

Plant
Breeding
Reviews



VOLUME 44

Edited by
IRWIN GOLDMAN

WILEY

PLANT BREEDING REVIEWS
Volume 44

Editorial Board, Volume 44

Jules Janick

Rodomiرو Ortiz

PLANT BREEDING REVIEWS

Volume 44

Edited by

Irwin Goldman

University of Wisconsin–Madison
Madison, WI, USA

WILEY

This edition first published 2021
© 2021 John Wiley & Sons, Inc.

All rights reserved. No part of this publication may be reproduced, stored in a retrieval system, or transmitted, in any form or by any means, electronic, mechanical, photocopying, recording or otherwise, except as permitted by law. Advice on how to obtain permission to reuse material from this title is available at <http://www.wiley.com/go/permissions>.

The right of Irwin Goldman to be identified as the author of this editorial material has been asserted in accordance with law.

Registered Office

John Wiley & Sons, Inc., 111 River Street, Hoboken, NJ 07030, USA

Editorial Office

The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK

For details of our global editorial offices, customer services, and more information about Wiley products visit us at www.wiley.com.

Wiley also publishes its books in a variety of electronic formats and by print-on-demand. Some content that appears in standard print versions of this book may not be available in other formats.

Limit of Liability/Disclaimer of Warranty

While the publisher and authors have used their best efforts in preparing this work, they make no representations or warranties with respect to the accuracy or completeness of the contents of this work and specifically disclaim all warranties, including without limitation any implied warranties of merchantability or fitness for a particular purpose. No warranty may be created or extended by sales representatives, written sales materials or promotional statements for this work. The fact that an organization, website, or product is referred to in this work as a citation and/or potential source of further information does not mean that the publisher and authors endorse the information or services the organization, website, or product may provide or recommendations it may make. This work is sold with the understanding that the publisher is not engaged in rendering professional services. The advice and strategies contained herein may not be suitable for your situation. You should consult with a specialist where appropriate. Further, readers should be aware that websites listed in this work may have changed or disappeared between when this work was written and when it is read. Neither the publisher nor authors shall be liable for any loss of profit or any other commercial damages, including but not limited to special, incidental, consequential, or other damages.

Library of Congress Cataloging-in-Publication data applied for

HB: 9781119716914

Cover Design: Wiley

Cover Illustration: © browndogstudios/Getty Images

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

Contents

Contributors	ix
1 Salvatore Ceccarelli: Plant Breeder, Mentor, and Farmers' Friend	1
<i>Stefania Grando</i>	
I. Biographical Sketch and Background	2
II. Research	6
III. The Man	17
IV. The Mentor and Inspirer	19
V. The Innovator	20
VI. The Supporter of National Programs	21
VII. The Advocate of Farmers	21
Acknowledgments	22
Literature Cited	22
Selected Publications of Salvatore Ceccarelli	25
2 Maize Cross Incompatibility and the Promiscuous <i>Ga1-m</i> Allele	31
<i>Major M. Goodman, Zachary G. Jones, G. Jesus Sanchez, and Jerry L. Kermicle</i>	
I. Historical Background	33
II. <i>Ga1</i> (Gametophyte-Factor 1), <i>Ga2</i> (Gametophyte-Factor 2), and <i>Tcb1</i> (Teosinte-Crossing-Barrier 1)	34
III. <i>Ga1-m</i> (Gametophyte-Factor 1-Male)	35
IV. Locus Composition	35
V. Gametophytic Selective Advantage	36
VI. Silk Reactions	36
VII. Mapping Gametophytic Loci	38
VIII. Geographical Distribution of <i>Ga1</i> Alleles	38
IX. Distribution of <i>Ga1</i> Alleles in Commercial Materials	41
X. Teosinte and Maize	41
XI. Popcorn and Organic Isolations	43
XII. Exceptionally Strong Cross-Incompatible Sources Within Maize	44

XIII.	Cautions Concerning Use of <i>Ga1-m</i>	45
XIV.	Genetic Modifiers	46
XV.	Molecular Characterizations	47
XVI.	Recent Conclusions	47
XVII.	Practical Use of Pollen-Blockers	47
XVIII.	Future Prospects	50
	Acknowledgments	54
	Literature Cited	54
3	Development of the Genetically Modified Innate[®] Potato	57
	<i>Craig M. Richael</i>	
I.	Introduction	58
II.	Innate [®] Generation 1 Potato Varieties	65
III.	Innate [®] Generation 2 Potato Varieties	71
IV.	Future Innate [®] Potato Varieties	74
V.	Conclusions	75
	Literature Cited	76
4	<i>Cucumis sativus</i> Chromosome Evolution, Domestication, and Genetic Diversity: Implications for Cucumber Breeding	79
	<i>Yiqun Weng</i>	
I.	Introduction	81
II.	Chromosome Evolution in the Making of Cucumber	83
III.	Chromosome Evolution During Cucumber Domestication	86
IV.	Diffusion of Cucumber to the World From its Center of Diversity and the Formation of Market Groups	90
V.	Types of Cucumbers: Fresh Market vs Processing	92
VI.	Genetic Diversity and Population Structure of Cucumber Collection	94
VII.	Genetic Basis of Domestication-Related Traits in Cucumbers	96
VIII.	Chromosome Evolution, Domestication, and Genetic Diversity: Implications for Cucumber Breeding	101
	Acknowledgments	104
	Literature Cited	104
5	Freelance Plant Breeding	113
	<i>Carol S. Deppe</i>	
I.	Introduction	115
II.	Evolution of a Freelance Plant Breeder	116

