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Genetic survey of 10 Indian coconut landraces by simple sequence repeats (SSRs)

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ABSTRACT

A rich genetic diversity of coconut exists in farmer's fields, which represent valuable genetic resource for breeding. The study was conducted to assess the pattern of diversity in 102 coconut palms representing 10 landraces from 3 coconut-growing communities of India using 14 simple sequence repeat (SSR) markers. A total of 90 alleles were detected with an average of 6.42 alleles per locus and an average polymorphism information content of 0.61. Expected heterozygosity (H_e) was highest for the two tall landraces from Pallikkara community, while the least heterozygosity was observed for the dwarf coconut landraces from Vayalar community. Mean fixation index (F_{ST}) of 0.42 indicates a high level of population differentiation. A low gene flow (N_m) of 0.37 was observed. Based on molecular data, genetic similarities were calculated. The unweighted pair group method with arithmetic averages (UPGMA) cluster analysis grouped the landraces according to their geographical locations and breeding behaviour. The practical implications of this study in farmer participatory evaluation and conservation of coconut genetic resources are highlighted.

1. Introduction

Coconut palm (*Cocos nucifera* L.) is an important plantation crop of the tropics, which gives a multitude of products for human use. It is a diploid species ($2n = 2\times = 32$) belonging to the botanical family Arecaceae. It is mainly a small holder's crop, with 96% of the holdings less than 4 ha (Batugal and Oliver, 2003). Coconuts farmers are being subjected to miseries due to decline in farm productivity and unstable markets. Heavy losses in yield occur in coconut due to drought, debilitating and lethal pathogens and pests. Genetic enhancement of the productivity and tolerance to biotic and abiotic stress in coconut palm is impeded by slow growth and long pre-bearing period of the palm.

Gene pool enrichment has been one of the important means of improvement of coconut. A high degree of variability is available in landraces in farmers' fields, especially for adaptation to features of agro-ecosystem, which needs to be exploited. Landraces of crop plants have been found to be invaluable for providing sources of resistance against biotic and abiotic stress and also improvement of agronomic traits (Frankel et al., 1995). However, with the advent of modern agriculture and commercial cultivation of high yielding varieties, there is loss of landraces (Persson and von Bothmer, 2000). Effective *in situ* conservation strategies for crop plants need to be developed to prevent the loss of diversity in farmer's field and to sustain the process of evolution (Brush, 1991).

Diversity analysis in coconut palm has been carried out using morphological traits, biochemical and molecular markers. Morphometric traits were helpful in distinguishing the *typica*, *nana* and *javanica* forms of coconut (Sugimura et al., 1997). Foliar characters (Arunachalam et al., 2005), floral biology (Sangare et al., 1978; Ratnambal et al., 2003) and fruit components (Harries, 1978; Ashburner et al., 1997a) have also been used to understand the relationship between the coconut varieties. Molecular characterization of coconut landraces have been performed with RAPD (Ashburner et al., 1997b; Upadhyay et al., 2004), RFLP (Lebrun et al., 1998), AFLP (Perera et al., 1998), ISSR's (Zizumbo-Villarreal et al., 2006) and microsatellites/SSR's (Perera et al., 1999, 2001; Rivera et al., 1999; Merrow et al., 2003; Devakumar et al., 2006).

Diversity analysis carried out so far in coconut using morphological and molecular markers has been either restricted to accessions from different macro- or micro-geographical regions (N'Cho et al., 1993; Ashburner et al., 1997a,b; Lebrun et al., 1998; Teulat et al., 2000; Upadhyay et al., 2004) or accessions belonging to different botanical forms (Sugimura et al., 1997; Perera et al., 2001). Such efforts are minimal in landraces in a small village level agro-ecosystem, despite the urgent need to conserve these landraces.

Farmer participatory evaluation and conservation of forms of coconut is a long-term perspective plan to promote on-farm and *in*

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situ conservation of diversity. With this background, International Plant Genetic Resources Institute (IPGRI) and Coconut Genetic Resources Network (COGENT) have initiated a program to promote this objective in few identified sites in selected countries in order to fulfill the needs of poverty reduction along with conservation of diversity (Batugal and Oliver, 2003). In India, this program was implemented at three sites in Southern India, viz., Ariyankuppam community of Pondicherry Union Territory, Pallikkara community of Kasaragod District and Vayalar community of Alappuzha District, both of Kerala State (Rajagopal, 2003; Thampam, 2003).

