RESEARCH

Multiple Resistant and Nutritionally Dense Germplasm Identified from Mini Core Collection in Peanut

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ABSTRACT

Peanut (*Arachis hypogaea* L.) is extensively grown by resource-poor farmers in the semiarid tropics where many abiotic and biotic stresses limit the crop's productivity and seed quality. Peanut cultivars with enhanced host-plant resistance, adaptation to abiotic stress, input-use efficiency, and yield potential will maximize yield gains and minimize inputs to sustain production. The peanut mini core collection was evaluated for agronomic traits in multienvironment trials at Patancheru, India. The published information on 184 mini core accessions revealed 28 accessions resistant to abiotic stress, 30 resistant to biotic stress, and 18 that were agronomically desirable but susceptible to stresses, while 16 were seed nutrient dense. The mini core is part of the composite collection, which was previously genotyped using SSRs. The agronomic evaluation, stress response, and nutritional information together with genotyping data were used to identify genetically diverse germplasm with agronomically beneficial traits: ICG 12625 (resistance to drought, low temperature, late leaf spot [LLS], *Aspergillus flavus* Link, bacterial wilt; high oil and good oil quality) and ICG 442 (resistance to drought, salinity, P deficiency); ICG 12625 and ICG 2381 (resistance to rust, *A. flavus*; good oil quality); ICG 12697 (resistance to LLS, rust, *A. flavus*) and ICG 6022 (resistance to early leaf spot [ELS], LLS); ICG 14710 (high oil, Fe, Zn) and ICG 7963 (high protein, Fe, Zn); ICG 11426 (resistance to ELS, LLS, rust) and ICG 5221 (high Fe and Zn and good oil quality). Accessions with adaptation to rainy and/or post-rainy environments were ICG# 434, 5745, 8285, 10036, 11088, 11651, 12625, 15042, and 15419. These accessions are ideal genetic resources that may be used to develop agronomically superior and nutritionally enhanced peanut cultivars with multiple resistances to abiotic and biotic stresses.

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Abbreviations: AMOVA, analysis of molecular variance; ELS, early leaf spot; GRVD, *Groundnut rosette virus* disease; LLS, late leaf spot; MAGIC, multiparent advanced generation inter-cross; O/L, oleic/linoleic fatty acid ratio; PBND, peanut bud necrosis disease; REML, restricted maximum likelihood; TSWV, *Tomato spotted wilt virus*.

PEANUT (*Arachis hypogaea* L.) is one of the most important oilseed crops. It is widely grown in the tropical, subtropical, and warm temperate regions of the world. In 2011 the total acreage of peanut worldwide was 21.77 million ha with an annual production of 38.61 Tg (in shell) (www.faostat.fao.org; accessed on 26 Apr. 2013). Asia contributes 67.91% (26.22 Tg), Africa 24.45% (9.44 Tg), and the Americas 7.87% (3.03 Tg) to global peanut production. The average productivity of peanut was < 1 t ha^{-1} in Africa, while it was 2.4 and 3.0 t ha^{-1} in Asia and the Americas. China is the largest producer (16.11 Tg, 41.72% of world production), followed by India (6.93 Tg, 17.94%), Myanmar (1.39 Tg, 3.6%), Indonesia (0.69 Tg, 1.79%), and Vietnam (0.47 Tg, 1.22%), while Nigeria in Africa is the largest producer (2.96 Tg, 7.67%) followed by the United Republic of Tanzania (0.65 Tg, 1.69%), Cameroon (0.54 Tg, 1.39%), Senegal (0.53 Tg, 1.37%), the Democratic Republic of Congo (0.47 Tg, 1.21%), and Ghana (0.46 Tg, 1.20%).

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The other producers in Africa are Burkina Faso, Chad, Guinea, Mali, Malawi, and Niger, wherein the peanut production is approximately 0.27–0.39 Tg. In the Americas, the United States (1.65 Tg, 4.27%) and Argentina (0.70 Tg, 1.81%) dominate production. The regions and countries within a region show large variability in productivity. For example, productivity remained at < 1.0 t ha^{-1} in Africa (from 0.7 t ha^{-1} in Burkina Faso to 1.4 t ha^{-1} in Cameroon), while it rose to 2.4 t ha^{-1} in Asia (from 1.3 t ha^{-1} in Indonesia to 3.4 t ha^{-1} in China) and 3.0 t ha^{-1} in the Americas (from 2.9 t ha^{-1} in Brazil to 3.7 t ha^{-1} in the United States). Various factors, including abiotic and biotic stresses and technological innovations (cultivars, irrigation, herbicides, insecticides, fungicides, farm mechanization, and postharvest technologies, etc.) leading to highly mechanized agriculture in some countries, contribute to the variability in peanut productivity (Isleib and Wynne, 1991; Zeyong, 1991; Shuren et al., 1996). Farm mechanization, socioeconomic conditions, low inputs, and lack of adaptation to new technologies, beside susceptibility to abiotic and biotic stresses, contribute to large differences in peanut productivity between the developed and most of the developing countries. Drought, salinity, and heat are the major abiotic stresses, while the major biotic stresses include diseases (fungal, virus, and bacterial) and pests (both sucking and defoliators or pests as vectors of virus diseases). The major fungal diseases include early leaf spot (ELS; *Cercospora arachidicola* Hori.), late leaf spot [LLS; *Phaeoisariopsis personata* (Berk. and Curtis) Deighton], and rust (*Puccinia arachidis* Speg.); the predominant bacterial disease is bacterial wilt [*Ralstonia solanacearum* (E.F. Smith) Yabuchi et al.]; and the viral diseases include *Groundnut rosette virus* disease (GRVD), peanut bud necrosis disease (PBND), and *Tomato spotted wilt virus* (TSWV). Some of these pathogens, such as rust and leaf spots, are widely distributed, whereas others are localized, such as GRVD in Africa, PBND in South Asia, TSWV in the United States, and bacterial wilt in East and Southeast Asia. Likewise, many insect pests cause localized damage to peanut, such as the leafminer [*Aproaerema modicella* (Deventer)] in South Asia and *Spodoptera* in South and Southeast Asia. Most of these stresses often occur together to cause substantial loss to production and in the quality of the peanuts (Dwivedi et al., 2003). Aflatoxin caused by *Aspergillus flavus* and *A. parasiticus* Speare, is a serious quality problem that adversely impacts human health and trade (Williams et al., 2004).

Peanut is a rich source of protein, fat, minerals, and vitamins. Peanut is essentially grown for its oil in most countries; however, the demand for the peanut as wholesome food has been growing because of the health benefits associated with consumption of the nutrient-dense peanut kernels. Regular consumption of peanuts is associated with reduced risk of cardiovascular diseases, lower blood pressure, reduced incidence of cancers and type 2 diabetes (O'Byrne et al., 1997; Kris-Etherton, 2001; Alper and Mattes, 2003; Teres et al., 2008; Vassiliou et al., 2009), and proper body-weight maintenance, that is, malnourished infants gain weight and obese adults and children lose weight (Griel et al., 2004; Pelkman et al., 2004). The oil and protein contents and oil quality, as determined by the variation in oleic/linoleic (O/L) fatty acid ratio, are important seed quality traits. High O/L ratio determines the shelf life of the peanut products: the higher the ratio, the longer the products' shelf life (Mozingo et al., 2004). Peanut haulm is excellent forage for cattle because it is rich in protein and is more palatable than many other fodders (Cook and Crosthwaite, 1994). Peanut derives 41–63% of its total nitrogen by fixing atmospheric nitrogen through host–rhizobium symbiosis depending on the soil types, which is important for its growth and yield, especially in low-input production systems (Khan and Yoshida, 1994).