III.	Who and Where	119
IV.	How Freelancers Learn the Plant Breeding Trade	130
V.	Why—Motivations and Values	136
VI.	Crops	139
VII.	Goals	146
VIII.	Methods	151
IX.	Sources of Germplasm	161
X.	Economics of Freelance Plant Breeding	164
XI.	Freelance Plant Breeding That Doesn't Fit Commercial Models	174
XII.	Open Source Seed Initiative and Freelance Plant Breeding	176
XIII.	Future Prospects	180
	Acknowledgments	183
	Literature Cited	183
6	Meadowfoam Breeding	187
	<i>Jennifer G. Kling</i>	
I.	Introduction	189
II.	Botany and Taxonomy of <i>Limnanthes</i>	190
III.	Meadowfoam Breeding Organizations	195
IV.	Seed Production Requirements	197
V.	Greenhouse and Field Plot Techniques	201
VI.	Selection Methods	206
VII.	Breeding Populations and Molecular Resources	216
VIII.	Meadowfoam Seed Oil	222
IX.	Biotic Constraints	225
X.	Glucosinolates and Other Seed Meal Components	230
XI.	Meadowfoam in Cropping Systems	234
XII.	Conclusions and Future Directions	235
	Acknowledgments	237
	Literature Cited	237
7	Reconsidering Approaches to Selection in Winter Squash Improvement: Improved Quality and Breeding Efficiency	247
	<i>Michael Mazourek, Christopher Hernandez, and Jack Fabrizio</i>	
I.	Introduction	249
II.	Genomic Resources for Winter Squash Improvement	251
III.	Insight into Winter Squash Metabolism Related to Fruit Quality	253
IV.	Winter Squash Quality Phenotyping	258

V. Squash Breeding Schemes	260
VI. Applying Genomic Selection in <i>Cucurbita</i>	264
VII. Conclusion	268
Acknowledgments	268
Literature Cited	269
8 Development of the Arctic® Apple	273
<i>Evan Stowe and Amit Dhingra</i>	
I. Introduction	274
II. Genetic Engineering of Apple	275
III. Development and Evaluation of the Arctic® Apple	280
Literature Cited	292
Author Index	297
Subject Index	305

Contributors

Amit Dhingra

Washington State University, Pullman, WA, USA

Carol S. Deppe

Fertile Valley Seeds, Corvallis, OR, USA

Jack Fabrizio

Cornell University, Ithaca, NY, USA

Stefania Grando

Ascoli Piceno, Italy

Major M. Goodman

North Carolina State University, Raleigh, NC, USA

Christopher Hernandez

Cornell University, Ithaca, NY, USA

Zachary G. Jones

Corteva Agriscience, Windfall, IN, USA

Jerry L. Kermicle

University of Wisconsin–Madison, Madison, WI, USA

Jennifer G. Kling

Oregon State University, Corvallis, OR, USA

Michael Mazourek

Cornell University, Ithaca, NY, USA

Craig M. Richael

Simplot Plant Sciences, J.R. Simplot Company, Boise, ID, USA

G. Jesus Sanchez

University of Guadalajara, Guadalajara, Mexico

Evan Stowe

Washington State University, Pullman, WA, USA

Yiqun Weng

USDA-ARS Vegetable Crops Research Unit,
University of Wisconsin–Madison, Madison, WI, USA

Salvatore Ceccarelli: Plant Breeder, Mentor, and Farmers' Friend

Stefania Grando
Ascoli Piceno, Italy

ABSTRACT

Salvatore Ceccarelli is a geneticist, plant breeder, innovator, mentor, and farmers' friend with over 50 years of dedicated work to agricultural research for development. His major contributions have been in the development of breeding methodologies for barley and other important crops for the livelihoods of resource poor farming community in marginal environments. After a career in academia in Italy, in 1980 Salvatore moved to ICARDA, based in Aleppo, Syria, initially as a forage breeder and later as a barley breeder and manager of the barley improvement program until he left the center over 30 years later. It was while at ICARDA that he developed and adopted a new breeding strategy, based on decentralized selection for specific adaptation, a drastic departure from the dominant philosophy in plant breeding based on wide adaptation. A further development of this strategy was the idea of PPB, initially implemented in Syria and later extended to other Middle East countries, North Africa, Horn of Africa, and more recently to Italy, accompanied by a continuous refinement in experimental techniques and statistical analysis. When Salvatore recognized the limitation of PPB to ensure a continuous flow of new material to farmers, he proposed the use of EPPB to adapt crops to their specific environment and to climate change, while providing diversity for farmers to manage. His breeding program distributed new barley material to farmers worldwide and to numerous research institutions for basic and applied research, and generated information and methodologies to establish breeding programs for difficult and stressful environments. He has published over 270 scientific articles and been invited to countless national and international events. He has collaborated with researchers and mentored breeders and

technicians from around the world, helped establishing participatory breeding programs in several countries, supervised 25 MSc and PhD students, and conducted courses on participatory and evolutionary plant breeding in numerous countries. In 2017, he returned to Italy and continued to work as a consultant in national and international projects, which brings that decision-making process and seed ownership back in the hands of farmers. He is currently involved in projects in Bhutan, Ethiopia, Iran, Jordan, Nepal, Uganda, and Europe.

