Plant Breeding Reviews VOLUME 41

WILEY Blackwell

PLANT BREEDING REVIEWS Volume 41

PLANT BREEDING REVIEWS Volume 41

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WILEY Blackwell

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Editorial Office 9600 Garsington Road, Oxford, OX4 2DQ, UK

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Library of Congress Cataloging-in-Publication Data

Library of Congress Catalog Control Number: 83-641963

Cover Design: Wiley Cover Illustration: © browndogstudios/Gettyimages

Set in 10/12pt Melior by SPi Global, Pondicherry, India

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Hari Deo Upadhyaya: Plant Breeder, Geneticist and Genetic Resources Specialist

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ABSTRACT

This chapter discusses Hari Deo Upadhyaya, a plant breeder, geneticist and genetic resources specialist, and his contributions in management and utilization of genetic resources, molecular biology and biometrics, and in groundnut breeding. Hari's contributions in genetic resources include enriching germplasm collections; forming representative subsets in the form of core and/or mini-core collections in chickpea, groundnut, pigeonpea, pearl millet, sorghum, and six small millets; unlocking population structures, diversity and association genetics; and identifying genetically diverse and agronomically desirable germplasm accessions for use in crop breeding. The Consultative Group on International Agriculture Research (CGIAR) recognized his concept and process of forming mini-core collection as International Public Goods (IPGs) and researchers worldwide are now using mini core-collections as useful genetic resources in breeding and genomics of the aforementioned crops. A genebank manager's role isn't just confined to collection, maintenance, and archiving germplasm. Hari's spirited efforts prove so and they led many to realize the abundant opportunities to mine and enhance the value of the genetic resources in crop improvement programs. As a geneticist, his seminal work on wilt resistance in chickpea laid a strong foundation for the wilt resistance breeding programs globally. His contributions as a groundnut breeder resulted in the release of 27 cultivars in 18 countries, some widely grown, and 24 elite germplasm releases with unique characteristics made available to groundnut researchers

Plant Breeding Reviews, Volume 41, First Edition. Edited by Irwin Goldman.

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worldwide. Hari's inimitable ability and scientific competence allowed him to collaborate with diverse groups and institutions worldwide. His scientific contributions in germplasm research and groundnut breeding have been recognized with several prestigious global awards and honors. A prolific writer and with immense passion for teaching, Hari Upadhyaya has established a school of his own for the management, evaluation and use of genetic resources for crop improvement.

KEYWORDS: Breeding, Climate resilient germplasm, core and mini-core collections, crop wild relatives, cultivars, elite germplasm, farmers participatory variety selection, molecular breeding, population structure and diversity, on-farm conservation of germplasm

OUTLINE

ABBREVIATIONS

- I. INTRODUCTION
- II. BIOGRAPHICAL SKETCH
- III. CONTRIBUTIONS
 - A. Genetic Resources Management and Use
 - 1. Representative Subsets
 - 2. Climate-resilient Germplasm
 - 3. Seed Nutrient-dense Germplasm
 - 4. Bioenergy
 - 5. Germplasm Use in Breeding
 - 6. On-farm Conservation and Use of Diversity
 - 7. Wild Relatives and Cultigen Genepool
 - 8. Gaps in Collections
 - B. Molecular Biology and Biometrics
 - 1. Population Structure and Diversity
 - 2. Genome-wide Association Mapping
 - 3. Candidate Genes Associated with Agronomically Beneficial Traits
 - 4. Ethnolinguistic Groups Shaped Sorghum Diversity in Africa
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- IV. UPADHYAYA, THE MAN
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 - 1. Awards
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VI. PRODUCTS A. Cultivars B. Registrations REFERENCES CITED AND FURTHER READING

ABBREVIATIONS

ASA	American Society of Agronomy
CGIARC	Consultative Group on International Agricultural Research
	Consortium
CSSA	Crop Science Society of America
ICRISAT	International Crops Research Institute for Semi-Arid
	Tropics
NARS	National Agricultural Research Systems
R4D	Research for development
SNP	Single nucleotide polymorphisms