Identification of trait-specific genetic resources for the desired traits from large ex situ germplasm collections is a key to successfully introgressing new traits in crop improvement programs. The aims of this investigation were to (i) assess agronomic performance of the peanut mini core collection accessions and (ii) identify trait-specific genetically diverse germplasm for use in breeding programs. We evaluated the peanut mini core collection (Upadhyaya et al., 2002a) in multienvironment trials to assess agronomic performance. The agronomic performance together with genotyping information (Upadhyaya et al., 2008) and responses to abiotic (Upadhyaya et al., 2001, 2009; Upadhyaya, 2005; Biradar, 2007; ICRISAT, 2008, 2009, 2010; Srivastava, 2010; Hamidou et al., 2012, 2013) and biotic (Yugandhar, 2005; Ajay, 2006; Madhura, 2006; Kusuma et al., 2007; Khalid, 2008; Sujay et al., 2008; ICRISAT, 2009; Jianwei et al., 2010; Zhang, 2010) stresses and nutritional traits (oil, protein, O/L ratio, Fe, and Zn) (Upadhyaya et al., 2012a,b) of the mini core accessions were used to identify genetically diverse accessions with agronomically desirable traits for use in peanut breeding and genomics.

MATERIALS AND METHODS

One hundred and eighty-four germplasm accessions of the peanut mini core collection (Upadhyaya et al., 2002a), representing two subspecies (*fastigiata* and *hypogaea*) and six botanical varieties (*hypogaea*, 85 accessions; *vulgaris*, 58 accessions; *fastigiata*, 37 accessions; *peruviana*, two accessions; and *aequatoriana* and *hirsuta*, one accession each) together with four controls (ICGS 44, ICGS 76, Gangapuri, and M 13) were included in this study. Both ICGS 76 (also known as ICGV 87141 or ICG 13942) and M 13 (ICG 156) belong to the subspecies *hypogaea* var. *hypogaea*; ICGS 44 (also known as ICGV 87128 or ICG 13941) belongs to the subspecies *fastigiata* var. *vulgaris*; and Gangapuri (ICG 2738) belongs to the subspecies *fastigiata* var. *fastigiata*. ICGS 76 is adapted to rainfed conditions in peninsular India (Nigam et al., 1991), while M 13 is a late maturing large-seeded cultivar adapted to rainfed conditions in northern India (Isleib et al., 1994). Gangapuri is an early maturing cultivar

Table 1. Accessions providing sources of resistance to abiotic and biotic stress and those with nutrient-dense seeds after evaluation of the peanut mini core collection.

	Resistant genotype		
Stress	**Subsp. *fastigiata***	**Subsp. *hypogaea***	**Reference**
Abiotic stresses			
Drought	ICG 434, 442, 1274, 2106, 3584, 3673, 5475, 6646, 8567, 10554, 11088, 12625	ICG 862, 2511, 3053, 5663, 8285, 11855, 14475	Upadhyaya, 2005; ICRISAT, 2008, 2009, 2010; Hamidou et al., 2012
Heat	ICG 4729, 5236, 12879, 15042	ICG 862, 1668, 2925, 8285, 11219	Hamidou et al., 2013
Salinity	ICG 442, 2106	ICG 862, 8285, 9842, 11855	ICRISAT 2008, 2009; Srivastava, 2010
Low temperature	ICG 1274, 5475, 5609, 10554, 11088, 12625		Upadhyaya et al., 2001, 2009
P deficiency	ICG 442, 3584, 3673, 5609	ICG 5663, 9842, 14475	Biradar, 2007
Biotic stresses			
Early leaf spot	ICG 6022	ICG 2857, 6402, 11426	Yugandhar, 2005; Ajay, 2006; Kusuma et al., 2007; Khalid, 2008; Madhura, 2006; Sujay et al., 2008; ICRISAT, 2008, 2009, 2010
Late leaf spot	ICG 4684, 6022, 12625, 12697	ICG 76, 532, 1668, 2857, 2925, 4156, 4412, 6402, 6993, 7243, 8760, 9037, 9777, 9842, 9961, 11109, 12000, 11426, 12276, 12672, 13787, 15190	
Rust	ICG 12697	ICG 76, 532, 2381, 2857, 2925, 4412, 6993, 7243, 8760, 9037, 9842, 9961, 9777, 11109, 11426, 12000, 13099, 13787, 14008	Yugandhar, 2005; Ajay, 2006; Kusuma et al., 2007; Khalid, 2008; Sujay et al., 2008; ICRISAT, 2008, 2009, 2010
Aspergillus flavus	ICG 12625, 12697	ICG 76, 2381, 4156, 6402, 8760, 13787	Yugandhar, 2005; Kusuma et al., 2007; ICRISAT, 2009; Zhang, 2010
Peanut bud necrosis disease	ICG 4684	ICG 76, 1668, 4412, 11109, 12000, 12672, 13099, 14008, 14482, 15190	Khalid, 2008; ICRISAT, 2008, 2009, 2010
Bacterial wilt	ICG 12625	ICG 76, 1668	ICRISAT, 2008, 2009; Zhang, 2010;Jianwei et al., 2010
Seed quality			
Oil (%)	ICG 3681, 4955, 5475, 12625, 14710, 15309	ICG 5827, 6402, 14482	Upadhyaya et al., 2012a
Protein (%)		ICG 5051, 7963, 13982	Upadhyaya et al., 2012a
Oleic/linoleic ratio	ICG 1274, 5221, 5475, 12625	ICG 2381, 15419	Upadhyaya et al., 2012a
Fe (mg kg^{-1})	ICG 1274, 4955, 5221, 5475, 14710, 15309	ICG 5051, 5827, 6402, 7963, 13982, 14482, 15419	Upadhyaya et al., 2012b
Zn (mg kg^{-1})	ICG 3681, 5221, 14710, 15309	ICG 5051, 5827, 6402, 7963, 13982, 15419	Upadhyaya et al., 2012b

adapted to rainfed conditions in central India (Isleib et al., 1994). ICGS 44 is adapted to post-rainy, irrigated conditions in peninsular India (Nigam et al., 1990). The experiment was conducted in nine environments (three rainy and six post-rainy seasons at Patancheru (78°12′ E, 17°24′ N, and 545 m asl), India on an alfisol, in an α design (four blocks, each with 47 plots) with three replications during the 2001 to 2011 crop seasons. The two distinct cropping seasons, rainy (June to October) and post-rainy (October to May), represent diverse environments with the potential to impact the cultivar's adaptation. Plot size consisted of two rows, 4 m in length, with an inter- and intrarow spacing of 60 cm and 10 cm, respectively. The seeds were sown at a uniform depth, and the crop-specific agronomic practices, including plant protection, were followed in cultivating the crop. All plots received 60 kg ha^{-1} P_2O_5 as basal dose and 400 kg ha^{-1} gypsum at flowering. The rainy-season crop received 6 irrigations, whereas the post-rainy season crop received 12 irrigations; each time, the plots received 5 cm water, which was sufficient to avoid water stress. Data were recorded on a plot basis for days to 50% flowering (when 50% plants in a plot had at least one flower), shelling outturn (%), 100-seed weight (g), and pod yield (kg ha^{-1}). The plots were harvested, pods air dried and cleaned, and matured pods weighed. A 200-g, mature-pod sample was used to determine shelling outturn.

The GenStat 14.1 software (VSN International, 2011) was used for statistical analysis of the data following restricted maximum likelihood (REML) (Patterson and Thompson, 1971), with seasons as fixed and entries as random variables. The genotype (σ^2g) and genotype × environment interaction (σ^2ge) variances were further partitioned at subsp. level, that is, subsp. *fastigiata* (σ^2g_f or σ^2ge_f) and subsp. *hypogaea* (σ^2g_h or σ^2ge_h) and their residuals were calculated. The significance among environments was tested using Wald (1943) statistic.