KEYWORDS: Decentralized breeding, participatory breeding, evolutionary breeding

OUTLINE:

- I. BIOGRAPHICAL SKETCH AND BACKGROUND
- II. RESEARCH
- III. THE MAN
- IV. THE MENTOR AND INSPIRER
- V. THE INNOVATOR
- VI. THE SUPPORTER OF NATIONAL PROGRAMS
- VII. THE ADVOCATE OF FARMERS
- ACKNOWLEDGMENTS
- LITERATURE CITED
- SELECTED PUBLICATIONS OF SALVATORE CECCARELLI

ABBREVIATIONS

BLUP	best linear unbiased predictor
EP	evolutionary population
EPB	evolutionary plant breeding
EPPB	evolutionary participatory plant breeding
GEI	genotype x environment interactions
ICARDA	International Center for Agricultural Research in the Dry Areas
IFAD	International Fund for Agricultural Development
ILRI	International Livestock Research Institute
PPB	participatory plant breeding

I. BIOGRAPHICAL SKETCH AND BACKGROUND

Dr Salvatore Ceccarelli was born on September 7, 1941, in Fiume, today Rijeka in Croatia. At the outbreak of World War II, the family moved to central Italy, where he grew up with solid values of respect, personal responsibility, and accountability, and a strong commitment to perform to the best of his capabilities in the studies and all he was doing. He

also developed a profound sense of curiosity and a desire to discover new things and come up with new ideas.

After graduating from high school with the highest grades, Salvatore decided to undertake agricultural studies and enrolled in the degree course in agricultural sciences at the University of Perugia. He studied a range of subjects related to agricultural sciences from soil physics and chemistry, to biochemistry, botany, agronomy, animal and crop husbandry, hydrology, and plant breeding. In 1964, he graduated in Agricultural Sciences with the dissertation “Morphological traits and nutritive value of *Brachypodium pinnatum* L.”

From 1965 to 1967 he attended the Advanced Specialization Course on Applied Genetics at the Institute of Genetics of the University of Milan. The director of the Institute was Professor Claudio Bargozi, an Italian biologist and geneticist who had promoted genetic research in Italy since the early 1960s. During this period, Salvatore’s scientific preparation focused on genetics with particular attention to quantitative genetics, selection theory, mutation, cytogenetics, statistics, and advanced plant breeding. Salvatore refers often to this period as fundamental to setting the basis for his scientific formation and as very inspirational to developing his research, teaching, and mentoring approaches. In 1967, he obtained a PhD in Applied Genetics with a dissertation on “Biometrical analysis of natural populations of *Trifolium pratense*” (Ceccarelli 1968).

After serving in the military (at that time, service was unavoidable), Salvatore joined the Institute of Plant Breeding of the University of Perugia as assistant professor in plant breeding. To further strength his scientific knowledge, Salvatore spent a sabbatical year, from 1973 to 1974 at the Genetics Department of North Carolina State University in Professor Charles W. Stuber’s laboratory.

In 1979, while attending a meeting of the Italian Society of Agricultural Genetics, he was introduced by Professor Scarascia Mugnozza to the International Agricultural Research Centers, and in 1980 he joined the International Center for Agricultural Research in the Dry Areas (ICARDA) as senior scientist in the Pasture and Forage Improvement Program. Salvatore requested a two-year study leave from the university, keeping open the possibility of asking for an extension, but when he decided to do so, he encountered difficulties, and by the end of 1982 he went back to the University of Perugia, Italy. The following year he became associate professor in Plant Genetic Resources, and then in 1986 professor in Agricultural Genetics,

Shortly after his return to Italy, Salvatore became member of a Committee of the International Cooperation of the Italian Ministry of

Foreign Affairs, in charge of advising how the funds in the CGIAR system should be invested. In that role, he was invited to ICARDA for a visit that would have marked a big change in his professional and personal life. Despite his career advancements at the University of Perugia, Salvatore was very enthusiastic about his experience at ICARDA and was convinced that his knowledge could serve not only as a basis for becoming an author specialized in the field but also to make a difference in the lives of the poor and marginalized.