For adoption of *in situ* and on-farm conservation by the farmer's, a strategy to demonstrate the link between diversity of coconut landraces with socio-economic benefit should exist (Batugal and Oliver, 2003). The first step towards achieving this would be characterizing the available diversity in the coconut-growing communities. The present study was undertaken with an objective of understanding and characterizing diversity present in landraces of coconut from the above three communities in India using microsatellite DNA markers.

2. Materials and methods

2.1. Characterization of landraces

The major coconut-growing areas in India are located in the coastal agro-ecosystem. Among the three communities selected in Southern India, Pallikkara village of Kasaragod District and Vayalar village of Alappuzha District (both of Kerala State) represent the West Coast region and Ariyankuppam Community of Pondicherry represents the East Coast. Through participatory methods, farmers of the three communities were asked to characterize and rank the landraces of coconut available. Transect walk by a team of researchers and farmers to identify the agro-ecological situation and to identify the problems and opportunities also yielded information pertaining to the nature and distribution of diversity in coconut available in the community. Features such as stature of the palm, colour, size and shape of nuts, response to management practices, tolerance to stress situations, suitability to various uses, etc. were considered by the farmers for characterizing the varietal diversity in coconut. A coconut diversity fair was organized as part of the study on farmer characterization of coconut landraces. The primary objective of the programme was to characterize the existing coconut landraces in the local community from the point of view of the local farmers, ecology and uses. Coconut bunches of diverse features existing in their garden were brought and exhibited in the fair by the farmers. A total of 10 distinct types of coconut were identified from the three project sites in the participatory characterization process and these were used for the present study (Table 1).

2.2. Genomic DNA isolation

A total of 102 palms comprising the 10 landraces were used for molecular marker studies (Table 1). DNA was extracted from spindle leaves of palms following the method of Upadhyay et al. (1999).

2.3. Microsatellite analysis

A total of 14 highly polymorphic SSR primer pairs specific to coconut from the microsatellite kit developed by Baudouin and Lebrun (2002) were used in the present study. The sequences of the primers used are given in Table 2. PCR reaction was conducted in volumes of 20 μl containing 35 ng genomic DNA, 0.2 μM each of forward and reverse primers, 50 μM of each dNTPs (M/s Bangalore Genei Pvt. Ltd., Bangalore), 1× buffer [10 mM Tris–HCl (pH 8.3), 50 mM KCl, 1.5 mM $MgCl_2$] and 0.3 Unit of *Taq* DNA polymerase (M/s Bangalore Genei Pvt. Ltd., India).

Table 1
Details of the coconut landraces studied

S. No.	Name of the variety	Abbv.	Place of cultivation	Adaptation	No. of palms sampled for microsatellite studies
1.	Vayalar Tall	VLT	Vayalar Community, Kerala State	Root (wilt) disease-free tall palms	15
2.	Vayalar Green Dwarf	VGD	Vayalar Community, Kerala State	Root (wilt) disease-free dwarf palms with green nuts	7
3.	Vayalar Orange Dwarf	VOD	Vayalar Community, Kerala State	Root (wilt) disease-free dwarf palms with orange nuts. Sweet tender nut water.	7
4.	Pallikkara Tall I ('*Alakode Tall*')	PLK I	Pallikkara Community, Kerala State	Local tall variety well adapted to laterite soils	12
5.	Pallikkara Tall II ('*Koottakani Tall*')	PLK II	Pallikkara village, Kerala State	Local tall variety well adapted to laterite soils	15
6.	Pallikkara Tall III ('*Kuttiyadi Tall*')	PLK III	Pallikkara village, Kerala State	Tall variety well adapted to laterite soils	12
7.	East Coast Green Tall	ECGT	Ariyankuppam Community, Pondicherry UnioinTerritory	Typical local cultivar, widely distributed. Tall palms which produce medium to large sized, light green coloured, round to oblong-shaped nuts. Well adapted—best performance under irrigated conditions with good management (140 nuts/(palm year))	15
8.	East Coast Pink Tall ('*Sevvelanir*')	ECPT	Ariyankuppam Community, Pondicherry Union Territory	Tall palms which produce medium-sized light green nuts. Villagers believe tender nut water possess medicinal properties to cure jaundice and asthma. Premium price for tender nut. Rare	5
9.	East Coast Yellow Tall ('*Narimedu Yellow*')	ECYT	Ariyankuppam Community, Pondicherry Union Territory	Tall palms which produce yellow coloured, round to oblong-shaped nuts. Rare	7
10.	East Coast Tall Spicata ('*Panaithennai*')	ECSP	Ariyankuppam Community, Pondicherry Union Territory	Tall palms producing medium sized, oblong-shaped nuts. Unique feature is spikeless bunches (mutant). Nuts are preferred for culinary purposes. Tolerant to coconut stem bleeding disease and eriophid mite	7

