and Singh 2014). Thus, selection for high yield indirectly through yield associated and highly inheritable characters after eliminating environmental components of phenotypic variance should be the breeding objective. Improvement in a character by selection can be brought out only if a major portion of the variation is heritable which is governed completely by the magnitude of genetic variability in the source progeny.

Significant differences were observed for all the traits including the oil productivity among 15 genotypes sourced

Table 8 Cluster constituents and cluster mean values for all the traits in 15 CPTs of *J. curcas*

	Genotypes	BSD	NPB	DPB	NSB	DSB	PH	VPC	M:F	FL	FW	SL	SW	SFW	SSW
Cluster I	JCN01	146.94	4.22	63.85	10.11	35.35	227.78	8.69	16.1	28.51	21.27	18.6	8.9	2.31	0.5
Cluster II	JCN02, JCN03, JCN07, JCN08, JCN09, JCN11, JCN14	147.5	2.86	84.15	7.52	48.04	235.29	9.76	13.9	27.68	21.25	18.5	8.9	2.79	0.64
Cluster III	JCN04, JCN05, JCN06, JCN10, JCN12, JCN13	138.47	2.93	82.99	8.15	48.02	230.13	10.07	14.6	26.17	20.5	17.7	8.6	2.63	0.58
Cluster IV	JCN15	142.78	2.33	89.02	7.78	50.86	245.56	7.59	16.6	27.37	21.36	18.1	8.7	2.95	0.65

SWPF	SPF	SFCW	SYPP	TChl	Chl-*a*	Chl-*b*	CRT	*A*	Gs	Ci	*E*
1.34	2.69	0.96	0.33	2.09	1.43	0.64	0.69	17.5	0.29	233.71	3.57
1.75	2.72	1.04	1.15	1.94	1.24	0.67	0.59	18.67	0.24	191.42	3.4
1.56	2.71	1.07	0.69	1.79	1.18	0.58	0.57	18.47	0.22	179.21	3.17
1.84	2.83	1.11	0.22	1.72	1.06	0.63	0.56	16.43	0.21	199.53	2.3

WUE	OC	OYPP	PA	SA	LA	OA	SFA	USFA
4.92	27.68	91.41	16.94	10.26	30.95	41.85	27.2	72.8
5.53	35.55	408.04	16.53	8.77	32.88	41.77	25.3	74.7
5.91	32.83	228.78	16.19	8.34	33.23	42.24	24.53	75.47
7.19	33.26	74.11	16.76	7.96	33.72	41.56	24.72	75.28

Table 9 Distance between cluster centroids

	Cluster I	Cluster II	Cluster III
Cluster I			
Cluster II	7.13		
Cluster III	3.93	10.97	
Cluster IV	9.19	14.98	7.40

from diverse locations. The variability exhibited in the different traits may be attributed to heterogeneity and also to the geo-ecological dissimilarities from which the different germplasm were sourced. Among the germplasm, there were large differences between maximum and minimum values for seed yield (482 %), oil content (35 %) and oil yield (571 %) which underscored the importance of germplasm choice at the very outset for profitable *Jatropha* cultivation. Unfortunately, investments on *Jatropha* got way ahead of the plant science (Sanderson 2009), and the plantations were done hurriedly using seed material which had no known pedigree despite scientific cautions about imminent frustration over poor yields in the subsequent years by not focussing on germplasm quality (Ghosh et al. 2007), which eventually boomeranged. Moreover, untested germplasm are often not well-suited to the climate in which they are planted (Sanderson 2009), which necessitates that the selection of the plant genotype should be done after acclimatization of the plants in a particular environment for a sufficient period.

Variability and association of traits among germplasm

Genotypic coefficient of variation and genetic advance are the parameters that help to split the total variability into heritable and non-heritable components (Gangashetty et al. 2010). Phenotypic variances (σ^2p) were observed higher or similar as compared to the corresponding genotypic variances (σ^2g) for all the traits. Also, PCV was higher than the corresponding GCV for all the traits indicating that the traits interacted with the environment to some extent. The number of primary and secondary branches, stomatal conductance, internal leaf carbon dioxide concentration, water use efficiency, and chlorophyll-*b* had wide difference between PCV and GCV suggesting the role of environment on these characters. In yield, oil and fatty acid traits, the difference between PCV and GCV was much less indicating less effect of the environment on such traits. High heritability along with high genetic advance is known to be a good indicator for trait selection and is controlled by additive genes.