I. INTRODUCTION

Hari Deo Upadhyaya, whom many of us know as Hari, has been known to me since 1980, when he joined the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India, as a postdoctoral fellow in chickpea breeding. After completing his postdoctoral assignment at ICRISAT, Hari then moved for a short period to work as the Pool Officer at 'GB Pant' University of Agriculture and Technology (GBPUAT), Pantnagar, India, the first agricultural university established on a US 'Land Grant' pattern in India. He then took up a regular position at the University of Agriculture Sciences (UAS), Dharwad, India, where he worked for almost for eight years, first as a soybean breeder (as Assistant Professor), and then as the head of the oilseeds scheme and a groundnut breeder (as Associate Professor). He did a remarkable job as an oilseed breeder, and he set up and took the soybean and groundnut breeding programs to newer heights.

In 1991, Hari returned to ICRISAT as a Senior Groundnut Breeder. In late 1997, ICRISAT reorganized its research portfolio, and moved Hari on a part-time basis to the Genetic Resources Unit, as part of the Crop Improvement Program. In 2002, Hari was appointed as a Principal Scientist and Head of the Genebank, ICRISAT, Patancheru, India, a position he still holds in the 'new organizational structure', where he has to manage the ICRISAT administrative Research for Development (R4D) portfolios with respect to management and utilization of genetic resources in crop improvement programs.

Hari knows very well that greater use of germplasm in crop breeding is the way forward for better conservation and use of genetic resources, and to address food and nutritional security in the developing world. As a principal scientist (in genetic resources), Hari performed exceedingly well, while promoting the greater use of genetic resources in crop improvement. Today, the representative subsets (i.e. the core and minicore collections) of the ICRISAT crops (i.e. chickpea, groundnut, pearl millet, pigeonpea, sorghum, finger millet) and small millets (i.e. barnyard millet, foxtail millet, kodo millet, little millet, proso millet) have been made available, and globally researchers are using these subsets to identify new sources of variation to support crop breeding in their respective regions.

Hari's seminal work with Rodomiro Ortiz on the process and concept of forming the mini-core collection has been recognized as an 'International Public Good'. Hari has published a total of 812 articles, of which 291 have undergone international peer review. These include research articles, commissioned reviews, and book chapters, and he has averaged 11.6 such articles per year, with three articles per year as first author. Twenty-seven cultivars of groundnut that were bred by Hari are being cultivated in 18 countries in Africa and Asia.

Over my long association with Hari, I have found him to be a person with the highest scientific competence and integrity, and a successful plant breeder and genebank manager. Hari's leadership in managing one of the largest Consultative Group on International Agricultural Research (CGIAR) Consortium genebanks is very much reflected in a recently concluded external review, when the panel remarked that '*The ICRISAT* genebank is functioning to high technical and scientific standards, and is very good in comparison with other international genebank operations. The users of the ICRISAT genebank are satisfied and appreciation of the genebank is wide spread.'

II. BIOGRAPHICAL SKETCH

Hari was born on 12th August 1953, in the small village of Shiwala, in Khair Tehsil, District Aligarh, Uttar Pradesh, India. He is the seventh of the eight children of Mr Gopi Chand Upadhyaya and Mrs Longsri Devi Upadhyaya. He passed his high school examinations (X standard) with Biology as his main subject, and got a distinction in Mathematics. Hari did a BSc (with honours) at Aligarh Muslim University, Aligarh, India, and then moved to the GB Pant University of Agriculture and Technology, Pantnagar, India, to complete his MSc and PhD, both in Plant Breeding. Hari is married to Ms Sudha, and is blessed with two sons, Abhisheik Deo and Aaditya Deo. Interestingly, neither of his sons has followed in his footsteps, as they chose Information Technology for their career path. Hari derives great strength from his wife and children in his scientific endeavours.