After some negotiation, in 1984 Salvatore again joined ICARDA as a barley breeder, a position he held until he retired in 2006. His association with the center continued until 2015 as a consultant. This period has been certainly the most prolific of his scientific career, characterized by innovative research approaches, which included the use of what in the mid- to late-1980s was considered “unconventional” germplasm. Salvatore advocated the use of landraces and wild relatives in breeding barley for adaptation to stressful environments, when most of the breeding programs around the world would consider such material as “genetic garbage.” He also helped to develop a decentralized breeding approach that later evolved in a participatory breeding and more recently in evolutionary breeding.

His breeding program not only produced new barley material for distribution worldwide but also, more notably, generated information and methodologies to establish breeding programs that were facing difficult and stressful environments (Figure 1.1). The barley breeding program at ICARDA provided germplasm to numerous research institutions for both basic and applied research (some examples are Baum et al. 2003, Russell et al. 2003, Grando et al. 2005, Fufa et al. 2007, Russell et al. 2011, Varshney et al. 2010, 2012). Several of Ceccarelli’s papers from this period were a source of inspiration for a number of breeders in developing countries and have been used in breeding classes in US and European universities.

Ceccarelli received the 2000 CGIAR Chairman’s Excellence in Science Award for Outstanding Scientific Article on a methodological study on participatory barley breeding; the 2014 Farmers’ Friend award designed and promoted by the Girolomoni Cooperative to enhance the farmers activity in Italy and around the world; and the 2015 Bologna Sustainability and Food International Award.

In 2017, he returned to Italy and continued to work as a consultant to both national and international projects, promoting the development of breeding methodologies, such as evolutionary plant breeding, that will bring the decision-making process and seed ownership back in the hands of farmers.



Fig. 1.1. Salvatore in the field (Stefania Grando). Source: Stefania Grando.

As of 2019, Ceccarelli had published more than 270 scientific articles, of which over 150 appear in peer-reviewed journals. He has been invited to countless national and international events, spanning from local gatherings of organic farmers to international conferences.

Over the span of his career, he has collaborated on an ongoing basis with researchers from countries such as Algeria, Armenia, Bolivia, Brazil, Bhutan, Chile, Colombia, Cuba, Ecuador, Egypt, Ethiopia, Eritrea, the Philippines, India, Iran, Iraq, Kenya, Jordan, Libya, Mexico, Morocco, Nepal, Pakistan, Peru, Russia, Syria, Tunisia, Turkey and Uganda. He also worked occasionally with researchers in Afghanistan, China, Vietnam, South Korea, Spain, France, Germany, Great Britain, the United States, Denmark, Finland, Australia, The Netherlands, and Italy.

He has mentored several breeders and technicians from around the world, helped establishing participatory breeding programs in several countries, supervised 25 MSc and PhD students, and conducted several courses on participatory and evolutionary plant breeding in Australia, Bhutan, China, Eritrea, Ethiopia, Nepal, India, Iran, Jordan, Philippines, South Africa, Uganda, and Yemen.

He is currently involved in projects in Bhutan, Ethiopia, Iran, Jordan, Nepal, Uganda, and Europe. If anyone asks him when he will eventually

retire, he answers, quoting Professor Miguel Altieri: “you can retire from a job not from a passion.”

II. RESEARCH

A. Breeding for Low-Input, Stress Prone Environments – From Conventional to Decentralized Barley Breeding Program at ICARDA

Plant breeding has been beneficial to farmers in favorable environments and to those who could profitably ameliorate the environment by the use of inputs. It has been less beneficial to the resource-poor small-holder farmers who cannot modify their environments by the use of inputs (Byerlee and Husain 1993, Eyzaguirre and Iwanaga 1996, Trutmann 1996) and have not known the benefits of the “green revolution” (Francis 1986, Pimbert 1994).

Given their success in favorable environments, plant breeders have tried to solve the problems of farmers living in unfavorable environments by applying the same methodologies and breeding philosophy used in favorable, high-potential environments, without considering the limitations associated with genotype–environment interactions (GEI). This has led to almost negligible progress for crops grown in unfavorable environments, often attributed to the difficult nature of the target environment (Blum 1988) with a consequent widespread habit of conducting selection under favorable conditions and sometimes only final testing in the target environments.

GEIs are considered to be among the main factors limiting response to selection and therefore the efficiency of breeding programs (Ceccarelli 2015), and they become important when the rank of breeding lines or varieties is different for different environments. Plant breeders have tried to avoid GEIs by selecting for widely adapted varieties; however, breeders can also exploit GEIs by selecting for specific adaptation (Ceccarelli 1989). This is particularly relevant when breeding crops for adaptation to unfavorable environments grown by resource-poor farmers.

In many developing countries, barley is a typical crop grown in difficult environments because of either climate stresses, low soil fertility, or both. In these areas, barley is often the only possible rainfed crop and the last crop possible before the steppe, and the desert, with a high risk of crop failures, and therefore there is low or no use of external inputs.

To generate valuable germplasm for these conditions, in the mid-1980s Ceccarelli challenged several concepts that characterized conventional

plant breeding programs based on the assumption that breeding for environments with unpredictable and variable stresses is too slow and difficult. Many conventional plant breeders argued that the target was too difficult to define and heritabilities were too low to achieve significant results. As a result, the majority of the breeding for crops grown in stressful environments has been conducted using the same approach that was successful in favorable areas.