The published information on response of peanut mini core accessions to abiotic and biotic stresses or on nutritional traits (Table 1) was superimposed on agronomic data (days to 50% flowering, shelling outturn, 100-seed weight, and pod yield) to separate accessions into four distinct groups: abiotic stress resistant (28 accessions), biotic stress resistant (30 accessions), seed-nutrient dense (16 accessions), and agronomically desirable but stress susceptible (18 accessions). The common accessions were ICG 1668, 2925, 9842, and 12625 in the abiotic and biotic stress resistant groups; ICG 2381, 6402, 12625, and 14482 in the biotic-resistant and seed-nutrient-dense groups; and ICG 1274, 5475, and 12625 in the abiotic-resistant and seed-nutrient-dense groups. The mini core accessions were part of a composite collection (1000 accessions) in peanut that had been genotyped with 21 SSRs (Upadhyaya et al., 2008). Twenty-one SSR loci data on 86 accessions, including four controls, were used to estimate simple matching allele frequency-based distance matrix in DARwin 5.0 (Perrier et al., 2003) to identify genetically diverse accessions with agronomically desirable traits. Analysis of molecular variance (AMOVA) was performed with Arlequin 3.1 (Excoffier et al., 2005; http://cmpg.unibe.ch/software/arlequin3; accessed 13 Dec. 2013) to estimate variance components between groups and within groups (as detected in structure analysis). The F-value—the fixation index (or Wright's F-statistic, Fst)—from the AMOVA analysis provided genetic differentiation of the subgroups.

Table 2. Variance components for genotype (σ^2g) and genotype × environment interactions (σ^2ge) in peanut mini core accessions evaluated for four agronomic traits during the 2001–2011 crop seasons (three rainy and six post-rainy environments) at Patancheru, India.

Source of variation	Days to 50% flowering	Pod yield (kg ha^{-1})	Shelling outturn (%)	100-seed weight (g)
Pooled analysis over three rainy season environments				
σ^2g	4.90**	38,608**	9.05**	27.67**
σ^2g_f[†]	1.06**	33,224**	8.30**	16.21**
σ^2g_h	2.25**	42,214**	10.23**	28.05**
σ^2ge	0.36**	40,338**	3.97**	2.54**
σ^2ge_f	0.22*	31,228**	4.00	2.90*
σ^2ge_h	0.03	38,347**	1.50	2.36
Pooled analysis over six post-rainy season environments				
σ^2g	10.30**	71,480**	14.32**	85.72**
σ^2g_f	3.87**	53,125**	8.18**	43.93**
σ^2g_h	4.78**	104,745**	10.16**	103.77**
σ^2ge	2.65**	131,847**	3.58**	12.92**
σ^2ge_f	1.55**	74,716**	3.16**	3.00**
σ^2ge_h	1.69**	143,422**	2.71**	20.01**
Pooled analysis over nine environments (three rainy and six post-rainy seasons)				
σ^2g	8.10**	51,106**	11.02**	59.99**
σ^2g_f	2.69**	39,163**	8.09**	31.40**
σ^2g_h	3.69**	70,968**	9.45**	69.63**
σ^2ge	2.04**	110,708**	4.78**	14.59**
σ^2ge_f	1.31**	67,234**	3.34**	6.05**
σ^2ge_h	1.24**	12,138**	2.93**	21.07**
Error (residual)	3.79**	128,915**	21.90**	26.98**
Wald statistics (season)	13,630.77**	6847.47**	780.81**	2352.64**

*Significant at $p = 0.05$.

**Significant at $p = 0.01$.

[†] f, subsp. *fastigiata*; h, subsp. *hypogaea*.

RESULTS

REML analysis of results from individual environments (data not given) or pooled across environments (rainy or post-rainy or both) revealed that variances due to genotype (σ^2g) and genotype × environment interaction (σ^2ge) were highly significant for days to 50% flowering, shelling outturn, 100-seed weight, and pod yield (Table 2). Both σ^2g_f and σ^2g_h at the subspecies levels were also highly significant for all four traits. Also σ^2ge_f and σ^2ge_h in the rainy environments were highly significant for pod yield, while only σ^2ge_f was significant for days to flowering and 100-seed weight. In post-rainy environments as well across rainy and post-rainy environments, both σ^2ge_f and σ^2ge_h were highly significant for days to 50% flowering, shelling outturn, 100-seed weight, and pod yield.

None of the abiotic-stress-resistant accessions from subsp. *fastigiata* in the rainy environments significantly outyielded the higher-yielding control, ICGS 44 (Table 3). ICG 11088 produced a nearly significant increased pod yield relative to ICGS 44 (21.6% greater than ICGS 44, which yielded 1172 kg ha^{-1}), while in post-rainy environments it significantly outyielded ICGS 44 by 35.6% (ICGS 44, 2217 kg ha^{-1}). This accession across rainy and post-rainy environments produced a 33.4% greater pod yield than ICGS 44 (1879 kg ha^{-1}). ICG 11088 is similar to ICGS 44 for days to 50% flowering and 100-seed weight. Other accessions in subsp. *fastigiata* yielding on par with ICGS 44 were ICG 434, 2106, 12625, 12879, and 15042 with a mean pod yield of 1082 to 1259 kg ha^{-1} in rainy environments; ICG 434, 2106, 4729, 5236, 6646, 12625, and 15042, with a mean pod yield of 2129 to 2373 kg ha^{-1} in post-rainy environments; or ICG 434, 4729, 5236, 6646, 12625, 12879, and 15042, with a mean pod yield of 1795 to 1953 kg ha^{-1} across rainy and post-rainy environments. For shelling outturn, ICG 2106, 4729, 5236, and 12879 were similar to ICGS 44 (70%), while ICG 6646 and 12625 had similar 100-seed weights as ICGS 44 (50 g). In the subsp. *hypogaea* group, none of the accessions in either the rainy or post-rainy environments outyielded the better control, ICGS 76. ICG 8285 in post-rainy environments had a 14.7% greater pod yield than ICGS 76 (2320 kg ha^{-1}). Performance of ICG 8285 across the rainy and post-rainy environments was comparable with that of ICGS 76 (2040 kg ha^{-1}). ICG 8285 is comparable with ICGS 76 for days to 50% flowering, shelling outturn, and 100-seed weight. Other *hypogaea* accessions yielding on par with ICGS 76 in post-rainy environments were ICG 3053, 5663, 11219, and 11855, with most of these accessions being comparable with ICGS 76 for shelling outturn (except ICG 11855) and 100-seed weight (except ICG 3053). ICG 8285 is reported to be resistant to drought, heat, and salinity; ICG 2106 and 11855 to drought and salinity; ICG 11088 and 12625

Table 3. Abiotic-stress-resistant group of peanut mini core accessions for variation in days to 50% flowering, shelling outturn, 100-seed weight, and pod yield evaluated during the 2001–2011 crop seasons (3 rainy and 6 post-rainy seasons) at Patancheru, India.

Accession no.	Country of origin	Days to 50% flowering†	Shelling outturn†	100-seed weight†	Pod yield Rainy (three seasons)	Pod yield Post-rainy (six seasons)	Pod yield Pooled (nine seasons)
			%	g	kg ha^{-1}		
Subsp. *fastigiata*							
ICG 11088	Peru	31	64.4	47.0	1425	3006	2506
ICG 12625	Ecuador	31	62.1	51.9	1093	2368	1953
ICG 15042	Unknown	28	62.9	43.2	1203	2217	1891
ICG 434	USA	31	67.1	41.2	1190	2172	1855
ICG 6646	Unknown	30	60.5	51.3	748	2373	1830
ICG 5236	Chile	31	70.2	40.5	964	2250	1825
ICG 12879	Myanmar	32	71.3	36.9	1259	2056	1803
ICG 4729	China	32	69.6	37.7	976	2197	1795
ICG 2106	India	32	71.5	38.3	1082	2129	1787
ICG 3584	India	31	70.3	36.3	942	2059	1688
ICG 3673	Korea	31	69.7	43.6	665	2078	1602
ICG 8567	Uruguay	31	71.7	37.0	872	1852	1523
ICG 5609	Sri Lanka	28	67.6	46.6	874	1755	1458
ICG 442	USA	31	69.1	34.3	629	1877	1451
ICG 1274	Indonesia	29	65.1	51.3	818	1766	1444
ICG 5475	Kenya	30	69.9	42.8	947	1663	1422
ICG 10554	Argentina	34	59.9	31.4	709	1656	1330
Entry mean		30.8	67.2	41.8	964	2087	1715
Trial controls							
ICGS 44	India	31	70.3	50.6	1172	2217	1879
Gangapuri	India	28	68.8	45.0	1005	1810	1544
Trial control mean		29.5	69.6	47.8	1088	2013	1711
Subsp. *hypogaea*							
ICG 8285	USA	34	65.1	51.7	915	2660	2083
ICG 11855	Korea	34	62.1	56.3	984	2465	1979
ICG 5663	China	35	66.9	51.6	1052	2352	1925
ICG 3053	India	35	65.9	48.5	966	2197	1789
ICG 11219	Mexico	35	65.4	58.2	806	2219	1746
ICG 14475	Nigeria	34	66.9	55.7	789	2110	1668
ICG 862	India	36	66.0	38.0	879	2040	1652
ICG 1668	USA	36	63.5	52.4	925	1976	1626
ICG 2511	India	35	67.2	46.8	678	2028	1571
ICG 2925	India	35	69.5	46.9	686	1872	1468
ICG 9842	Tanzania	37	64.6	41.4	728	1491	1225
Entry mean		35.1	65.7	49.8	855	2128	1703
Trial controls							
ICGS 76	India	34	70.5	55.9	1222	2320	2040
M 13	India	35	68.1	58.3	1112	2221	1930
Trial control mean		34.5	69.3	57.1	1167	2270	1985
Subsp. *fastigiata* and subsp. *hypogaea*							
28-entry mean		32.5	66.6	45.0	922	2103	1711
Trial mean‡		32.4	66.3	44.6	913	1986	1628
Trial range‡		26–38	53.5–72.1	27.9–68.2	449–1617	1143–3122	879–2594
SE ±		1.34	2.17	3.59	100.13	141.98	101.44
LSD (p = 0.05)		3.7	6.0	9.9	278.0	394.0	281.0
CV (%)		6.0	7.1	11.6	27.8	20.6	22.0