III. CONTRIBUTIONS

Unlike traditional germplasm botanists and curators, whose vision is always centred on collection, conservation, characterization and documentation of germplasm, Hari's basic training in plant breeding and genetics helped him to think beyond routine genebank activities, to include enhancing the value of genetic resources in the breeder's perception. Plant breeders are often reluctant to use exotic germplasm, largely because of the fear of linkage drag, breakdown of co-adapted gene complexes, and lengthening of the breeding cycle for the development of new cultivars. Hari strongly believes in promoting the use of germplasm in crop improvement programs, the generation and use of new knowledge (i.e. physiological, genetic, molecular) of trait expression and inheritance in applied breeding, and the sharing of breeding populations and advanced varieties, and also of knowledge, to help the global community to increase the production and productivity of staple food crops. Hari invested heavily to add value to the germplasm collections, and uses this in the crop breeding at ICRISAT and in the national programs globally.

A. Genetic Resources Management and Use

1. Representative Subsets. The use of germplasm in crop improvement programs globally is restricted due to:

- (i) the large sizes of collections of many crop species;
- (ii) the non-availability of representative subsets; and
- (iii) the lack of accurate and precise information on the agronomic worth of individual germplasm.

Hari saw the need, as advocated by Frankel and Brown (1984) to form reduced subsets that represent the diversity of the entire collection of a given species preserved in the genebank, and he initiated work to develop representative sets for ICRISAT mandate crops and small millets. Using passport and characterization data and statistical tools, Hari first developed the core collections (10% of the entire collection of a species stored in the genebank) for chickpea and, later, for pigeonpea, groundnut, pearl millet, and small millets (Table 1.1).

Сгор	Number of accessions used	Number of traits involved	Number of accessions in core	Reference
Pearl millet	20,766	22	2,094	Upadhyaya <i>et al.,</i> 2009a
Chickpea	16,991	13	1,956	Upadhyaya <i>et al.,</i> 2001a
Pigeonpea	12,153	14	1,290	Reddy <i>et al.,</i> 2005
Groundnut	14,310	14	1,704	Upadhyaya <i>et al.,</i> 2003
Finger millet	5,940	14	622	Upadhyaya <i>et al.,</i> 2006c
Foxtail millet	1,474	23	155	Upadhyaya <i>et al.,</i> 2008b
Proso millet	833	20	106	Upadhyaya <i>et al.</i> , 2011i
Barnyard millet	736	21	89	Upadhyaya <i>et al.,</i> 2014c
Kodo millet	656	20	75	Upadhyaya <i>et al.,</i> 2014c
Little millet	460	20	56	Upadhyaya <i>et al.,</i> 2014c

Table 1.1. Core collections formed by Hari Deo Upadhyaya in chickpea, groundnut,pearl millet, pigeonpea, and small millets.

The chickpea core collection consisted of 1,956 accessions that had been selected from 16,991 accessions (Upadhyaya *et al.*, 2001a). Rodomiro Ortiz, the then Director of Genetic Resources and the Enhancement Program, ICRISAT, challenged Hari and Paula Bramel (a co-author with Hari) about how useful the core collections were, with such large numbers of accessions for screening a desired trait for further use in breeding. After evaluating 1,956 accessions, together with controls for one season, in an augmented design, Hari concluded that it was a Herculean task to accurately and cost-effectively generate datasets even for the core collection accessions.

Hari and Rodomiro Ortiz discussed this and adopted the approach of re-sampling the core collection to define a 'core of the core' or 'mini-core', subset. Here, they used the evaluation data (22 morphological and agronomic traits) of the core collection (1956 accessions) and statistical theory to sample the variability to form the mini-core collection (211 accessions) in chickpea. This represented the diversity that was present in the core collection, and also the entire collection, as shown by the similar means, variances, frequency distributions and preserved co-adapted gene complexes, both for the core and mini-core collections (Upadhyaya and Ortiz, 2001).