Breeding programs around the world share some of the following concepts: (a) selection has to be conducted under the optimum conditions of research stations where environmental influences can be controlled, error variances are smaller and responses to selection are higher (Ceccarelli et al. 1992, 1994); (b) cultivars must be genetically homogeneous and widely adapted (Ceccarelli 1989), locally adapted landraces must be replaced on the assumption that are low yielding and susceptible to diseases; (c) seed of improved varieties must be approved and dissemination through seed certification schemes and often inaccessible seed-production organizations; (d) the farmers or other end-users are only involved in the final stage of field testing of few promising lines, only to verify whether the choices made by others are suitable or not for them.

When breeders started questioning those concepts, it was found that: (a) selection under the optimum conditions of research stations produces varieties that are superior to local landraces only under improved management, not under the unfavorable conditions of resource-poor farmers, resulting on few or any new varieties grown by farmers in difficult environments; (b) resource-poor farmers in unfavorable environments tend to maintain genetic diversity by growing different crops or different and heterogeneous varieties of the same crop to retain adaptability (Simmonds 1962); diversity and heterogeneity are used to diffuse the risk of a total crop failure due to environmental variation; (c) resource-poor farmers often rely on their own or neighbors' seed and seldom rely on formal seed-supply systems (Almekinders et al. 1994); (d) when farmers participate in the selection process, their selection criteria may differ from those of the breeder (Sperling et al. 1993, Ceccarelli et al. 2000, 2001).

Because for so long those conventional plant breeding concepts were not questioned, the lack of adoption of new varieties was often attributed to the ignorance of farmers, the malfunctioning of extension services, and the inefficiency of seed systems – the hypothesis that the breeder might have bred the wrong varieties was rarely considered.

Ceccarelli demonstrated that breeding to improve the productivity of a low-input crop such as barley, grown in marginal environments

by resource-poor farmers with limited or no access to inputs, is indeed possible provided is conducted using strategies and methodologies that little have in common with those used in breeding for favorable environment (Ceccarelli 1994, Ceccarelli and Grando 1996). He then developed a methodological package that comprised the use of four strategies:

1. Decentralized selection for specific adaptation in the target environment
2. Locally adapted and often neglected germplasm, such as landraces and wild relatives
3. Proper plot techniques and experimental designs to control environmental variation
4. Participation of farmers in selection in later stages

This resulted in the production of varieties adapted to the environments in which they must be grown. This approach has also been adopted by other international and national plant breeding programs (Ceccarelli et al. 1994).

This was a drastic departure from the dominant philosophy in plant breeding, based on the production of varieties that, with the input of water, fertilizers, pesticides and herbicides, hence with major environmental changes, were able to provide high production with a high cost in terms of environmental damage and genetic erosion.

International breeding programs usually aim to assist national programs to increase agriculture production through the development of superior varieties. This has been traditionally done through large breeding programs that develop and distribute fixed or semi-fixed lines selected with average good performance across environments, often high-input research stations. This approach has favored the distribution of widely adapted material, excluding the use of locally adapted germplasm. Although international breeding programs distributed segregating populations, those were the same for all countries and were not targeted to a specific environment.

To fully exploit specific adaptation and make a positive use of GEI, Ceccarelli et al. (1994) proposed that international breeding programs decentralize most of the selection work to national programs by gradually replacing the traditional distribution of breeding material with targeted segregating populations. This will reduce the risk of useful material being discarded simply because it had not been tested in the target environment.

In 1991, ICARDA's barley improvement program initiated a gradual process of decentralization of selection work to Morocco, Algeria, Tunisia, and Libya (Ceccarelli et al. 1994). The process was extended to Iraq in

1992, to Egypt in 1995, and later to Ethiopia, Eritrea, Yemen, Uzbekistan, Kazakhstan, and Armenia. An important feature of the decentralization process was the active role of national program scientists in identifying the parental material, designing of crosses, deciding on material to be selected, and adapting the process to their own needs and capabilities.

While national programs were responding with enthusiasm to the idea of decentralization, Ceccarelli and co-workers recognized that decentralization *per se* may not respond to the needs of resource-poor farmers in unfavorable environments. In fact, the process, as originally designed, was from ICARDA's research stations to the research stations of the national programs that often did not represent unfavorable environments. However, the most serious limitation of decentralized selection for specific adaptation to unfavorable environments is in the large number of potential target environments. Moreover, while decentralized selection is a powerful methodology to fit crops to the physical environment, crop breeding-based decentralized selection can still miss its objectives if it does not consider the producers and the end-users of the crop (Ceccarelli et al. 2000, 2001). Therefore, in 1995, Ceccarelli proposed decentralizing the barley breeding program from research stations to farmers' fields, and to have farmers participating in the very early stages of selection as a solution to fit the crop to a multitude of target environments and users' preferences (Ceccarelli et al. 1996). This allowed for the development of methodologies to implement a decentralized-participatory barley breeding program.