† Nine season average.

‡ For the entire trial.

to drought and low temperature at germination; ICG 434, 3053, 5663, and 6646 to drought; and ICG 4729, 5236, 11219, 12879, and 15042 to heat (Table 1).

Most of the biotic-stress-resistant accessions either yielded poorly or on par with the best control in their respective group (subsp. *fastigiata* or *hypogaea*) (Table 4).

Table 4. Biotic-stress-resistant group of the peanut mini core accessions evaluated for variation in days to 50% flowering, shelling outturn, 100-seed weight, and pod yield, evaluated during the 2001–2011 crop seasons (three rainy and six post-rainy seasons) at Patancheru, India.

Accession no.	Country of origin	Days to 50% flowering†	Shelling outturn†	100-seed weight†	Pod yield		
					Rainy (three seasons)	Post-rainy (six seasons)	Pooled (nine seasons)
			%	g	kg ha^{-1}		
Subsp *fastigiata*							
ICG 6022	Sudan	31	62.0	58.5	1057	2532	2049
ICG 12625	Ecuador	31	62.1	51.9	1093	2368	1953
ICG 12697	India	31	71.5	37.9	1239	2154	1861
ICG 4684	USA	32	70.9	36.9	1009	1969	1652
Entry mean		31.3	66.6	46.3	1099	2256	1879
Trial controls							
ICGS 44	India	31	70.3	50.6	1172	2217	1879
Gangapuri	India	28	68.8	45.0	1005	1810	1544
Trial control mean		29.5	69.6	47.8	1088	2013	1711
Subsp. *hypogaea*							
ICG 12672	Bolivia	33	63.5	50.6	943	2659	2094
ICG 11426	India	33	66.6	52.2	1572	2231	2034
ICG 15190	Costa Rica	36	65.9	49.0	838	2343	1843
ICG 14008	Central African Republic	36	66.3	48.9	1109	2171	1834
ICG 14482	Nigeria	34	70.0	62.7	1065	2200	1830
ICG 13099	Unknown	35	67.0	47.4	1264	2080	1819
ICG 9961	Unknown	37	66.3	44.8	911	2191	1766
ICG 532	Unknown	37	64.3	45.5	982	2113	1739
ICG 12276	Bolivia	32	63.5	55.8	589	2254	1693
ICG 2381	Brazil	34	65.3	63.0	1005	2008	1677
ICG 1668	USA	36	65.1	44.3	919	1976	1627
ICG 9777	Mozambique	35	61.7	52.1	548	2133	1594
ICG 7243	USA	35	66.8	49.8	828	1860	1510
ICG 8760	Zambia	35	58.4	62.0	633	1942	1496
ICG 4156	Unknown	36	63.0	39.8	754	1854	1480
ICG 4412	USA	36	63.6	41.7	748	1850	1475
ICG 2925	India	35	69.5	46.9	686	1872	1468
ICG 6402	Unknown	33	66.1	36.6	834	1704	1408
ICG 76	India	35	63.5	40.1	778	1689	1377
ICG 2857	Argentina	36	64.9	58.7	607	1737	1349
ICG 6993	Brazil	36	58.0	63.3	688	1708	1347
ICG 9037	Cote d’ Ivoire	37	64.8	34.5	751	1597	1306
ICG 11109	Taiwan	36	65.3	39.8	625	1601	1261
ICG 9842	Tanzania	37	64.6	41.4	728	1491	1225
ICG 13787	Niger	36	64.1	46.8	684	1486	1207
ICG 12000	Mali	38	60.5	39.8	698	1289	1081
Entry mean		35.3	64.6	48.4	838	1925	1559
Trial controls							
ICGS 76	India	34	70.5	55.9	1222	2320	2040
M 13	India	35	68.1	58.3	1112	2221	1930
Trial control mean		34.5	69.3	57.1	1167	2270	1985
Subsp. *fastigiata* and subsp. *hypogaea*							
30-entry mean		34.8	64.8	48.1	873	1969	1602
Trial mean‡		32.4	66.3	44.6	913	1986	1628
Trial range‡		26–38	53.5–72.1	27.9–68.2	449–1617	1143–3122	879–2594
SE ±		1.34	2.17	3.59	100.13	141.98	101.44
LSD ($p = 0.05$)		3.7	6.0	9.9	278.0	394.0	281.0
CV (%)		6.0	7.1	11.6	27.8	20.6	22.0

[†] Nine season average.

[‡] For the entire trial.

The promising accessions in subsp. *fastigiata* were ICG 12697 in the rainy environments, and ICG 6022, 12625, and 12697 in the post-rainy environments. ICG 6022 in post-rainy environments had a 14.2% greater pod yield than ICGS 44 (2217 kg ha^{-1}). ICG 6022 is reported to be resistant to ELS and LLS, ICG 12697 to LLS, rust, and *A. flavus*, while ICG 12625 is resistant to LLS, *A. flavus*, and bacterial wilt (Table 1). ICG 12697 for shelling outturn and ICG 6022 and ICG 12625 for 100-seed weight were similar to ICGS 44 (shelling outturn, 70%; 100-seed weight, 50 g). In the subsp. *hypogaea* group, ICG 11426 in rainy environments significantly outyielded ICGS 76 by 28.6%. ICG 12672 in post-rainy environments outyielded ICGS 76 by 14.6%. ICGS 76 had a pod yield of 1222 kg ha^{-1} in rainy and 2320 kg ha^{-1} in post-rainy environments. Other accessions yielding on par (2171–2343 kg ha^{-1}) with ICGS 76 in post-rainy environments were ICG 9961, 11426, 12276, 14008, 14482, and 15190. Of these, ICG 11426 and 14482 were similar for shelling outturn and 100-seed weight with ICGS 76 (shelling outturn, 70%: 100-seed weight, 56 g). ICG 9961, 12276, 14008, and 15190 in comparisons to ICGS 76 recorded a 6–9% lower shelling outturn. For 100-seed weight, ICG 11426 and 12276 had similar seed weights as ICGS 76, while ICG 9961, 14008, and 15190 had 7–11 g lower seed weights than ICGS 76 (56 g). ICG 11426 is reported to be resistant to three foliar fungal diseases (ELS, LLS, and rust), ICG 12672 and 15190 to LLS and PBND, ICG 9961 to LLS and rust, ICG 12276 to LLS, ICG 14008 to rust and PBND, and ICG 14482 to PBND.