Hari and Rodomiro jointly wrote a manuscript on the chickpea mini core collection, with Rodomiro as corresponding author, and submitted it to *Theoretical Applied Genetics*. To their surprise, exactly two weeks later, they got a response from the editor to say that the manuscript was accepted for publication. This development encouraged Hari to follow this approach, and in subsequent years, he developed mini-core collections for other crops as well (Table 1.2). In all cases, both the core and mini-core collections fulfilled the statistical tests for the preservation of

Crop	Entire collection	Mini-core number	% of entire collection	Traits used	Reference
Sorghum	22,473	242	1.08	21	Upadhyaya <i>et al.</i> , 2009b
Pearl millet	20,766	238	1.14	18	Upadhyaya <i>et al.,</i> 2011 l
Chickpea	16,991	211	1.24	22	Upadhyaya and Ortiz, 2001
Pigeonpea	12,153	146	1.2	34	Upadhyaya <i>et al.,</i> 2006e
Groundnut	14,310	184	1.28	34	Upadhyaya <i>et al.,</i> 2002a
Finger millet	5,940	80	1.34	20	Upadhyaya <i>et al.</i> , 2010c
Foxtail millet	1,474	35	2.37	21	Upadhyaya <i>et al.,</i> 2011e

Table 1.2. Mini-core collections formed by Hari Deo Upadhyaya in chickpea, groundnut, pearl millet, pigeonpea, sorghum, and small millet.

means, variances, and frequency distributions, and the co-adapted gene complexes of the entire collections (in the case of the core collections) or core collections (in the case of the mini-core collections).

2. Climate-resilient Germplasm. Global warming is putting significant stress upon agricultural production and the nutritional quality of staple crops in many parts of the world. Southern Asia and Sub-Saharan Africa will be the most adversely affected regions, due to climate change and the variability effects. ICRISAT-mandated crops are widely grown and consumed in these regions (http://faostat.fao.org/site/567/default. aspx#ancor).

The identification and use of climate-resilient germplasm in crop breeding is the way forward to develop 'climate-smart' crop cultivars. Hari adopted a two-pronged strategy, first by working with ICRISAT researchers, and second by providing the seeds of several sets of minicore collections to NARS partners and working with them to evaluate these subsets for agronomic traits, including stress tolerance. The end result was the identification of several sources of resistance to abiotic and biotic stresses in chickpea and groundnut, with some accessions combining stress resistance and tolerance in good agronomic backgrounds (Upadhyaya *et al.*, 2013a, 2014d). Using a similar approach, Hari and his colleagues identified a number of drought-tolerant and salinity-tolerant germplasm accessions in finger millet and/or foxtail millet (Krishnamurthy *et al.*, 2014a, 2014b, 2016).

Blast (*Pyricularia grisea*) is a devastating disease in pearl millet and finger millet, which has many pathotypes. The work of Hari and his colleagues on screening the pathogenic variability led them to identify accessions that were resistant to multiple pathotypes in pearl millet (Sharma *et al.*, 2015), finger millet (Babu *et al.*, 2013b, 2015) and foxtail millet (Sharma *et al.*, 2014). Downy mildew (*Sclerospora graminicola* [Sacc.] Schröt) is a highly destructive and widespread disease of pearl millet, while grain mould and downy mildew (*Peronosclerospora sorghi*) are also important diseases of sorghum. Hari and his colleagues identified a number of accessions with resistance to multiple pathotypes in pearl millet (Sharma *et al.*, 2015) and sorghum (Sharma *et al.*, 2010, 2012). In addition, they identified some lines with good agronomic value, such as early maturity and resistance, and resistance and high seed/fodder yield potential, in both finger millet and pearl millet.

3. Seed Nutrient-dense Germplasm. Widespread micronutrient malnutrition in human beings, as a result of deficiency of iron (Fe), zinc (Zn)

and β -carotene, has an enormous socio-economic cost for society in the developing world (Stein, 2010). Hari saw the need to identify seed nutrient-dense (i.e. Fe, Zn) germplasm to support crop breeding. After evaluating the mini-core collections for two seasons, Hari identified a number of different germplasm sources with high seed Fe and/or Zn concentrations in groundnut (Upadhyaya *et al.*, 2012d), pearl millet (Rai *et al.*, 2015), sorghum (Upadhyaya *et al.*, 2016c), finger millet (Upadhyaya *et al.*, 2011d), and foxtail millet (Upadhyaya *et al.*, 2011e). Finger millet and foxtail millet are rich sources of seed protein and calcium (Ca), with some accessions in both of these crops showing exceptionally high protein and Ca contents (Upadhyaya *et al.*, 2011d, 2011e).

