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Genetic diversity and adaptive variations under static and dynamic management: a case of rice landraces from parts of Odisha in India

M. Logapriyan[1], I. S. Bisht[1]*, K. V. Bhat[1] and D. Pani[2]

[1]*National Bureau of Plant Genetic Resources, Pusa Campus, New Delhi 110 012, India and* [2]*National Bureau of Plant Genetic Resources, Base Centre, CRRI Campus, Cuttack, Odisha 753 006, India*

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Abstract

In the present study, inter- and intrapopulation diversity of five named rice landraces from parts of Odisha state of India representing static and dynamic management was examined using 14 sequence-tagged microsatellite site primer pairs. A total of 64 alleles were detected in ten populations of the five named landraces. The number of alleles ranged from 2 to 7, with an average of 4.57 alleles per locus. Of the 64 alleles, 60 were common and four were rare. Moderate-to-low diversity was observed in the landrace populations, with the number of alleles per population ranging from 16 to 25 and the percentage of polymorphism ranging from 14.29 to 64.29, respectively. The analysis of molecular variance indicated a highest variation of 75.7% among populations within groups (static *vs.* dynamic). The pairwise estimates of F_{ST} revealed very high significant population differentiation, which ranged from 0.68 to 0.89, indicating that the populations share limited genetic diversity among them. However, not many variations were observed in the phenotypes of populations representing static and dynamic management. This shows that adaptations of a population apparently persist over generations, but the underlying genotypes change and new alleles or combinations may arise and increase in frequency at the expense of other alleles that have disappeared. The importance of population biology research for *in situ* conservation requires both descriptive and hypothesis testing to guide technical improvement and management of landrace populations.

Keywords: adaptive variations; *Oryza sativa* L; population structure; rice landraces; static and dynamic management

Introduction

The threats faced by crop landraces grown in traditional farming by large-scale adoption of improved cultivars have led to the creation of conservation programmes to preserve crop resources for future generations. One type of crop genetic resource conservation is *ex situ* (static) conservation, i.e. maintenance of genetic resources in genebanks under subzero temperatures (Plucknett *et al.*, 1987), and another type is *in situ* (dynamic) conservation, i.e. maintenance of genetic resources on farm under traditional production conditions (Brush, 1991, 2000; Maxted *et al.*, 1997). *Ex situ* conservation is well suited to capture and store alleles and genotypes and is also well suited to users who need ready access. It also acts as a back-up for existing diversity that might otherwise be lost in human-managed

* Corresponding author. E-mail: bishtis@nbpgr.ernet.in, bishtis@rediffmail.com

agricultural landscapes (Cohen *et al.*, 1991). However, *ex situ* conservation is not suited to conserve the other components of the agroecosystem that generate crop genetic resources (Brush, 2000). *In situ* conservation is specifically intended to maintain these components in living, viable agroecosystems. Considering that *in situ* conservation is ecologically dynamic, it would fail if we stop change or preserve agroecosystem in a particular state (Brown, 2000). Sources of change that can be expected and must be tolerated include the introduction of new crops and crop varieties; the exchange of varieties between farmers and localities; the use of inputs to improve the productivity of land and labour, such as fertilizers and pesticides; and commercialization (Brush, 2000).

There is now widespread recognition globally within the plant genetic resource community that attention should be paid to *in situ* conservation of cultivated populations on farms. Certain case studies of crop diversity indicate that substantial diversity still persists on farms in regions of crop origin and diversity, despite the advent of modem cultivars of crops to these regions (Brush, 1995; Kumar, Bisht *et al.*, 2010; Pandey *et al.*, 2011, 2012). There is now widespread recognition of the need to plan for *in situ* conservation to continue and indeed to improve its capacity to maintain genetic diversity as an adjunct to conservation of *ex situ* collections (Brown, 2000). However, limited information is available on the scientific basis and optimal procedures for on-farm conservation of crop landraces. As a basis for guiding the supporting research in population biology for on-farm conservation, the present study was carried out on the genetic structure of traditional rice landraces from parts of Odisha state of India, under both static and dynamic management.