The previous research reported 16 accessions, 8 each from subsp. *fastigiata* and *hypogaea*, that were found promising for seed quality traits (oil and oil quality or grain protein, Fe, and Zn) (Table 1). In the present study, none of the accessions in the subsp. *fastigiata* group outyielded ICGS 44 either in rainy or post-rainy or across rainy and post-rainy environments (Table 5). ICG 12625 across rainy and post-rainy environments yielded on par with ICGS 44 (1879 kg ha^{-1}). However, ICG 12625 has about an 8% lower shelling outturn but is similar to ICGS 44 for 100-seed weight (ICGS 44: shelling outturn 70%; 100-seed weight, 50 g). ICG 12625 is reported to possess high oil and good quality oil and has resistance to LLS, *A. flavus*, bacterial wilt, drought, and low temperature at germination (Table 1). In the subsp. *hypogaea* group (Table 5), ICG 15419 significantly outyielded ICGS 76, by 34.6%, in post-rainy, and 27.2% across rainy and post-rainy environments. ICGS 76 on average produced a pod yield of 1222 kg ha^{-1} in rainy, 2320 kg ha^{-1} in post-rainy, and 2040 kg ha^{-1} across rainy and post-rainy environments. ICG 15419 is reported to possess high grain Fe and Zn, and its oil quality is better than that of ICGS 76; however, ICG 15419 had a 100-seed weight similar to that of ICGS 76 (56 g) but a poorer shelling outturn (62% as compared with 70% in ICGS 76). Interestingly, ICG 15419 had no resistance to either abiotic or biotic stresses (Table 1). Upadhyaya et al. (2012b) detected the highest O/L ratio (6.9 compared with 2.7 in ICGS 76) in ICG 2381 (subsp. *hypogaea*) among the mini core collection accessions evaluated for two seasons. This accession in the present study yielded poorly in rainy, post-rainy, and across rainy and post-rainy environments. However, it is reported to be resistant to rust and *A. flavus* (Table 1). The accessions with high grain Fe, Zn, and/or protein contents—ICG 5051, 5827, 6402, 7963, and 13982 (Table 1)—were found to have low yields (19–57% pod yield of ICGS 76) across rainy and post-rainy environments. These accessions (except ICG 5051), however, were similar to ICGS 76 in shelling outturn and had lower 100-seed weight than ICGS 76 (shelling outturn, 70%; 100-seed weight, 56 g) (Table 5).

In the agronomically-desirable-but-susceptible group, a subsp. *fastigiata* accession ICG 11651 significantly outyielded ICGS 44 by 38.0% in the rainy environments; however, ICG 11651 yielded on par with ICGS 44 in the post-rainy and across rainy and post-rainy environments (Table 6). The mean pod yield of ICGS 44 was 1172 kg ha^{-1} in rainy, 2217 kg ha^{-1} in post-rainy, and 1879 kg ha^{-1} across rainy and post-rainy environments. Other accessions that yielded statistically on par with ICGS 44 were ICG 397, 10036, and 14985 in rainy and ICG 3102, 10036, and 14985 in post-rainy environments. The first three accessions had 13–19% greater pod yields, whereas the latter three accessions produced 6–11% greater pod yield than ICGS 44. ICG 10036 across rainy and post-rainy environments yielded a 12.8% greater pod yield than ICGS 44 (1879 kg ha^{-1}). Although none of the accessions from subsp. *hypogaea* group statistically outyielded ICGS 76 in rainy-season environments, ICG 5745 and 11322 produced 18 and 22% greater pod yields than ICGS 76 (1222 kg ha^{-1}). ICG 5745, 10185, and 14705 in post-rainy environments yielded on par (2218–2492 kg ha^{-1}) with ICGS 76 (2320 kg ha^{-1}). Most of these accessions were similar to the controls (ICGS 44 or ICGS 76) in shelling outturn and 100-seed weight.

A neighbor joining hierarchical tree diagram broadly separated 86 accessions including four controls into two clusters (Fig. 1A). Most of the *hypogaea* accessions grouped into cluster 1, whereas those of *fastigiata* types in cluster 2, with a few exceptions in both the groups. The results of AMOVA also showed a significant difference between the two groups (subsp. *fastigiata* vs. subsp. *hypogaea* accessions), which accounted for 18.94% of the total genetic variation detected by 21 SSR loci, but genetic variation among the populations within groups was low (13.59%), relative to within populations, which was 67.47% (Table 7). The Fst between two groups for individual markers varied from 0.026 to 0.559 and was significant for all 21 marker loci (data not given). Some of the markers, 7H6, 1B9, 13E9, 18C5, 19B1, TC3E02, and TC6G09, had high Fst values of 0.551,

Table 5. Seed-nutrient-dense group of the peanut mini core accessions for variation in days to 50% flowering, shelling outturn, 100-seed weight, and pod yield, evaluated during the 2001–2011 crop seasons (three rainy and six post-rainy seasons) at Patancheru, India.

Accession no.	Country of origin	Days to 50% flowering†	Shelling outturn†	100-seed weight†	Pod yield Rainy (three seasons)	Pod yield Post-rainy (six seasons)	Pod yield Pooled (nine seasons)
			%	g	kg ha^{-1}		
Subsp. *fastigiata*							
ICG 12625	Ecuador	31	62.1	51.9	1093	2368	1953
ICG 5221	Argentina	29	64.8	44.9	974	2178	1780
ICG 4955	India	29	70.2	44.7	993	1990	1659
ICG 15309	Brazil	29	68.0	37.8	955	1983	1643
ICG 14710	Cameroon	28	68.3	43.9	1080	1665	1475
ICG 3681	USA	28	67.1	44.1	917	1727	1456
ICG 1274	Indonesia	29	65.1	51.3	818	1766	1444
ICG 5475	Kenya	30	69.9	42.8	947	1663	1422
Entry mean		29.1	66.9	45.2	972	1917	1604
Trial controls							
ICGS 44	India	31	70.3	50.6	1172	2217	1879
Gangapuri	India	28	68.8	45.0	1005	1810	1544
Trial control mean		29.5	69.6	47.8	1088	2013	1711
Subsp. *hypogaea*							
ICG 15419	Ecuador	29	61.9	57.2	1454	3122	2594
ICG 14482	Nigeria	34	70.0	62.7	1065	2200	1830
ICG 2381	Brazil	34	65.3	63.0	1005	2008	1677
ICG 5827	USA	35	65.8	47.6	941	1996	1645
ICG 7963	USA	32	67.1	45.0	1238	1872	1642
ICG 13982	USA	32	66.5	43.7	1071	1848	1574
ICG 6402	Unknown	33	66.1	36.6	834	1704	1408
ICG 5051	USA	33	59.2	57.7	449	1143	879
Entry mean		32.8	65.2	51.7	1007	1987	1656
Trial controls							
ICGS 76	India	34	70.5	55.9	1222	2320	2040
M 13	India	35	68.1	58.3	1112	2221	1930
Trial control mean		34.5	69.3	57.1	1167	2270	1985
Subsp. *fastigiata* and subsp. *hypogaea*							
16-entry mean		30.9	66.1	48.4	989	1952	1630
Trial mean‡		32.4	66.3	44.6	913	1986	1628
Trial range‡		26–38	53.5–72.1	27.9–68.2	449–1617	1143–3122	879–2594
SE ±		1.34	2.17	3.59	100.13	141.98	101.44
LSD (p = 0.05)		3.7	6.0	9.9	278.0	394.0	281.0
CV (%)		6.0	7.1	11.6	27.8	20.6	22.0

† Nine season average.

‡ For the entire trial.