4. Bioenergy. Sorghum is a crop that is used for food, feed, and bioenergy. The stalks are rich in sugar (as measured by Brix). However, the stalk sugar content is greatly influenced by the environment and the crop stage at which the stalks are harvested. Hari evaluated the sorghum mini-core collection accessions for stalk sugar content for two post-rainy seasons under irrigated and drought-stressed conditions. He found that drought stress significantly increased the mean Brix by 12–27%. A few germplasm lines had significantly greater mean Brix (14.0–15.2%), but were agronomically inferior, while some others were agronomically comparable but with similar Brix, such as IS 33844 (Brix, 12.4%) (Upadhyaya et al., 2014a). This indicated that it is possible to select for even higher Brix content in agronomically superior genetic background in germplasm collections. IS 33844 is the local landrace Maldandi that was collected from Maharashtra, India, and it is the most popular sorghum cultivar that is widely grown under decreasing soil moisture conditions during the rabi (post-rainy) season in India. IS 33844 is tolerant to terminal drought and has excellent grain quality.

5. Germplasm Use in Breeding. Plant genetic resources are the basic raw materials for genetic progress, and they provide insurance against unforeseen threats to agricultural production. Hari firmly believes that the use of germplasm in crop improvement is one of the most sustainable ways to conserve valuable genetic resources and to broaden the genetic base of crops. Hari partnered with researchers globally to get these subsets (Tables 1–2) evaluated for stress tolerance, yield and seed nutritional traits, and collaborated with molecular biologists to dissect out the population structure and diversity in these representative subsets. This exercise resulted in the identification of several agronomically beneficial and genetically diverse germplasm sources that fulfil the needs of crop breeders. Armed with this valuable information, Hari

interacted with crop breeders at ICRISAT and elsewhere, to promote the use of such germplasm in breeding programs.

An analysis of the uptake of germplasm in crop improvement programs at ICRISAT showed that germplasm use has increased since the formation of the mini-core collections in some crops. For example, there was increased use (≈15% increase) of stress-tolerant chickpea germplasm during the 2000–2004 and 2005–2009 periods, while in recent years (i.e. 2010–2014), more emphasis (22% increase) has been on the use of germplasm that has agronomic (vield *per se*) and seed nutritional traits. The trend noted in groundnut was opposite: namely, more emphasis (17% increase) on the use of yield and quality-enhancing germplasm from 2000–2004, which changed to increased (42% increase) the use of stresstolerant germplasm from 2005–2009, with emphasis (46% increase) from 2010-2014 on stress tolerance, vield, and guality enhancement. All of this was possible because of the consistent efforts led by Hari and his colleagues (including those from ICRISAT and NARS countries) to use representative subsets in the identification of new sources of variation with agronomically beneficial traits, and to promote the breeders' willingness to use new germplasm as a resource in crop breeding.

6. On-farm Conservation and Use of Diversity. On-farm conservation and evaluation of genetic resources provides farmers with the opportunity to select germplasm adapted to their climate conditions. In addition, it also allows evolution of new genetic variants as a result of climate change and variability effects. This facilitates greater and more rapid dissemination of promising seeds among the farming community. Hari's collaborative work with NARS partners on the evaluation of core/mini-core collections of finger and foxtail millets, through a project on farmers' fields in Africa and Asia, provided the farmers with opportunities to access and appreciate the diversity of these neglected crops. Today, farmers own and cultivate some finger millet germplasm sources, such as IE 2440 and 4625 in Uganda, and IE 2872 and 4115 in Kenva, or finger millet (e.g. IE 3575, 4415, 4425, 6045, 6337) and foxtail millet (e.g. ISe 156, 1575) in India. In addition, the NARS partners from these countries have identified stress-tolerant germplasm that they are using in breeding programs to enhance the genetic potential of these crops.