Table 2
List of coconut-specific microsatellite primer pairs with their sequences

S. No.	Primer	Sequence (5′–3′)		Annealing temperature (°C)
		Forward primer	Reverse primer	
1.	CnCir A3	AATCTAAATCTACGAAAGCA	AATAATGTGAAAAAGCAAAG	52
2.	CnCir A9	AATGTTTGTGTCTTTGTGCGTGTGT	TCCTTATTTTTCTTCCCCTTCCTCA	59
3.	CnCir B6	GAGTGTGTGAGCCAGCAT	ATTGTTCACAGTCCTTCCA	58
4.	CnCir B12	GCTCTTCAGTCTTTCTCAA	CTGTATGCCAATTTTTCTA	56
5.	CnCir C3′	AGAAAGCTGAGAGGGAGATT	GTGGGGCATGAAAAGTAAC	58
6.	CnCir C7	ATAGCATATGGTTTTCCT	TGCTCCAGCGTTCATCTA	58
7.	CnCir C12	ATACCACAGGCTAACAT	AACCAGAGACATTTGAA	54
8.	CnCir E2	TCGCTGATGAATGCTTGCT	GGGGCTGAGGGATAAACC	55
9.	CnCir E10	TGGGTTCCATTTCTTCTCTCATC	GCTCTTTAGGGTTCGCTTTCTTAG	57
10.	CnCir E12	TCACGCAAAAGATAAAACC	ATGGAGATGGAAAGAAAGG	58
11.	CnCir F2	GGTCTCCTCTCCCTCCTTATCTA	CGACGACCCAAAACTGAACAC	58
12.	CnCir G11	AATATCTCCAAAAATCATCGAAAG	TCATCCCACACCCTCCTCT	58
13.	CnCir H4′	TTAGATCTCCTCCCAAAG	ATCGAAAGAACAGTCACG	54
14.	CnCir H7	GAGATGGCATAACACCTA	TGCTGAAGCAAAAGAGTA	58

PCR amplifications were performed on an Eppendorf gradient thermal cycler with a PCR profile of 94 °C for 5 min followed by 30 cycles of 1 min at 94 °C, 2 min at the different annealing temperatures for the individual SSR locus, and 2 min at 72 °C with a final extension for 5 min at 72 °C. After amplification, a volume of 8 μl of loading buffer (98% formamide, 10 mM EDTA, 0.005% each of xylene cyanol and bromophenol blue as tracking dyes) was added to each of the amplified product and denatured at 94 °C for 5 min, snap cooled using ice and separated on 5% denaturing polyacrylamide gels containing 7 M urea at a constant power of 100 W. The patterns of amplified products across the samples were resolved by silver staining following procedure described by Panaud et al. (1996).

2.4. Data analysis

The alleles were scored individually based on comparison with the molecular ladder and also the control samples (*West African Tall* and *Malayan Yellow Dwarf*). Observed number of alleles, effective number of alleles, Shannon's Information Index and F-Statistics were worked out for the 14 microsatellite loci using the software POPGENE version 1.31 (Yeh et al., 1999). The expected and observed heterozygosity across the 10 coconut landraces were worked out using the software GDA (Genetic Data Analysis; Lewis and Zaykin, 2002). A cluster analysis was performed on the similarity matrix using the unweighted pair group method with arithmetic averages (UPGMA) and the resultant phenogram was constructed.

3. Results

14 polymorphic SSR markers were used to amplify DNA of 102 palms representing 10 landraces form India. A total of 90 alleles were detected with most markers revealing four alleles or more. The number of alleles at each locus varied from 3 (CnCir A9) to 16 (CnCir E2) with a mean of 6.42 alleles per locus. The effective number of alleles per locus (N_e) ranged from 1.68 (CnCir A3) to 8.84 (CnCir E2) with a mean of 3.28 (Table 3). Shannon's Information Index ranged from 0.80 (CnCir A3) to 2.43 (CnCir E2) with a mean of 1.28. The polymorphism information content (PIC) value, which is a measure of polymorphism for a marker locus, varied from 0.41 (CnCir A3) to 0.89 (CnCir E2) among the 14 microsatellite loci, the average being 0.61 (Table 3).