0.226, 0.208, 0.302, 0.559, 0.305, and 0.373, respectively, and contributed maximally to the variation between two groups. No such differentiation in hierarchical clustering of accessions among the four groups (abiotic stress resistant, biotic stress resistant, seed-nutrient dense, or agronomically desirable but susceptible) could be seen (Fig. 1B). Marker-based genetic distance was used to identify in each group the 20 most diverse accession pairs (Table 8). The nutrient-dense group was genetically less diverse (range 0.480 among 120 pair comparisons), as evidenced by a smaller range of genetic distance between accessions, whereas abiotic-stress-resistant group was genetically more diverse (range 0.836 among 378 pair comparisons). The range diversity in the biotic-stress-resistant and agronomically-desirable-but-susceptible groups was, however, comparable (biotic: range 0.781 among 435 pair comparisons; agronomically desirable but susceptible: range 0.690 among 153 pair comparisons). A number of genetically diverse pairs with resistance to abiotic and/or biotic stresses, those possessing good seed quality and resistance to abiotic and/or biotic stresses, or those that are agronomically desirable but susceptible have been identified for enhancing the trait values: for example, ICG 11088 (drought, low temperature) and ICG 3673 (drought, P deficiency) in the abiotic-stress-resistant group; ICG 11426 (ELS, LLS, rust) and ICG 4684 (LLS, PBND), ICG 12697 (rust, LLS, *A. flavus*) and ICG 4156, and ICG 12697 (LLS, *A. flavus*) and ICG 6022 (ELS, LLS) in the biotic-stress-resistant group; ICG 12625 (tolerance to low temperature at germination; resistance to LLS, *A. flavus*, bacterial wilt; high oil and improved oil quality) and ICG 434

Table 6. Agronomically-desirable-but-susceptible (abiotic and biotic stress) group of the peanut mini core accessions for variation in days to 50% flowering, shelling outturn, 100-seed weight, and pod yield, evaluated during the 2001–2011 crop seasons (three rainy and six post-rainy seasons) at Patancheru, India.

Accession no.	Country of origin	Days to 50% flowering[†]	Shelling outturn[†]	100-seed weight[†]	Pod yield: Rainy (three seasons)	Pod yield: Post-rainy (six seasons)	Pod yield: Pooled (nine seasons)
			%	g		kg ha^{-1}	
Subsp. *fastigiata*							
ICG 10036	Peru	31	64.2	48.8	1389	2458	2119
ICG 14985	Unknown	29	67.1	55.0	1324	2374	2042
ICG 11651	China	31	62.6	51.7	1617	2086	1953
ICG 3102	India	30	68.9	45.2	1052	2348	1925
ICG 9315	USA	28	68.8	41.8	1179	2255	1908
ICG 397	USA	26	68.8	40.8	1388	2047	1844
ICG 12988	India	31	70.7	35.3	992	2142	1764
ICG 11249	Tanzania	31	70.6	37.1	929	2167	1756
ICG 4750	Paraguay	29	70.8	39.0	985	2098	1729
ICG 297	USA	29	64.1	53.3	1006	2028	1692
ICG 118	India	34	68.2	53.0	1050	1992	1683
ICG 3421	India	32	71.4	37.3	960	1991	1648
ICG 9809	Mozambique	32	71.3	37.8	870	2004	1624
Entry mean		30	68.2	43.5	1135	2157	1825
Trial controls							
ICGS 44	India	31	70.3	50.6	1172	2217	1879
Gangapuri	India	28	68.8	45.0	1005	1810	1544
Trial control mean		29.5	69.6	47.8	1088	2013	1711
Subsp. *hypogaea*							
ICG 5745	Puerto Rico	35	68.3	61.3	1441	2447	2132
ICG 10185	USA	36	66.5	55.0	822	2492	1937
ICG 14705	Cameroon	31	70.2	47.5	1291	2218	1924
ICG 11322	India	34	68.4	50.9	1492	2040	1876
ICG 5662	India	32	66.9	68.2	1105	2132	1796
Entry mean		34	68.1	56.6	1230	2266	1933
Trial controls							
ICGS 76	India	34	70.5	55.9	1222	2320	2040
M 13	India	35	68.1	58.3	1112	2221	1930
Trial control mean		34.5	69.3	57.1	1167	2270	1985
Subsp. *fastigiata* and subsp. *hypogaea*							
18-entry mean		31.0	68.2	46.6	1158	2183	1851
Trial mean[‡]		32.4	66.3	44.6	913.0	1986.3	1628.1
Trial range[‡]		26–38	53.5–72.1	27.9–68.2	449–1617	1143–3122	879–2594
SE ±		1.34	2.17	3.59	100.13	141.98	101.44
LSD (p = 0.05)		3.7	6.0	9.9	278.0	394.0	281.0
CV (%)		6.0	7.1	11.6	27.8	20.6	22.0

[†] Nine season average.

[‡] For the entire trial.

(drought), ICG 6022 and ICG 3673 (drought, phosphorous deficiency), and ICG 12625 and ICG 442 (drought, salinity, P deficiency) in the multiple-abiotic-stress-resistant and multiple-biotic-stress-resistant groups; ICG 3673 (drought, P deficiency) and ICG 2381 (oil quality), ICG 12625 and ICG 2381 (oil quality), and ICG 11426 (ELS, LLS, rust) and ICG 5221 (high Fe, Zn, oil quality) combining resistance to stresses and seed nutritional quality; and ICG 14710 (high oil, Fe, Zn) and ICG 7963 (high protein) in the seed-nutrient-dense group.

DISCUSSION

Cultivated peanut has a narrow genetic base as the result of an evolutionary bottleneck associated with its origin and domestication (Kochert et al., 1996). Globally the crop suffers from abiotic and biotic stresses, which often occur together and cause substantial losses to production and quality. Aflatoxin is a serious quality problem in peanut and affects human and animal health and international trade. The challenge before the crop genetic enhancers in the 21st century will be to make peanut more competitive

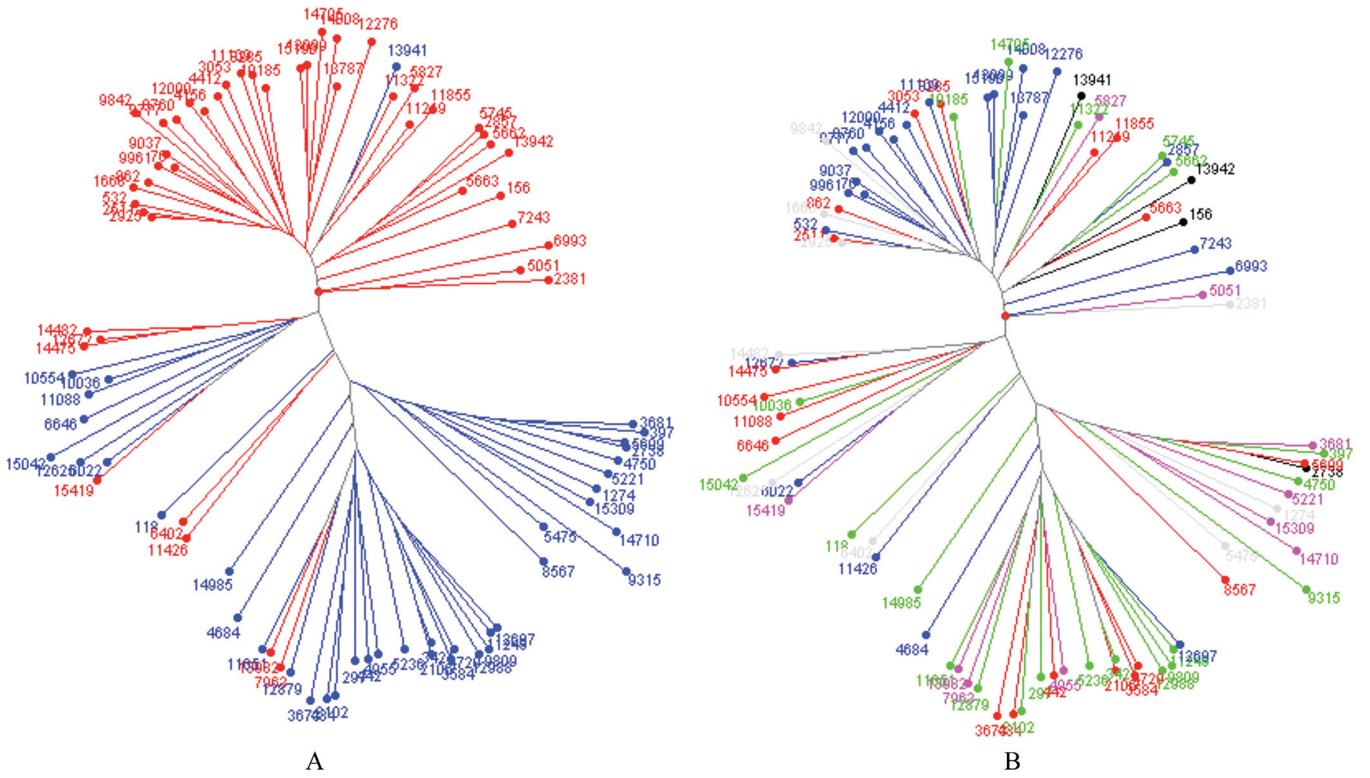

Figure 1. Neighbor joining tree diagram based on 21 SSR loci data on 82 peanut mini core accessions and four controls, representing two subsp. (*fastigiata* and *hypogaea*) classified into four groups (abiotic, biotic, seed-nutrient dense, and agronomically desirable but susceptible) based on responses to stresses and seed quality traits. (A) Red color represents subsp. *hypogaea* and blue, subsp. *fastigiata*. (B) Red represents the abiotic-stress-resistant group; blue, the biotic-stress-resistant group; purple, the nutrient-dense group; green, the group agronomically superior but susceptible to abiotic and biotic stresses; gray, the group resistant to multiple abiotic and biotic stresses; black, control cultivars.