Two sets of attributes can be considered as important indicators of the genetic composition of rice landraces. The first set is marker diversity or the extent of differences between individual copies of genes at DNA level and is informative as to the ancestry or breeding history of the populations (Brown, 2000). This set comprises indicators of the recency of bottlenecks in population size, the prevalence of outcrossing, the ease with which genes are recombined, and the level of gene flow between populations. The second set is variation in adaptation. This set comprises indicators of the degree to which populations are adapted to their environment and of their potential for continued performance or being donors of characteristics in plant breeding. Both biotic and abiotic aspects of the environment are involved.

Materials and methods

Five named rice landraces obtained from parts of Odisha (Orissa) state of India, representing both static (*ex situ* in genebanks) and dynamic (*in situ* on-farm) conservation, were included in the present study (Table 1). The genebank-conserved populations were collected during 1986 and 1987, whereas the on-farm managed accessions were collected during 2008, as these landraces are still continuously cultivated under a traditional farming system. As none of these named landraces maintained on farm could be collected from the same household, utmost care was taken to explore and collect landrace populations from the close-by areas from where populations were collected earlier and conserved *ex situ* in the National Genebank at the National Bureau of Plant Genetic Resources (NBPGR), New Delhi, India.

Molecular characterization

Sample preparation

Thirty individual plants were taken for each landrace population. The seeds were selected randomly from the sample and planted in the field nursery for collecting leaf samples. Young actively growing leaves of 30-d-old

Table 1. Rice landraces studied for population genetic structure under static and dynamic management

Landrace	IC number	Conservation status	Area of landrace collection	Frequency of occurrence
Asamchudi	98 721	Static	Kalahandi	Locally common
	569071	Dynamic	Kalahandi	Locally common
Bhuta	86 063	Static	Keonjhar	Locally common
	568854	Dynamic	Keonjhar	Locally common
Kalakadamba	85 972	Static	Keonjhar	Locally common
	568859	Dynamic	Keonjhar	Locally common
Narada	85 999	Static	Keonjhar	Locally common
	568856	Dynamic	Keonjhar	Locally common
Saleijhati	86 055	Static	Keonjhar	Locally common
	568873	Dynamic	Keonjhar	Locally common

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plants were collected and used for DNA extraction. Leaves were harvested and immediately stored at −80°C until total genomic DNA was extracted using a modified cetyltrimethylammonium bromide method (Saghai-Maroof *et al.*, 1984). DNA quantification was carried out using the Nanodrop™ 1000 Spectrophotometer (Thermo Scientific). These estimates were confirmed by staining DNA with ethidium bromide after electrophoresis in 0.8% agarose gel at 100 V for 1 h in Tris-acetate-EDTA (TAE) buffer (0.04 M Tris acetate and 0.001 M EDTA, pH 8.0) using known DNA concentration standards.

Sequence-tagged microsatellite site genotyping

A group of 14 highly polymorphic and diverse primer pairs representing 11 rice chromosomes were chosen for the sequence-tagged microsatellite site (STMS) analysis. Polymerase chain reactions (PCRs) were carried out in a Bioer XP cycler (Bioer Technology Co. Ltd, Hangzhou, PR China) using PCR microplates (Axygen Inc., Union City, CA, USA). The total PCR reaction volume was 25 µl, comprising 2.0 µl of 40 ng genomic DNA, 2.5 µl 10× PCR buffer (Tris with 15 mM $MgCl_2$, conc. 10×), 2.5 µl deoxynucleotides, 2.0 µl primer, 0.33 µl Taq DNA polymerase (conc. 3 U/µl) (GeNei™ Bangalore Genei, Bangalore, India) and 15.67 µl sterile deionized water. The samples were subjected to the following thermal profile for amplification in a thermocycler: an initial extended step of denaturation at 94°C for 6 min followed by 32 cycles of denaturation at 94°C for 1 min, primer annealing at the respective annealing temperature for 1 min, primer extension at 72°C for 1 min and a final extension step at 72°C for 10 min. After amplification, the PCR tube was stored at 4°C until electrophoresis. The amplified products were electrophoresed on 3% agarose gels at 110 V in 1× TAE buffer. The gels were stained with ethidium bromide and photographed using a G:Box XT^4 gel documentation system (Syngene, Henry B. Gonzalez Convention Centre, Headquarter Hotel-Grand Hyatt, San Antonio).