Among the landraces, expected heterozygosity was highest for the two tall populations from Pallikkara community, Pallikkara Tall III (0.58) and Pallikkara Tall I (0.51) (Table 4). Least heterozygosity was observed for the dwarf coconut landraces from Vayalar community (0.03–0.05). Among Talls, Vayalar Tall exhibited the least heterozygosity (0.37). The observed heterozygosity for all the landraces was less than expected indicating a tendency towards inbreeding within the population.

The fixation index (F_{ST}) ranged from 0.29 to 0.64 with a mean of 0.42, indicating a high level of population differentiation (Table 5). Even though negative inbreeding coefficient (F_{IS}) was noticed for four of the loci (CnCir A3, CnCir C7, CnCir F2 and CnCir C12), F_{IS} for most of the remaining loci was high. Mean F_{IS} (0.24) and F_{IT} (0.58) were both positive and greater than zero indicating a heterozygote

Table 3
Diversity statistics for the 14 SSR markers studied

S. No.	Locus	Allele size (bp)	No. of alleles	Effective no. of alleles (N_e)	Shannon's information index (I)	PIC
1.	CnCir E12	162–174	4	1.85	0.84	0.46
2.	CnCir A9	89–103	3	1.97	0.85	0.49
3.	CnCir B12	155–179	8	3.31	1.47	0.70
4.	CnCir C3′	176–210	8	4.84	1.77	0.80
5.	CnCir A3	228–240	4	1.68	0.80	0.41
6.	CnCir C7	157–169	7	3.57	1.47	0.72
7.	CnCir H4′	218–236	6	1.77	0.91	0.44
8.	CnCir E2	115–177	16	8.84	2.43	0.89
9.	CnCir F2	191–211	7	1.88	0.90	0.47
10.	CnCir H7	133–139	4	2.70	1.17	0.63
11.	CnCir B6	196–208	7	5.22	1.77	0.81
12.	CnCir E10	232–246	5	2.10	0.99	0.53
13.	CnCir G11	168–188	6	4.22	1.57	0.77
14.	CnCir C12	154–174	5	2.02	0.97	0.51
Mean			6.42	3.28	1.28	0.61

Table 4
Observed and expected heterozygosity for the 10 landraces of coconut

S. No.	Variety	Observed heterozygosity (H_o)	Expected heterozygosity (H_e)
1.	Vayalar Tall	0.31	0.37
2.	Vayalar Green Dwarf	0.03	0.05
3.	Vayalar Orange Dwarf	0.03	0.03
4.	East Coast Green Tall	0.34	0.50
5.	East Coast Pink Tall	0.32	0.48
6.	East Coast Yellow Tall	0.35	0.49
7.	East Coast Tall Spicata	0.33	0.47
8.	Pallikkara Tall I	0.32	0.51
9.	Pallikkara Tall II	0.34	0.48
10.	Pallikkara Tall III	0.36	0.58

Table 5
F-statistics (Wright, 1951) and gene flow for the 14 microsatellite loci

S. No.	Locus	F_{IS}	F_{IT}	F_{ST}	Gene flow (N_m)
1.	CnCir E12	0.67	0.82	0.46	0.29
2.	CnCir A9	0.87	0.92	0.36	0.44
3.	CnCir B12	0.26	0.57	0.41	0.36
4.	CnCir C3′	0.40	0.63	0.39	0.39
5.	CnCir A3	−0.10	0.60	0.64	0.14
6.	CnCir C7	−0.01	0.32	0.33	0.51
7.	CnCir H4′	0.16	0.44	0.33	0.49
8.	CnCir E2	0.36	0.57	0.32	0.53
9.	CnCir F2	−0.12	0.50	0.55	0.20
10.	CnCir H7	0.95	0.97	0.39	0.39
11.	CnCir B6	0.07	0.47	0.43	0.33
12.	CnCir E10	0.12	0.51	0.45	0.31
13.	CnCir G11	0.11	0.37	0.29	0.60
14.	CnCir C12	−0.32	0.39	0.53	0.22
Mean		0.24	0.58	0.42	0.37

F_{IS}, coefficient of inbreeding among individuals in the subpopulations; F_{IT}, degree of genetic differentiation among the total populations; F_{ST}, degree of genetic differentiation among the subpopulations.

deficit within populations. The mean gene flow (N_m) was 0.37 (Table 5).