7. Wild Relatives and Cultigen Genepool. Wild relatives and their derivatives are sources of variation for agronomic traits, which include stress tolerance, yield, and seed quality. Wild *Cicer* species, and particularly those from secondary and tertiary genepools that have high levels of resistance to stress tolerance, require vernalization and/or extended day-length treatments to synchronize their flowering with cultivated chickpea, for interspecific crosses. The use of vernalization and/or photoperiod response enabled Hari and his colleagues to introduce synchronized flowering into a few *Cicer* species, similar to that of cultivated chickpea (Sharma and Upadhyaya, 2015a). This contributes significantly not only to enhanced use of *Cicer* species for chickpea improvement, but also to improvements in the regeneration efficiency of *Cicer* species and their rapid generation turnover.

Cajanus albicans (Wight & Arn.) van der Maesen is a species from the secondary genepool of pigeonpea, and it is known for the long life of its large leaves (leaflet length, 4.4–6.8 cm; leaflet width, 3.1–5.8 cm). Hence, it is an important source of animal feed in semi-arid tropical regions. It possesses broader pods (9.6–15.0 mm) and high seed numbers (5–7 per pod), is resistant to abiotic (e.g. drought, salinity) and biotic (e.g. pod fly, pod wasp, *Alternaria* blight, sterility mosaic) stresses, and its high seed protein content (up to 32%) make it particularly attractive (Figure 1.1). Hari had to wait for about 500 days to see



Figure 1.1. *Cajanus albicans*, a wild species from a secondary genepool with many desirable characteristics, and a potential source for gene introgression in cultivated pigeonpea.

the flowering in *C. albicans*, and another 50–58 days to harvest the mature pods to complete the characterization data on this species. Notably, this produces partial fertile hybrids (Mallikarjuna *et al.*, 2011 and references therein), thus, providing a potential source to broaden the cultigen genepool in pigeonpea.

8. Gaps in Collections. Identifying gaps in collections and enriching collections with new sources is a critical function of genebank curators. Hari's work on gap analysis, using geo-referenced pearl millet landraces from Asian countries (5,768 accessions), revealed parts of the Bihar, Madhya Pradesh, Maharashtra, Rajasthan, and Uttar Pradesh provinces of India as the major geographical gaps in the world collection of pearl millet at ICRISAT (Upadhyaya *et al.*, 2010b).

His similar studies involving pearl millet landraces from southern and eastern Africa (3,750 accessions), and those from west and central Africa (6,434 accessions) also allowed Hari to identify regions in Africa that were not fully represented in ICRISAT collection (i.e. central Sudan and Tanzania, eastern Botswana, west and central Zambia, eastern and central Zimbabwe, southern Mauritania, Niger and Chad and northern Benin, Ghana, and Nigeria) (Upadhyaya *et al.*, 2009c, 2012f). Based on this gap analysis by Hari and requests from NARS partners, the ICRISAT regional genebanks in Africa organized collection missions and collected 6,625 new samples of mandate crops from west and central Africa and southern and eastern Africa regions. These, in my opinion, are important milestones achieved by Hari and his group that further enriched the germplasm collection at ICRISAT.

Hari's work further revealed that when landraces from the 5°-10°N latitude regions were grown at Patancheru, India, these flowered late and grew tall, and they also produced more tillers. Conversely, those from the 10°–15°N latitude regions had fewer tillers, but with long and thick panicles and larger seeds. Also, landraces from the 10°-15°S and 20°-25°S latitudes are good sources of resistance to bird damage (longbristled panicle). Furthermore, Hari found that the landraces of the lower latitude regions (<20°N and S) in both hemispheres are better sources of fodder types (i.e. high tillering, tall, long duration), while those from mid-latitude regions $(15^{\circ}-20^{\circ})$ in both hemispheres are good sources for enhancing productivity (i.e. early, long and thick panicle, large seeds). Similarly, landraces on both sides of the equator (i.e. within the 10°-20° latitudes) are highly sensitive to the photoperiod (>12.5 hours) and/or temperature $(<12 \degree C)$, while those from higher latitudes (20°-35°) in both hemispheres showed low sensitivity to both the photoperiod and temperature. The photoperiod and temperature

insensitive accessions are represented mostly from the mid-latitudes (15°–20°) in both hemispheres (Upadhyaya *et al.*, 2012e, 2014f).