Data analysis

The molecular weights of the bands were estimated using a standard 50 bp DNA ladder, and the homology of the bands was based on the distance of migration in the gels. STMS amplicons obtained from each entry were resolved as a single band on the agarose gel system and the dataset was used to conduct the analysis. The polymorphism information content (PIC) value for each STMS locus was calculated using the PIC calculator http://www.liv.ac.uk/~kempsj/pic.html (Jan, 2002). The PopGene Version 1.32 software (Yeh *et al.*, 2000) was used to estimate the various genetic diversity parameters. NTSYS-PC (version 2.02; Exeter Software, Setauket, NY, USA; Rohlf, 2000) was used to prepare the dendrogram based on Nei's genetic distance.

Analysis of molecular variance (AMOVA) was carried out among groups, among populations within groups, and among individuals within populations in Arlequin 3.5 (Excoffier and Lischer, 2010) to determine the distribution of variation at different hierarchical levels. Population structure by AMOVA is based on an analysis of variance of gene frequencies, taking into account the number of mutational differences between molecular haplotypes. Fixation indices (Weir and Cockerham, 1984) and population pairwise F_{ST} (pairwise estimates of the correlation of alleles between populations) values were also computed using the above-mentioned software. Rcmd (R software) was used in the Arlequin version 3.5 software to generate a plot of pairwise F_{ST} values. Population average pairwise differences were also computed using the software.

Morphological characterization

The rice landrace populations were also grown for morphological characterization in on-station field trials at the NBPGR Base Centre, Cuttack (Odisha), during the 2012 cropping season, and data were recorded on 24 qualitative morphological traits. The descriptors for qualitative traits were recorded at different stages of growth for all the ten landrace populations of rice, as per Bioversity-IRRI guidelines (2007). Data were also subjected to cluster analyses using the INDOSAT statistical package developed at the INDOSTAT Services, Hyderabad, India.

Results

Molecular diversity analyses

Fourteen STMS primer pairs were used for the molecular diversity analyses of the five named rice landraces, each representing both static and dynamic conservation (Table 2). A total of 64 alleles were detected in the ten populations of the five named landraces. The number of alleles ranged from 2 to 7, with an average of 4.57 alleles per locus. Of the 64 alleles, 60 were common and four were rare. Summary diversity of each landrace population is given in Table 3. The effective number of alleles and expected heterozygosity ranged from 1.08 to 1.25 and from 0.07 to 0.17, respectively, across the populations. The total number of alleles per landrace population ranged from 16 to 25, and the percentage of polymorphic loci ranged from 14.29 to 64.29 (Table 3). The PIC values ranged from 0.148 to 0.760, with a mean average value of 0.519 (Table 2).

Individual landrace pairwise distributions of allele frequencies under static and dynamic management are

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Table 2. Repeat motif, number of alleles per locus (*n*), PIC and allele size range for all the 14 STMS loci

				Allele size (bp)	
Locus	SSR motif	Alleles (*n*)	PIC	Range	Difference
RM206	$(GA)_{21}$	5	0.674	140–180	40
RM19	$(ATC)_{10}$	4	0.557	210–250	40
RM218	$(GA)_{24}$	5	0.557	130–200	70
RM233B	$(GA)_{20}$	6	0.355	140–180	40
RM234	$(GA)_{17}$	3	0.442	140–160	20
RM241	$(GA)_{31}$	7	0.636	100–160	60
RM249	$(GA)_{14}$	3	0.254	110–150	40
RM217	$(GA)_{20}$	6	0.647	120–170	50
RM11	$(GA)_{17}$	2	0.148	130–150	20
RM223	$(GA)_{25}$	5	0.499	140–180	40
RM242	$(GA)_{26}$	4	0.572	150–240	90
RM216	$(GA)_{18}$	4	0.578	130–160	30
RM222	$(GA)_{18}$	4	0.582	200–240	40
RM224	$(GA)_{13}$	6	0.760	130–180	50
Total		64	–	–	–
Mean		4.57	0.519	–	–