Genetic similarity was calculated for the ten landraces of coconut. A dendrogram was constructed using UPGMA clustering (Fig. 1). Two major clusters were observed, the tall and dwarf landraces clustering separately. Two sub-clusters were observed within the tall landraces—Vayalar Tall clustering closer to the four East Coast Talls and the Pallikkara Talls forming a separate cluster.

4. Discussion

Genetic diversity is necessary to sustain the productivity of a crop as it furnishes new genes for yield, adaptation, disease resistance, high value uses and characters (Frankel and Soule, 1981). About 12 million hectares of coconut are grown worldwide. To date, 1416 accessions of coconut have been recorded worldwide in the Coconut Genetic Resources Database. Rich diversity of coconut exists in the farmers' field and there is tremendous scope for utilizing this diversity for providing various options and opportunities while formulating strategies for solving the problems of coconut farmers, the majority of whom are smallholders. The present study on characterization of 10 landraces of coconut using molecular tools was taken up in three coconut communities in Southern India mainly to quantify the extent of genetic diversity present coconut landraces.

The high percentage of polymorphic loci (100%), the mean number of alleles per locus (6.42) and the mean expected heterozygosity (0.61) observed indicate the immense potential of the 14 SSR markers from the coconut microsatellite kit (Baudouin and Lebrun, 2002) for genetic diversity studies in coconut from different geographical regions.

The expected heterozygosity was much higher in the tall landraces (0.37–0.58) compared to dwarfs (0.03–0.05). Earlier studies using microsatellites in coconuts (Perera et al., 2000; Rivera et al., 1999; Teulat et al., 2000; Merrow et al., 2003; Devakumar et al., 2006) have also reported higher heterozygosity and gene diversity of the talls genotypes compared to dwarfs. This is basically related to their breeding habit: talls are primarily allogamous, while dwarfs are autogamous. The mean expected heterozygosity value as seen in the present study was substantially

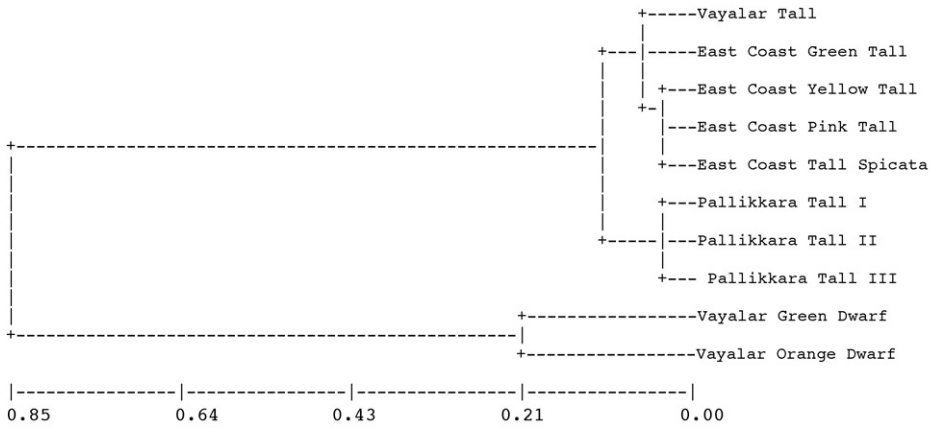

Fig. 1. UPGMA phenogram based on Nei's (1973) genetic distance showing the relationships among the 10 landraces of coconut.

higher than the mean value of plant species with an outcrossing mating system in general (Hamrick and Godt, 1989).

The overall degree of genetic differentiation was high (0.42) indicating a high genetic differentiation among the populations. The high level of population differentiation was supported by low mean gene flow across the landraces ($N_m = 0.37$), which can be considered insufficient for significant divergence of the populations caused by genetic drift. According to Hall et al. (1994), there exists an inverse relationship between geographic distance and N_m. The high genetic differentiation between landraces of coconut could be mainly due to regional differences as they covered a vast geographic area extending from the East coast to the West Coast of India. Restricted pollen and seed dispersal could also contribute to the high genetic divergence among the populations. In earlier studies in coconut, while a higher level of population differentiation ($F_{ST} = 0.36$) was observed in Mexican coconut populations analyzed using 15 enzymatic systems (Zizumbo-Villarreal et al., 2002), a moderate level of population differentiation ($F_{ST} = 0.054$) was observed in Sri Lankan coconut populations (Perera et al., 2001) analyzed using 8 SSR primer pairs.