B. Molecular Biology and Biometrics

1. Population Structure and Diversity. Understanding how diversity is structured so as to unlock its potential for crop improvement is an emerging area that has been made possible by rapid advances in the scale, robustness, and reliability of marker technologies, and the sharp fall in the unit costs of their deployment. Hari is probably one of the few CGIAR scientists who used Generation Challenge Program (www. generationcp.org) grants to develop global composite collections, which the molecular biologists at ICRISAT genotyped using high-throughput assays and simple sequence repeats (SSRs). Hari then used genotyping data and his statistical knowledge to form reference sets in chickpea. pigeonpea, groundnut, pearl millet, sorghum, finger millet and foxtail millet. These reference sets accounted for 78-95% of the allelic variations observed in global composite collections (Table 1.3). Genotyping of reference sets has revealed abundant allelic diversity that grouped the accessions into distinct clusters, with many of the alleles unique in a particular accession in each crop (Upadhvava et al., 2008a; Billot et al., 2013). This can be further explored, possibly to associate such allelic diversity with temporal and eco-geographical diversity, or in proprietary germplasm protection.

2. Genome-wide Association Mapping. The diversity panels of germplasm collections, such as the conventional core and mini-core collections, or genotype-based reference sets, are ideal germplasm resources for studying linkage disequilibrium and association mapping in crop plants. Identification of candidate genes associated with abiotic stress responses will accelerate breeding efforts that are aimed at enhancing productivity in drought-stressed environments.

Hari's collaborative work with molecular biologists led to the identification of 18 single nucleotide polymorphisms (SNPs) in chickpea reference accessions that were significantly associated with droughtavoidance root traits, carbon isotope discrimination, heat tolerance, harvest index, and 100-seed weight under drought-stressed conditions (Roorkiwal *et al.*, 2014a). Similar work using SSRs in groundnut reference accessions revealed significant marker-trait associations for drought-tolerance traits (e.g. chlorophyll readings, harvest index) and seed weight, under both well-watered and drought-stressed conditions (Pandey *et al.*, 2014).

 Table 1.3.
 Composite collections and reference sets formed by Hari Deo Upadhyaya in chickpea, groundnut, pearl millet, pigeonpea, sorghum, finger millet, and foxtail millet.

		Composite collection		Reference set				
Crop	Number of SSRs used			Number of accessions	Number of alleles [<i>n</i> (%)]	-] Reference		
Sorghum	41	3367	783	383	613 (78.3)	http://genebank.icrisat.org/GB_ReferenceSet/ ReferenceSet_Sorghum.aspx; Billot <i>et al.</i> , 2013		
Pearl millet	19	1021	230	300	218 (94.8)	http://genebank.icrisat.org/GB_ReferenceSet/ ReferenceSet_Pearlmillet.aspx		
Chickpea	48	2915	1683	300	1315 (78.1)	http://genebank.icrisat.org/GB_ReferenceSet/ ReferenceSet_Chickpea.aspx; Upadhyaya <i>et al.</i> 2008b		
Pigeonpea	20	952	197	300	187 (94.9)	http://genebank.icrisat.org/GB_ReferenceSet/ ReferenceSet_Pigeonpea.aspx		
Groundnut	21	852	490	300	466 (95.1)	http://genebank.icrisat.org/GB_ReferenceSet/ ReferenceSet_Groundnut.aspx		
Finger millet	20	959	231	300	206 (89.2)	http://genebank.icrisat.org/GB_ReferenceSet/ ReferenceSet_Fingermillet.aspx		
Foxtail millet	19	452	362	200	316 (87.3)	http://genebank.icrisat.org/GB_ReferenceSet/ ReferenceSet_Foxtailmillet.aspx		