Among the growth characters, the number of secondary branches plant^{-1} was not found suitable as a trait of interest for direct selection for seed source on account of having low GCV, heritability and genetic advance and likelihood of it to be more influenced by environment. This trait was strongly and negatively correlated with oil yield. The negative correlation of yield with number of branches may be explained on account of excess branching and leaf formation which might use the majority of assimilates towards vegetative growth while adversely affecting reproductive growth (Ghosh et al. 2011). Significant association of basal stem diameter with oil yield was found in the present study, which was in conformity with an earlier report (Wani et al. 2012). Even then, this trait may not be a good selection index for the selection of high oil yielders in *Jatropha* because of inherent low PCV and GCV.

In the present study, plant height was positively correlated with seed yield, but not with oil yield. However, in contrast, another study reported it to correlate positively with both (Shabanimofrad et al. 2013). In our study, plant canopy volume did not correlate with seed and oil yield. PCV and GCV were moderate for plant height whereas it was high for plant canopy volume. Both of these characters had high heritability and genetic advance and thus can be taken forward for breeding high yielding plants with compact stature. Plants at a low height with a compact canopy are desirable from a harvesting point of view as fruit are then at comfortable harvesting distances, thereby reducing the cost of seed production (Ghosh et al. 2011).

Among the yield attributes, number of seeds fruit^{-1} neither had any correlation with oil content, seed yield or oil yield, nor had high values for PCV, GCV and genetic advance even though its heritability was high. So this trait may not be targeted for direct selection. Fruit length and fruit width, seed length and seed width had high association with oil yield as well as seed yield. These traits also had low values of GCV, PCV and genetic advance and therefore are not to be viewed as best gain traits for *Jatropha* improvement through selection. Genetic advance was also reported to be lower for seed characters as compared to growth and yield traits (Rao et al. 2008). Fruit weight and seed weight as well as seed weight fruit^{-1} had moderate GCV as well as PCV but high heritability and high genetic advance. Low to moderate PCV and GCV for seed weight was also reported by Tripathi et al. (2013). High heritability was also reported for seed weight in *Jatropha* (Rao et al. 2008; Das et al. 2010). These traits had a high correlation towards oil yield. Thus, these characters can be inferred to be important for direct selection purposes. In conformity with our results, seed weight was reported to be positively correlated with oil yield (Tripathi et al. 2013) and oil content (Nietsche et al. 2015; Tripathi et al. 2013; Kaushik et al. 2007; Shabanimofrad et al. 2013) and seed yield plant^{-1} (Rao et al. 2008; Das et al. 2010). Therefore, seed weight can be considered as an important trait for selection. Similarly, seed yield plant^{-1} was an important trait found suitable for direct selection as it had the highest variability as well as heritability and genetic advance. Similar to the finding of another study (Wani et al. 2012), seed yield plant^{-1} had a high correlation with oil yield in our study. Selection for the characters, among genotypes having high heritability combined with high genetic advance, is likely to add more additive genes leading to further improvement. Our results are in accordance with other researchers (Das et al. 2010; Shabanimofrad et al. 2013), who reported high values of PCV and GCV for seed and oil yield, respectively. A correlation matrix of yield attributing characters revealed a positive correlation among fruit length and width, seed length and width, fruit and seed weight and seed weight/fruit. Similar findings were also reported by Ginwal et al. (2004) and Rao et al. (2008).

The male-to-female flower ratio was inversely correlated with oil yield. The male-to-female flower ratio had moderate PCV and GCV coupled with high heritability and genetic advance and, thus, was found to be a candidate trait for selection. The male-to-female flower ratio was significantly negative correlated with seed and oil yield and the similar findings were also reported by Nietsche et al. (2015) and Rao et al. (2008).