B. From Decentralization to Participatory Plant Breeding

The idea of farmers' participation in the development of new technologies can be traced back to the inspiring paper by Rhoades and Booth (1982), introduced as "the farmer-back-to-farmer" model. The paper, together with the one that followed (Rhoades et al. 1986), emphasized the importance, when developing a new agricultural technology, of involving the farmers from the start, rather than ignoring them and then handing over a ready-to-use technology.

Although plant breeding programs differ from each other depending on the crop, the facilities, and the breeder, they all have in common three main stages defined by Schnell (1982):

1. Generate genetic variability (includes selection of parents, making crosses, choice of type and number of crosses, induced mutation, introduction of germplasm from genebanks, other breeding programs, and farmers).

2. Select the best genetic material within the genetic variability created or acquired in stage 1.
3. Test breeding lines emerging from stage 2. The number of crosses generated at the beginning of each cycle can vary from a few hundred to several thousand.

During stages 2 and 3, genetic variability is gradually reduced, and breeding lines are identified. While the number of breeding lines decreases, the amount of seed per line increases, as does the number of locations in which the material can be tested (Ceccarelli 2009). A breeding program handles considerable amounts of material on a yearly basis, whether a new cycle starts every year, or twice a year. Other important stages in a breeding program are social targeting and demand analysis (Weltzien and Christinck 2009), and dissemination of cultivars (Bishaw and van Gastel 2009).

A breeding program becomes participatory when farmers as well as other partners, such as extension staff, seed producers, traders, and final users participate in the development of a new variety. Participatory plant breeding (PPB) is expected to produce varieties that are targeted to the right users, respond to real needs, concerns and preferences, and have a high likelihood of being adopted (Bellon et al. 2006).

A decentralized PPB program follows the same process as described earlier, with three main differences:

1. Most of the process takes place in farmers' fields.
2. The decisions are taken jointly by farmers, breeders, and other partners.
3. The process can be implemented in several locations and involve a large number of farmers with different breeding material (Ceccarelli and Grando 2005).

PPB replaced the traditional linear sequence of scientist→extension→farmer with a team approach including farmers, scientists, extension agents, and other end-users.

In September 1995, Ceccarelli and coworkers met with a group of farmers in Jurn El Aswad, a village in the Raqqa province in Northeast Syria. The idea was to explore the feasibility of transferring most of the selection work from ICARDA's research stations to farmers' fields and of having farmers participating in selection and other major decisions. The farmers of Jurn El Aswad showed a strong interest in the proposal, so eight more villages, representing different agro-climatic environments and different ethnic groups, were visited. The first experiment,

comprising 200 extremely variable breeding accessions (from modern varieties to landraces), was designed with the objective of exposing these communities to as much barley diversity as possible (Ceccarelli et al. 2000). The set was planted in the fall of 1995.

This methodology, successfully implemented initially in Syria and in several other countries, has been described by Ceccarelli and Grando (2005, 2007), Mangione et al. (2006), and Ceccarelli et al. (2007). Crosses were done in stations, where also the F_1 and F_2 were grown, and then from the F_3 the bulks were tested in farmers' fields over a period of four years. The number of new entries shared every year with farmers varied from about 50 in Egypt, to 75 in Algeria and Eritrea, to 165 in Jordan and Syria. Breeding material was selected from one year to the next based on both qualitative and quantitative observations made by both farmers and breeders. Data collected were subject to statistical analysis, and a summary tables were provided to the farmers for final selection. PPB trials were implemented in a way that could generate the same amount and quality of data as in a conventional breeding program, plus additional information on farmers' preferences.

The methodology evolved in the course of time, while maintaining the fundamental aspects of a breeding program. The trials have been shaped and, with time, modified, in consultation with farmers, who indicated the preferred type of germplasm and the preferred plot size based on the land area they could make available. The trials also evolved as a consequence of the progress in experimental designs and statistical analysis made by conventional breeding programs. Over the years, the augmented design was replaced with the partially replicated design; the randomized block design with the row and column design allowing for spatial analysis. Eventually, optimized randomization was also introduced. A key feature of the PPB program Ceccarelli developed was the maintenance of a robust scientific basis. All the data generated by the program were amenable to the most advanced statistical analyses, such as spatial analysis that generated BLUPs (best linear unbiased predictors), which were tabulated and translated in the local language. The tables were then made available to farmers for the final selection. In this way, farmers had access to the same quality and quantity of information usually available to breeders for the final selection. Breeders participated also in the final selection, with the objective of answering questions and recording farmers' choices. This, in turn, would maximize the efficiency of their selection.

He demonstrated that farmers' selection was mostly influenced by the environment, with a large preference for landraces in drier locations. Farmers were able to handle a large number of breeding materials

(this was in contrast to scientists' belief that farmers can only handle a small number of lines); farmers were slightly more efficient than the breeder in identifying the highest yielding entries, while the breeder was more efficient than the farmers in selecting in the research station located in a favorable environment, but less efficient than the farmers in a research station located in a unfavorable environments. Ceccarelli et al. (2000) indicated that "it is possible to transfer the responsibility of selection to farmers in their fields, that farmers can handle selection choices among a large number of lines, and that farmers' selections are objectively high yielding and yet different from one location to another." The paper received the 2000 CGIAR Chairman's Excellence in Science Award for Outstanding Scientific Article.