F_{IS} values for most of the loci was high indicating an excess of homozygotes, which probably may be due to the inbreeding having occurred in the tall landraces and the inclusion of two dwarf landraces. One reason for occurrence of inbreeding in the tall landraces, which are otherwise allogamous, could be the isolation of the populations, which could have experienced limited gene flow resulting from restricted pollen and seed dispersal. Zizumbo-Villarreal et al. (2002) attributed a high F_{IS} in Mexican coconut populations to local endogamy and/or genetic drift.

Among the tall variety, Vayalar Tall showed lowest value for expected heterozygosity (H_e) across the microsatellite loci studied. Farmers of the Vayalar village are facing the serious malady of root (wilt) disease. In the disease hotspot areas of the community, few disease-free palms are found, which have remained free from disease symptoms despite being surrounded by severely infected palms (Nair et al., 1996). These palms are preferred by farmers in the village for collecting seed nuts due to the possibility of obtaining disease-free progenies. This must have resulted in stringent selection pressure, resulting in the evolution of Vayalar Tall variety. Vayalar Tall also formed a distinct variety when the dendrogram was constructed with molecular data. Usually dwarf landraces, rather than talls, exhibit such uniformity in morphometric traits (Arunachalam et al., 2005) and also in molecular data (Teulat et al., 2000). Correlation of uniformity/homozygosity in foliar traits and disease tolerance in Vayalar Tall needs further investigation. Two of the Pallikkara talls, Pallikkara Tall II and Pallikkara Tall III, showed high degree of heterozygosity for molecular marker data.

The expected heterozygosity of Spicata palms (0.47) was lower than most tall landraces. The Spicata palms exhibit distinct floral characters compared to normal palms; they produce a large number of female flowers on the unbranched spadix with a conspicuous reduction in the number of male flowers. The Spicata palms are known to occur in most of the coconut-growing countries (Sugimura et al., 1994). Due to the reduction in male flower production, there exists a possibility of high level of cross-pollination in Spicata palms. The low level of genetic diversity could be due to genetic bottleneck during its development history, being mostly derived from a single mother palm. Spicata of Philippines clustered together with Rennel Tall and Polynesian Tall than with the other seven tall and ten dwarf landraces (Rivera et al., 1999). Spicata of Philippines was found closely related to Southeast Asian Talls (Perera et al., 2000). These studies indicate the possible parent landraces from which Spicata mutant in their study might have evolved.

The present study revealed the clustering of Talls from each of the three communities depending on the geographical location. Geographic affinity of the relationship between tall coconut landraces was previously reported from Mexico (Zizumbo-Villarreal et al., 2002) and South Pacific Islands (Ashburner et al., 1997a). Dwarfs also recorded high level of uniformity in microsatellite loci and form distinct group different from tall landraces in the dendrogram (Perera et al., 1999; Teulat et al., 2000; Devakumar et al., 2006).

This study has practical implications in farmer participatory evaluation and conservation of coconut genetic resources. Coconut landraces which are adapted to the local conditions, high-yielding and possessing valuable characteristics are under threat of genetic erosion. Only few palms of East Coast Pink Tall (tender nut water with medicinal properties) and East Coast Yellow Tall could be located. The Vayalar palms exhibited relative tolerance to coconut root (wilt) disease, while the Pallikkara palms were well adapted to laterite soils. Farmers find it difficult to conserve their precious diversity unless it translates into economical value to them. To aid the conservation of coconut genetic resources, it is necessary to evaluate the extent of genetic diversity present in the landraces, which would go a long way in promoting conservation of coconut germplasm in farmer's fields through *in situ* and on-farm conservation (Batugal and Oliver, 2003). A thorough understanding of the diversity available in farmers' gardens would also enable the stakeholders to utilize the range of germplasm for the sustainable production of coconut and enhancing income of farmers and also plan conservation strategies. Selected palms from these communities will be used as sources of seed nuts for planting and community-managed seedling nurseries will be raised. This would serve as effective mechanisms for the introduction and promotion of farmer-preferred coconut diversity that could effectively support sustainable coconut production.

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