given in Table S1 (available online). The population structures of rice landrace populations under static and dynamic management were strikingly different, as revealed by the frequency of private alleles. The mean frequency of private alleles, under both static and dynamic management, was more than 50% (Table S1, available online). The AMOVA indicated a highest variation of 75.7% among populations within groups (static *vs.* dynamic) followed by that among individuals within populations (11.22%), among groups (6.66%) and within individuals (6.41%) (Table 4).

The pairwise estimates of F_{ST} revealed very high significant population differentiation, which ranged between 0.68 and 0.89 (Fig. 1; Fig. S1 (available online)). High population differentiation was observed even between populations of the same named landrace under static and dynamic management. This shows that the populations share limited genetic diversity among them. Even no pairs of a named landrace population representing static and dynamic conservation grouped together in the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) dendrogram (Fig. S2, available online) based on Nei's genetic distance.

Analyses of adaptive variations

Minor variations were observed both within and among the landraces under static and dynamic management. All the ten landraces analysed for qualitative traits were non-scented and had medium green-coloured leaf blades. They were monomorphic for traits such as the

Table 3. Summary diversity of rice landrace populations based on 14 STMS markers

Landrace	Accession	Na	Ne	*I*	He	Nei He	*n*	*P*	*P*%
Asamchudi	98 721 (S)	1.50 ± 0.52	1.22 ± 0.25	0.23 ± 0.25	0.15 ± 0.17	0.15 ± 0.16	21	7	50.00
	569071 (D)	1.64 ± 0.50	1.25 ± 0.28	0.26 ± 0.25	0.17 ± 0.17	0.16 ± 0.17	23	9	64.29
Bhuta	86 063 (S)	1.57 ± 0.51	1.10 ± 0.14	0.15 ± 0.17	0.08 ± 0.10	0.08 ± 0.10	22	8	57.14
	568854 (D)	1.29 ± 0.47	1.18 ± 0.34	0.15 ± 0.26	0.10 ± 0.18	0.10 ± 0.18	18	4	28.57
Kalakadamba	85 972 (S)	1.14 ± 0.36	1.08 ± 0.27	0.06 ± 0.17	0.04 ± 0.14	0.04 ± 0.13	16	2	14.29
	568859 (D)	1.36 ± 0.50	1.11 ± 0.26	0.11 ± 0.20	0.07 ± 0.14	0.07 ± 0.14	19	5	35.71
Narada	85 999 (S)	1.36 ± 0.50	1.19 ± 0.35	0.16 ± 0.27	0.11 ± 0.19	0.11 ± 0.19	19	5	35.71
	568856 (D)	1.36 ± 0.50	1.15 ± 0.26	0.15 ± 0.23	0.10 ± 0.16	0.10 ± 0.16	20	5	35.71
Saleijhati	86 055 (S)	1.71 ± 0.61	1.09 ± 0.11	0.16 ± 0.15	0.08 ± 0.08	0.08 ± 0.08	24	9	64.29
	568873 (D)	1.79 ± 0.70	1.25 ± 0.27	0.28 ± 0.25	0.17 ± 0.16	0.17 ± 0.16	25	9	64.29

Na, observed number of alleles; Ne, effective number of alleles; *I*, Shannon's information index; He, expected heterozygosity; Nei He, Nei's expected heterozygosity; *n*, total number of alleles present; *P*, number of polymorphic loci; *P*%, percentage of polymorphic loci; S, static; D, dynamic.