Table 7. Analysis of molecular variance of 86 peanut mini core accessions, including controls, based on structure analysis, separating subsp. *hypogaea* accessions from those of subsp. *fastigiata* accessions.

Source of variation	df	Sum of square	Variance components	Percentage of variation	*P* (1023 permutations)
Among groups	1	108.916	1.2486	18.94	0.0000
Among populations within groups	84	524.118	0.8961	13.59	
Within populations	86	382.500	4.4477	67.47	
Total	171	1015.564			
F-statistic = 0.1894					0.0000

(with respect to other crops), productive, and nutritionally superior. The best way to compete is to breed cultivars with enhanced host–plant resistance, adaptation to abiotic stress, input-use efficiency, and yield potential. Such cultivars will maximize yield gains while minimizing inputs for sustenance and to compete with other crops. Identification of genetically diverse germplasm with multiple beneficial traits is key to the success of any breeding program.

Agronomic desirability of resistant sources and its combining ability is the key factor in a breeder's choice of germplasm for use in breeding programs. In the present study, a peanut mini core collection (184 accessions) was evaluated for three rainy and six post-rainy irrigated environments at Patancheru, India. The significance of σ^2g and σ^2ge not only reveals the presence of heritable genetic variation for days to 50% flowering, shelling outturn, 100-seed weight, and pod yield, but also shows that these traits are sensitive to environmental variations (Table 2). Subsp. *fastigiata* accession ICG 11651, which is in the agronomically-desirable-but-susceptible group, and ICG 11088, which is in the abiotic-stress-resistant group, significantly outyielded the control ICGS 44 in the rainy environment (Table 6) and in the post-rainy (Table 3) environment, respectively. Likewise, a *hypogaea* accession ICG 15419 significantly outyielded the control ICGS 76 in post-rainy as well across rainy and post-rainy environments (Table 5). Seven accessions in the rainy environment and ten *fastigiata* accessions in the post-rainy environment yielded on par with (or better than) ICGS 44 (Tables 3–5). In the *hypogaea* group, one accession in the rainy and nine

Table 8. Twenty pairs of genetically most diverse mini core accessions selected in each of the four subsets (abiotic stress resistant, biotic stress resistant, nutrient-dense, and the susceptible-but-agronomically-desirable) in peanut.

Genotype pair	Genetic distance	Genotype pair	Genetic distance
Multiple abiotic stress resistance			
ICG 862 and ICG 434	1.000	ICG 5663 and ICG 434	0.952
ICG 12625 and ICG 434	1.000	ICG 1668 and ICG 434	0.952
ICG 10554 and ICG 3673	1.000	ICG 2925 and ICG 434	0.952
ICG 12625 and ICG 3673	1.000	ICG 15042 and ICG 434	0.952
ICG 12625 and ICG 3584	0.976	ICG 6646 and ICG 3584	0.952
ICG 6646 and ICG 3673	0.976	ICG 11088 and ICG 3584	0.952
ICG 11088 and ICG 3673	0.976	ICG 12879 and ICG 5663	0.952
ICG 4729 and ICG 12625	0.976	ICG 4729 and ICG 6646	0.952
ICG 8285 and ICG 434	0.975	ICG 4729 and ICG 11088	0.952
ICG 14475 and ICG 3673	0.975	ICG 12625 and ICG 442	0.950
Mean diversity: 0.769; diversity range among 378 pairs: 0.836 (min. 0.164 and max. 1.000)			
Multiple biotic stress resistance			
ICG 6022 and ICG 3673	1.000	ICG 13787 and ICG 4684	0.921
ICG 11426 and ICG 5221	0.952	ICG 12697 and ICG 6022	0.921
ICG 4684 and ICG 2925	0.947	ICG 4684 and ICG 532	0.917
ICG 15190 and ICG 4684	0.944	ICG 12697 and ICG 4412	0.900
ICG 12697 and ICG 2381	0.925	ICG 9037 and ICG 4684	0.900
ICG 9842 and ICG 4684	0.921	ICG 12697 and ICG 9842	0.900
ICG 11109 and ICG 4684	0.921	ICG 12697 and ICG 4156	0.895
ICG 12276 and ICG 4684	0.921	ICG 11426 and ICG 4684	0.895
ICG 12625 and ICG 4684	0.921	ICG 12000 and ICG 4684	0.895
ICG 13099 and ICG 4684	0.921	ICG 12697 and ICG 11109	0.895
Mean diversity: 0.623; diversity range among 435 pairs: 0.781 (min. 0.219 and max. 1.000)			
Seed-nutrient dense			
ICG 3673 and ICG 2381	0.976	ICG 12625 and ICG 7963	0.925
ICG 14482 and ICG 4955	0.950	ICG 14710 and ICG 7963	0.925
ICG 13982 and ICG 5827	0.944	ICG 15419 and ICG 7963	0.925
ICG 12625 and ICG 1274	0.929	ICG 15309 and ICG 12625	0.925
ICG 3681 and ICG 2381	0.929	ICG 7963 and ICG 5051	0.921
ICG 4955 and ICG 2381	0.929	ICG 7963 and ICG 5827	0.921
ICG 12625 and ICG 3681	0.929	ICG 13982 and ICG 12625	0.921
ICG 12625 and ICG 4955	0.929	ICG 15419 and ICG 13982	0.921
ICG 12625 and ICG 5475	0.929	ICG 14710 and ICG 2381	0.905
ICG 14482 and ICG 3681	0.925	ICG 12625 and ICG 2381	0.786
Mean diversity: 0.792; diversity range among 120 pairs: 0.480 (min. 0.472 and max. 0.952)			
Agronomically desirable but susceptible			
ICG 14705 and ICG 3421	1.000	ICG 14985 and ICG 9315	0.950
ICG 9315 and ICG 5745	1.000	ICG 10036 and ICG 9315	0.944
ICG 10036 and ICG 9809	1.000	ICG 5662 and ICG 4750	0.929
ICG 14705 and ICG 12988	1.000	ICG 9315 and ICG 5662	0.929
ICG 10185 and ICG 9315	0.975	ICG 14705 and ICG 9809	0.929
ICG 5745 and ICG 3102	0.952	ICG 14705 and ICG 11249	0.929
ICG 11322 and ICG 9315	0.952	ICG 10185 and ICG 9809	0.925
ICG 14705 and ICG 9315	0.952	ICG 5745 and ICG 397	0.921
ICG 10185 and ICG 3102	0.950	ICG 10036 and ICG 297	0.912
ICG 10185 and ICG 4750	0.950	ICG 5745 and ICG 4750	0.905
Mean diversity: 0.773; diversity range among 153 pairs: 0.690 (min. 0.310 and max. 1.000)			