The barley participatory program at ICARDA was initially scientist-driven, as the scientists introduced it to the farmers and decided the type of germplasm to use. However, as it should happen in a truly participatory program, the roles soon changed. The farmers gradually started influencing the methodology on how to organize field selection, suggesting suitable scoring methods, and choosing the type of germplasm, and organizing the harvesting. PPB considerably enriched farmers' knowledge, improved their negotiation capability, and enhanced their dignity (Soleri et al. 2002).

Even though the PPB programs were relatively young, by 2007, Ceccarelli had promoted, developed, and fully implemented PPB programs on different crops in partnership with farmers and various institutions in Syria, Jordan, Egypt, Eritrea, Yemen, Morocco, Tunisia and Algeria, and Iran (Ceccarelli and Grando 2009). In Syria, the PPB program started in 8 villages and reached 24 villages covering the majority of the barley-growing areas in Syria; each year, over 170 trials were planted, and an average of more than 200 farmers were involved in the selection process. By the same year, 19 new barley varieties were identified and adopted by farmers in Syria, one in Jordan, five in the drier areas of Egypt, three in Eritrea, and two in the highlands of Yemen. In addition, in Yemen farmers identified and adopted two lentil varieties (Ceccarelli and Grando, 2009).

In Syria, for the first time, adoption took place in low-rainfall areas (Ceccarelli and Grando 2009), where farmers started naming new varieties. Moreover, different varieties were selected in different areas within the same country, thus increasing crop biodiversity (Ceccarelli et al. 2001). For example, in Syria, the number of varieties selected after three cycles of selection was four to five times higher than the number of varieties entering the final test in the conventional breeding program.

To achieve the benefits of PPB, as described earlier, the seed of the new varieties has to become available to farmers in sufficient amounts. Ceccarelli and coworkers implemented a seed production based on the integration between the formal and the informal seed systems. Through the provision of basic equipment and of farmers' training on quality seed production, village-based seed production was promoted (Ceccarelli 2012).

In all countries where PPB was implemented, policy makers and scientists showed mounting interest in the ability of PPB to generate relevant results quicker.

Ceccarelli's work on PPB received a specific mention in the World Development Report 2008: Agriculture for Development (World Bank 2007). Here "it was found that participatory plant breeding and varietal selection speeds varietal development and dissemination to 5–7 years, half the 10–15 years in a conventional plant-breeding program" and "participatory plant breeding is now paying off with strong early adoption of farmer-selected varieties that provide 40 percent higher yields in farmers' fields." Eventually, PPB and decentralized participatory research were among the key recommendations in the report of the special rapporteur on the right to food to the United Nations (De Schutter 2014).

One of the most notable impacts of Ceccarelli's PPB programs was of a psychological and ethical nature (Figure 1.2). When farmers were asked which benefits they had receive from PPB, they often reported that their quality of life had improved, that they felt happier as a consequence of changing their role from passive receivers to active protagonists, that their opinion was valued, and that, as an Eritrean farmer said: "PPB has taken science back into my own hands."

Unfortunately, despite the positive reaction of the farmers and its solid scientific basis (Ceccarelli 2015), PPB suffered of lack of institutionalization, with some notable exceptions. Some countries such as Jordan, Algeria, and Yemen adopted PPB as part of their national breeding programs. In Jordan and Algeria, PPB is continuing while in Yemen the war has not allowed its continuation.

C. From PPB to Evolutionary Participatory Plant Breeding

The proposal of participatory research in general came from social scientists who also conducted early PPB experimentation often not involving breeders and other biophysical scientists. That could be one of the reasons explaining why professional breeders did not receive the idea of PPB with enthusiasm. In parallel, mainly social scientists developed a new vocabulary that described, for example, PPB as being



Fig. 1.2. Salvatore discussing with Eritrean farmers (Mohamed El Hadi Maatougui).
Source: Stefania Grando.

“conventional or contractual, consultative, collaborative, collegial, farmer experimentation” (Sperling et al. 2001). This gave the impression of PPB as a static phenomenon – whereas field experience demonstrated that as the farmers become more empowered, the process itself evolves further (Desclaux et al. 2012).

This resulted in a confidence gap, and several breeders felt that the proponents of PPB were driven by a social agenda, while the technical issues related to breeding were subordinate (Ashby 2007). A review of PPB programs by Ceccarelli and Grando (2019a) reported that there are no scientific objections raised against PPB, but the major obstacle to institutionalizing PPB lies in the difficulties of sharing power, authority, and control in the private and the public sectors. One of the major consequences of the lack of institutionalization of PPB is that participating institutions can suddenly interrupt the collaboration due to change of priorities and/or lack of funds, thus interrupting the flow of new material to farmers and the entire process.