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Table 4. AMOVA design and results

Source of variation	df	Sum of squares	Variance components	Percentage of variation
Among groups	1	207.00	0.30 Va	6.66
Among populations within groups	8	1653.35	3.42 Vb	75.70
Among individuals within populations	290	378.37	0.51 Vc	11.22
Within individuals	300	87.00	0.29 Vd	6.41
Total	599	2415.72	4.52	–

Fixation indices: $F_{IS} = 0.64$; $F_{SC} = 0.81$; $F_{CT} = 0.07$; $F_{IT} = 0.94$.

shape of the ligule (two-cleft), attitude of branches in the panicle (drooping) and panicle: secondary branching (sparse) (Table S2, available online). There were distinguishable differences within and between the landraces for traits such as the colour of basal leaf sheath, auricle, collar, stigma, lemma epiculus and pericarp. Traits such as the attitude of the leaf blade and flag leaf, which is very well correlated with the yield in rice crops, displayed significant variations, which were helpful in distinguishing diversity within landraces. The colour of the ligule ranged from white to purple, which further indicated differences within the landraces (Table S2, available online). With regard to culm strength, an important trait for judging the lodging resistance of a plant, among the

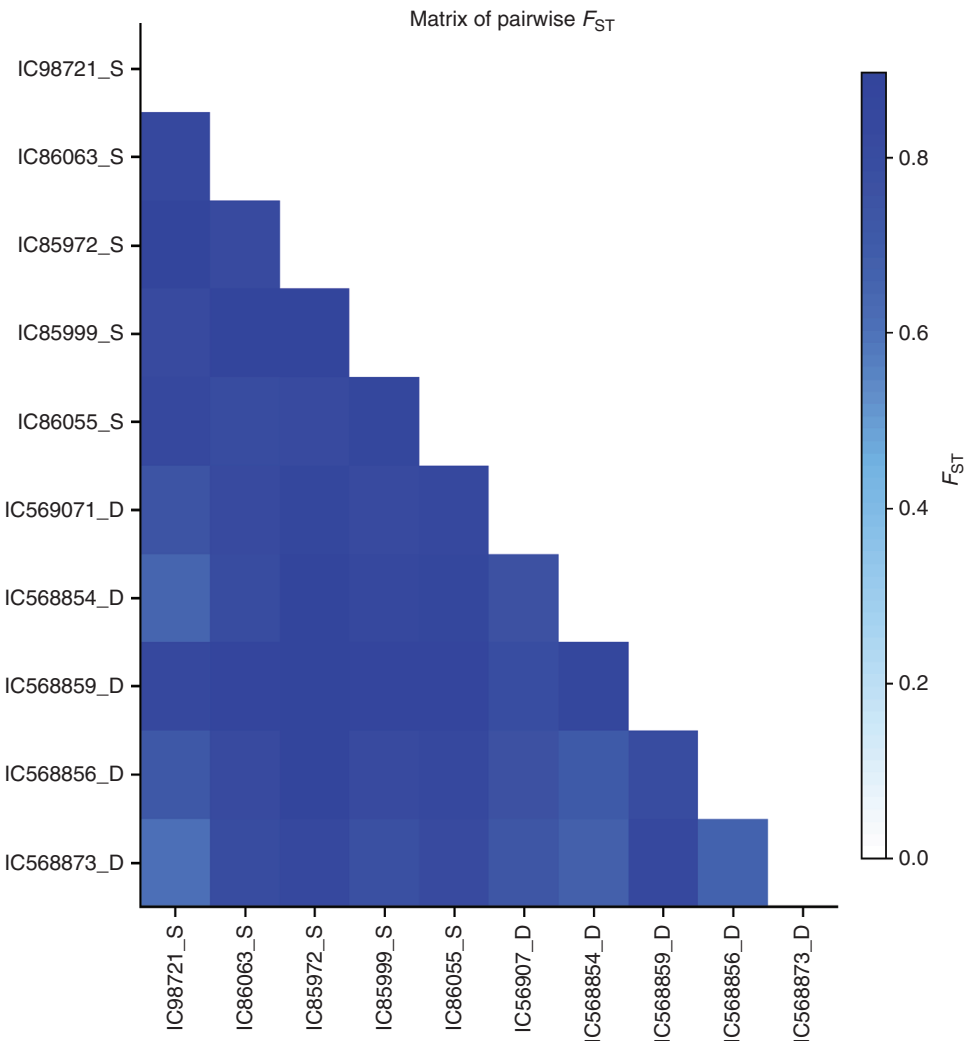

Fig. 1. Population pairwise F_{ST} estimates of rice landraces (S and D indicate static and dynamic conservation status).