Photosynthesis rate, transpiration rate, stomatal conductance, intercellular CO_2 concentration and the water use efficiency, i.e. the ratio of photosynthesis and transpiration rate are important physiological traits used for new cultivars in water scarce environments (Richards 2006; Passioura 2007; Sunil et al. 2013). The physiological parameters are important from the point of view of imparting stress tolerance to *J. curcas* under moisture stress condition. Sunil et al. (2013) identified Jatropha accessions with low stomatal conductance and transpiration rates coupled with high photosynthetic rates for growing under moisture stress condition. The present study found high correlation between photosynthetic rate and transpiration rate, photosynthetic rate and stomatal conductance and stomatal conductance and transpiration and the findings corroborated with those reported by Sunil et al. (2013). Further, our study found that all the physiological parameters observed had high heritability which indicates the possibility of greater success in transferring these traits by crossing with high biomass and oil yielding lines. Our result is in agreement with that of Avenson et al. (2005) who also reported that the chlorophyll content positively correlated to photosynthetic rate which increased biomass and yield. All the photosynthetic pigments had high variability and heritability. They did not correlate with seed or oil yield but correlated with oil content. The gas exchange parameters, viz., net photosynthesis and transpiration rate were highly correlated with pigments, seed and oil yield and had moderate values of genetic variability parameters. Though the trait oil content correlated highly with seed yield and oil yield its GCV and PCV were found to be low, which was in conformity with an earlier study by Tripathi et al. (2013). However, the trait was found to be highly heritable in nature with moderate genetic advance. The fatty acids were not found preferred traits of interest due to their low GCV, PCV, and genetic advance. Similar results were reported in earlier studies where palmitic acid, linoleic acid and oleic acid were reported to have high heritability coupled with low genetic advance indicating the occurrence of non-additive gene action (Nechifor et al. 2011).

Divergence of genotypes

Genetic divergence analysis helps to categorize the germplasm into subsets from which a genetically diverse parent can be chosen. In our study, highest mean value of important characters like seed yield plant^{-1}, oil content, oil yield plant^{-1} were observed in cluster II and comprised genotypes that had the lowest mean value for male-to-female flower ratio. On the other hand, genotypes in cluster IV (JCN15) had high water use efficiency, while the other distinct cluster III had germplasm that had more adaptability to dry condition characterized by low stomatal conductivity, transpiration rate along with good photosynthetic rate (JCN05) and biotic stress against pest (JCN13). Plants from such distinct group of germplasm associated with particular characters may be utilized as parents for breeding purpose to develop stress-resistant high oil-yielding elite varieties. The wide inter-cluster distance between cluster II and IV and that between cluster II and IV indicated extensive genetic diversity between these groups. Selection of parent materials from such clusters for a hybridization programme will help develop elite *Jatropha* plants with desirable characters. The minimum inter-cluster distance between clusters I and III indicated that plants in these groups are closely related. Therefore, the selection of parent trees within these clusters should be avoided. The diversity and associations found in this study may further be confirmed by suitable molecular techniques.

Conclusion

The study indicated the presence of high levels of variations among the traits such as oil content, seed yield and oil yield plant^{-1}. Traits with low environmental influence, high variability, heritability and genetic advance in addition to having significant bearing on oil yield were identified as the best gain characteristics which would help in transferring these traits by hybridization followed by recurrent selection. The study also helped to identify the promising germplasm among the population of diverse genotypes of *J. curcas* that can serve as parents with favourable characters for further breeding purposes. Moreover, the germplasm identified to be superior only should be propagated in large numbers to serve as quality planting material, failing which the consequences would render the plant to be irrelevant commercially.

Author contribution statement Sarnam Singh, carried out the experiment; field work; statistical analysis; writing the article. Aruna Prakash, supervised implementation in field; writing the article. N. R. Chakraborty, analysis and interpretation; writing the article; Candace Wheeler, overall project support; manuscript improvement. P. K. Agarwal, useful suggestions during experiment; final approval of the article. Arup Ghosh, designed and implemented the experiment; monitored data collection; writing the article; analysis and interpretation; final draft.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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