accessions in the post-rainy environments yielded on par with (or better than) ICGS 76. ICG 8285 among these also performed well across rainy and post-rainy environments (Tables 3). Many of these accessions had resistance to multiple stresses, and some also had good seed quality; for example, ICG 11088 and ICG 12625 are resistant to drought and low temperatures at germination; ICG 8285 to drought, heat and salinity; ICG 11426 to rust, ELS, and LLS; ICG 12697 to rust, LLS, and *A. flavus*; ICG 5221 has high Fe, Zn, and O/L ratio; ICG 5827 and ICG 15309 high oil, Fe, and Zn; ICG 5051 and ICG 13982 high protein, Fe, and Zn; ICG 6402 combines high oil, Fe, and Zn with resistance to ELS, LLS, and *A. flavus*, and ICG 5475 possesses high oil, O/L ratio, and Fe and resistance to drought and low temperatures at germination (Table 1). In the agronomically-desirable-but-susceptible group, a *fastigiata* accession ICG 11651 in rainy environments significantly outyielded ICGS 44. Other accessions yielding on par with (or better than) ICGS 44 were ICG 397, 10036, and 14985 in rainy; ICG 3102, 10036, and 14985 in post-rainy; and ICG 3102, 10036, 11651, and 14985 across rainy and post-rainy environments. In the subsp. *hypogaea* group, ICG 5745 and 11322 in rainy; ICG 5745, 10185, and 14705 in post-rainy; and ICG 5745 across rainy and post-rainy environments yielded on par with (or better than) ICGS 76 (Table 6). ICG 2381, an accession with a high O/L ratio (6.9; Upadhyaya et al., 2012b), yielded very poorly among the group of seed-nutrient-dense accessions (Table 5); however, it is reportedly resistant to rust and *A. flavus* (Table 1). Preliminary reports indicate that high-oleate peanut germplasm is more susceptible to cold injury (at the seed-filling stage; Sun, 2005), susceptible to aflatoxin contamination (Xue et al., 2003, 2005), and poor in germination at low temperatures (16 and 14°C; Jungman and Schubert, 2000), results that should be further investigated with germplasm and cultivars having extreme differences in their O/L ratios.

Resistance to stress imposes a cost on the fitness of plants, which means that when breeders select for one trait, such as yield, fewer resources remain for other functions. Peanut, unlike other crops, has also a high metabolic cost associated with maintaining high oil and protein fractions in the seeds (Sinclair and de Wit, 1975; Hall, 2004). Such trade-offs, which may result either from genetic linkage or pleiotropic effects, have been reported between yield and stress (pathogen, herbivore, or herbicide) resistance, yield and nutrition, and seed size and seed number (Brown, 2002; Burdon and Thrall, 2003; Morris and Sands, 2006; Sadras, 2007; Vila-Aiub et al., 2009). However, deviation from this widely accepted view has also been found in the literature. For example, reports on barley indicate a cost associated with the *mlo* gene for resistance to powdery mildew [*Blumeria graminis* (DC.) Speer, f. sp. *hordei* Ém. Marchal] (Schwarzbach, 1976; Bjørnstad and Aastveit, 1990), while others detect no cost associated with resistance to barley powdery mildew (Kølster et al., 1986; Kølster and Stølen, 1987). The agronomically-desirable-but-susceptible group across rainy and post-rainy environments produced an 8–16% greater mean pod yield (1851 kg ha^{-1}) than those in the abiotic-stress-resistance (1711 kg ha^{-1}), biotic-stress-resistance (1602 kg ha^{-1}), and seed-nutrient-dense (1630 kg ha^{-1}) groups. However, the four subgroups were similar between themselves for mean days to 50% flowering (31–35), shelling outturn (65–68%), and 100-seed weight (45–48 g). The challenge is to minimize any possible negative trade-offs between yield (or yield components), nutritional traits, and stress resistance. Trade-offs arising from linkage could be easily overcome through recombinant breeding coupled with rigorous selection for desired traits using applied genomic tools (Brown, 2002 and references therein). Near-isogenic lines are the ideal genetic resource to study the trade-off between resistance gene(s) and yield and yield-contributing traits. The breeder's best approach in the situation of the negative trade-off would be to select moderate resistance along with good agronomic traits. An incremental increase in level of resistance might be the best approach to address negative trade-offs in crop breeding. Breeding efforts at ICRISAT and elsewhere have been successful in combining stress resistance and/or good seed quality into improved genetic backgrounds with high yield potential and specific adaptation, with some of these already under cultivation. For example, the rust- and LLS-resistant cultivars ICGV 86590 and ICGV 87160 have been released in India (Reddy et al., 1992, 1993). US peanut breeders have successfully introgressed high oleate trait and resistance to TSWV and/or white mold (*Sclerotium rolfsii* Sacc.) in 'Florida 07', 'Georgia-09B', 'Georgia-11J', 'Georgia-08V', 'Red River Runner', 'Tamrun OL07', and 'Tamrun OL11' (Baring et al., 2006; Gorbet and Tillman, 2009; Branch, 2009, 2010, 2011; Melouk et al., 2013; Baring et al., 2013); high oleate and multiple pest resistance in 'Georgia-05E' and 'Webb' (Branch, 2006; Simpson et al., 2013); and high oleate, early maturity, and TSWV resistance in 'Andru II' (Gorbet, 2006), some of which are commercially grown in the United States. Likewise, researchers at ICRISAT have combined resistance to defoliators and PBND in ICGV 86031 (Dwivedi et al., 1993); to resistance to rust and LLS and low-temperature tolerance at germination in ICGV 92267 (Upadhyaya et al., 2002b); and multiple resistance to diseases and insects in ICGV 86699 (Reddy et al., 1996).

The neighbor joining tree diagram, which is based on a genotype-based distance matrix, clearly separated subsp. *hypogaea* accessions from those of subsp. *fastigiata*, the former represented in cluster 1, and the latter in cluster 2 (Fig. 1A), but with one *fastigiata* type (ICGS 44) falling into cluster 1 (subsp. *hypogaea*), and eight *hypogaea* types into cluster 2 (subsp. *fastigiata*). The subsp. *fastigiata* accessions have an erect to semi-spreading (decumbent 2 or decumbent 3) growth habit, whereas those of subsp. *hypogaea* mostly trail on the ground with various expressions (procumbent 1, procumbent 2, decumbent 1, decumbent 2, or decumbent 3) (IBPGR and ICRISAT, 1992). Growth habit in cultivated × cultivated crosses in peanut is governed by only a few genes, with some involvement of gene–cytoplasm interaction (Ashri, 1964, 1968), which could have been the reason for such clear separation between the two subspecies, with few exceptions. The eight *hypogaea* accessions that grouped with subsp. *fastigiata* (cluster 2)—five are landraces (ICG 6402, 12672, 14475, 14482, and 15419) of diverse origins, and three are breeding lines (ICG 7963 and 13982 from USA and ICG 11426 from India)—have decumbent 2 to decumbent 3 growth habit (except for ICG 15419), which is quite often the case with many advanced breeding lines originating from subsp. *fastigiata* × *hypogaea* crosses. Proximity of these accessions to subsp. *fastigiata* with respect to growth habit probably could have been the reason that these accessions fell into cluster 2 (subsp. *fastigiata* accessions), while subsp. *fastigiata* accession ICGS 44, a natural selection originating from the subsp. *hypogaea* cultivar Robut 33-1 (also known as Kadiri 3), which has a procumbent 1 growth habit, is in cluster 1 (subsp. *hypogaea* accessions). Likewise, ICG 15419, though belonging to the subsp. *hypogaea* var. *hirsuta* but having an erect growth habit, a trait mostly associated with typical subsp. *fastigiata*, is part of cluster 2 (subsp. *fastigiata* accessions). A number of genetically diverse pairs with superior agronomic and seed quality traits and resistance to abiotic and/or biotic stresses have been identified, which offer peanut breeders a unique opportunity to combine these desired traits into improved genetic background. All these genetically diverse germplasm accessions with beneficial agronomic and nutritional traits, including resistance to abiotic and/or biotic stresses, may be used as trait-specific donors or as founder lines to develop multiparent advanced generation inter-cross (MAGIC) populations (Huang et al., 2012) as sources for cultivar development or mapping quantitative trait loci for complex traits. Researchers worldwide may obtain small seed samples of these accessions for research purposes from ICRISAT after signing the appropriate Materials Transfer Agreement form.

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