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accessions in the Kalakadamba landrace, the accession representing static conservation had strong culm compared with on-farm managed populations. The population representing the dynamic management of the Narada landrace had awn, whereas the other landraces were awnless (Table S2, available online).

The data on some important qualitative traits were subjected to a cluster analysis (Fig. S3, available online). Three groups were formed, with the Narada (static) landrace clustering separately. The diversity pattern did not follow a set pattern, and the same named landraces clustered separately and even did not match the pattern observed in the molecular diversity analyses.

Discussion

The genotypes of different rice landrace populations representing static and dynamic conservation were different for most of the STMS loci analysed in the present study. Population differentiation based on F_{ST} measures was very high even for the same named landrace. Some recent studies have assessed the population genetic structure of named rice landraces (Pusadee *et al*., 2009; Kumar, Pandey *et al*., 2010; Sreejayan *et al*., 2011; Pandey *et al*., 2012) and found very high partitioning of total variability among individual populations.

Variation in the diversity pattern of the same named landrace under dynamic and static conservation was also observed for qualitative traits (Fig. S3, available online). Even the clustering pattern based on a few important qualitative morphological traits did not match with the pattern observed in the molecular diversity analyses (Fig. S2, available online). The only similarity in the clustering pattern was observed for the Narada landrace under static management, which was quite distinct from all the other landrace populations in clustering carried out based on molecular data and a few important qualitative characters. Therefore, consistency in farmer naming needs to be duly validated. Furthermore, the variation in static and dynamic conservation for qualitative traits could not be conclusively discussed as the differences might be due to sampling variations. The greater population differentiation in the molecular diversity analyses could be attributed to genetic drift.

Far fewer studies have been carried out on the multilocus structure of landrace populations, i.e. the extent to which genetic variants at one locus are correlated in occurrence with variants at another locus. Such a structure arises from selection, genetic drift or fragmentation of the population and is retained through selection, isolation and the lack of migration, and restrictions on outcrossing and genetic recombination (Brown, 2000).

In diversity assessment, the importance of variations due to adaptation and molecular diversity has long been argued. In the present study, it was observed that under on-farm management while the particular attributes, characters or adaptations of a population apparently persisted over generations in different named landrace populations, the underlying genotypes changed substantially. New alleles or combinations may arise and increase in frequency at the expense of other alleles that have disappeared (Tables S2, available online). As has been argued by Brown (2000), *in situ* strategies fail to preserve all the extant biodiversity at the gene level. As better alleles or combinations arise and enjoy selective advantage, others thereby will be less fit and decline. This is the cost of evolutionary substitution and the price paid for allowing evolution to continue.

The above-mentioned findings can also be argued in support of the neutral theory of molecular evolution (Kimura, 1968). Kimura's neutral theory claims that the overwhelming majority of evolutionary changes at the molecular level is caused not by selection acting on advantageous mutants, but by random fixation of selectively neutral or very nearly neutral mutants through the cumulative effect of sampling drift under continued input of new mutations (Kimura, 1991).

The *in situ* approach to conserving landraces undoubtedly holds several advantages over *ex situ* strategies. In view of the existing findings, a few hypotheses towards which research should be directed could be made (Brown, 2000). The important areas of research on *in situ* conservation of landrace diversity on farm in the context of population structure may include allelic richness and genotypic diversity, specific adaptations, localized divergence, diversity to meet temporal and environmental adaptations, and continuance of crop evolutionary processes. On-farm populations have the capacity to support a much greater number of rare alleles and of different (multilocus) genotypes than accessions in genebanks (Marshall, 1989). Diversity itself confers long-term population fitness because it helps populations to cope with variable environments. Landrace populations of crops have survived centuries of selection for reliable production in subsistence agriculture, yielding a definite, known but probably limited benefit to the farmers who grow them (Frankel *et al*., 1995). Presumably, they are selected for resilience and stability, though of modest productivity. The *in situ* strategy conserves the crop evolutionary processes (mutation, migration, recombination and selection). It provides scope for ongoing evolution, particularly in response to environmental changes and pathogen and pest pressures fluctuating in numbers and genetic composition. The key variables include (i) genetic diversity within populations, which is the essential raw material for evolution; (ii) breeding

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system variation (such as changes in outcrossing rate); (iii) variation in resistance in space and time, related to pest pressure and diversity; and (iv) the dynamics of seed systems, persistence and migration. Furthermore, regeneration of *ex situ* collections is currently considered a serious and enormous challenge (Brown *et al.*, 1997). Viability is inevitably lost at rates depending on the resources for and the management regimens of such collections. The task is to regenerate accessions without incurring genetic drift or genetic shift (Breese, 1989).

Diversity conserved on farm is subject to a range of forces and is likely to be in a dynamic state. As yet, the data are far too limited to assess the various factors – human, biological, edaphic or climatic – to determine the requirements for optimal outcomes. The challenge is to plan for the assessment of these factors in relation to changes in genetic structure over time. Population biology research for *in situ* conservation thus needs to be both descriptive and hypothesis testing in order to guide technical improvement and management of landrace populations (Brown, 2000).

Of the five rice landraces, two populations of the Narada landrace representing static and dynamic conservation grouped separately in the UPGMA dendrogram and Principal Components Analysis (PCA). One probable reason could be that farmers often are not consistent in naming and describing landraces. It is important to investigate across the area of study that the same named landraces are genetically similar. As the populations of the same named rice landraces in the present study were distinct genetically and highly differentiated, for population genetic parameters and also for monitoring allele loss/change over time and space, one needs to collect these landraces at periodic intervals from the same household. The landraces also need to be under continuous cultivation to make precise comparisons. Clarification on what constitutes a landrace at each scale (village, community and region) is the first step towards defining the amount and distribution of crop diversity maintained by farmers (Jarvis *et al.*, 2000).

It was observed that all these rice landraces were under continuous cultivation for several years. As long as farmers themselves find it in their own best interests to grow these populations, both farmers and society will benefit at no extra cost to anyone (Jarvis *et al.*, 2000). Furthermore, varietal dynamics based on average area and households growing the landrace are important for its on-farm management. The landraces can be categorized as common or rare based on average area and average number of households planting them. All the populations analysed in the present study were categorized as locally common as these were grown in more fields of above-average sizes. Qualset *et al.* (1997) suggested that small land holdings isolate landrace populations from one another, thus reducing the generation of new genetic material by natural recombination. In common with biogeography theory (MacArthur and Wilson, 1967), they say that without human management, the genetic diversity in small 'patches' of crops would suffer genetic drift and inbreeding depression. They suggest that human inputs may offset these processes, as isolated populations can rely on seed exchange and farmer selection for the introduction of new genetic material (Louette *et al.*, 1997). However, if two populations are isolated, they will diversify genetically to a greater extent and therefore interpopulation diversity will increase.

The population structure of named landraces in traditional farming would help decide the optimum number of landrace populations to be collected and conserved *ex situ* and level of adaptive variations in niche environments including biotic and abiotic stresses. The complementarity of *in situ* and *ex situ* conservation is based on the recognition that crop genetic resources involve more than the alleles and genotypes of crop populations. Besides the genetic raw material of landraces, crop genetic resources also comprise related species, agro-ecological interrelationships and human factors (Brush, 2000). For the on-farm conservation of crop landraces, the traditional cultures and cropping systems that grow and use such populations are fundamental aspects of the habitats to which they are adapted. The systems shape their present genetic structure and determine the changes within landrace populations (Brown, 2000).

Supplementary material

To view supplementary material for this article, please visit http://dx.doi.org/10.1017/S1479262113000440

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