To overcome that problem, Ceccarelli proposed using evolutionary participatory plant breeding (EPPB), which combines evolutionary plant breeding (EPB) and PPB. EPPB retains many of desirable features of PPB, such as farmers’ empowerment, recognition and utilization

of indigenous knowledge and breeding for specific adaptation, while providing farmers with large genetic diversity for them to manage over time (Murphy et al. 2005, Ceccarelli 2017). The science of EPB is based on research initiated by Harlan and Martini (1929), while Suneson (1956) used the term “evolutionary populations” for the first time and defined EPB as a method that “requires assembly and study of seed stocks with diverse evolutionary origin, recombination by hybridization, bulking of the F_1 progeny and subsequent prolonged mass selection for mass sorting of the progeny in successive natural cropping environments.” Despite the solid science behind it, EPB has been rarely used. EPB becomes participatory when the evolutionary populations (EP) are planted in farmers’ fields and the farmers use them as source populations to select new varieties.

Ceccarelli has been promoting EPPB to bring crop genetic diversity back into farmers’ fields and into farmers’ hands – taking advantage from the collaboration with the institutions without necessarily being dependent on it, as farmers can assemble and manage EPs by themselves. The EPs are planted and harvested year after year, thus evolving to become progressively better adapted to the environment in which they are grown. While they are evolving, farmers, or farmers and breeders together, can use them as source for the development of varieties. As climatic conditions vary from one year to the next, the genetic makeup of the population will fluctuate to better adapt to those conditions that will gradually become more frequent (Ceccarelli 2014, 2019).

In 2008, Ceccarelli constituted a barley EP resulting from mixing an equal number of seeds of nearly 1600 F_2 obtained by crosses done at ICARDA. The EP was deployed in a number of locations in Syria, Jordan, Iran, Algeria, Egypt, and Eritrea. In Jordan, Algeria, Iran, and Syria, farmers are still growing the barley EP. “Despite the difficult circumstances in Syria, I am still cultivating some of the varieties that we have selected together [with Dr. Ceccarelli] in addition to the population composed of seeds of different types. During the bitter displacement journey, these varieties have been multiplied and grown over large areas” (Mahmood Shlash, farmer in Aleppo Province, Syria, translated from Arabic by Adnan Al Yassin).

The following year, with the support of wheat breeders at ICARDA, Ceccarelli established one EP of bread wheat and one of durum wheat. Since then Ceccarelli contributed to the establishment and diffusion of EPs of different crops that are currently being grown by farmers in Jordan, Ethiopia, Iran, Italy for cereal crops (barley, bread and durum wheat, and rice), grain legumes (common bean), and horticultural crops (tomato and summer squash). In informal interviews during meeting

with scientists, farmers growing these populations have reported higher crop yields and lower levels of weed infestation, disease presence, and insect damage, as compared to the uniform varieties they used to grow.

Iranian and Italian farmers growing EPs of bread wheat and durum wheat have begun marketing bread and pasta from EPs flour and semolina (Ceccarelli and Grando 2019b). Anecdotal evidence from farmers growing wheat EPs in Italy shows that these EPs not only have greater yield stability, but also the bread and the pasta have more aroma and higher quality. Recent experimental evidence has shown that, with evolutionary breeding, it is possible to combine high yield and stability (Raggi et al. 2017).

In 2018, the International Fund for Agricultural Development (IFAD) approved a four-year IFAD project, “Use of genetic diversity and evolutionary plant breeding for enhanced farmer resilience to climate change, sustainable crop productivity, and nutrition under rainfed conditions.” Ceccarelli, as consultant to Bioversity International, has been enthusiastically promoting EPPB in Uganda and Ethiopia in Africa, Jordan and Iran in the Near East, and Nepal and Bhutan in South Asia (Figures 1.3 and 1.4). EPs of wheat, barley, rice, and beans have been designed and are being tested in a number of villages in the six countries.

Ceccarelli has shown that it is indeed possible to organize plant breeding programs, and therefore to guide plant evolution, in a way that combines modern science and local knowledge. Over the years, working with different crops in a number of countries, Ceccarelli has



Fig. 1.3. With a rice farmer in Bhutan (Dejene Mengistu, Bioversity International). Source: Stefania Grando.



Fig. 1.4. Salvatore with Ethiopian farmers (Stefania Grando). Source: Stefania Grando.

demonstrated that farmers are excellent partners and they readily share their knowledge with scientists. Participatory and evolutionary plant breeding can increase crop biodiversity, promote the use of landraces and wild relatives, and allow crops to continue to evolve – and therefore are the most dynamic way to cope with climate changes. Participatory and evolutionary plant breeding integrates greater production of more readily available and accessible food with various ecosystem services – including increases in agrobiodiversity, ecosystem maintenance through less use of chemicals, and farmers’ intellectual enrichment – while maintaining the evolutionary potential necessary for crops to cope with climate change.

III. THE MAN

Mohamed El Hadi Maatougui, independent consultant and former Ceccarelli’s colleague at ICARDA, describes Ceccarelli in this way (Figure 1.5):

[He is] a genius scientist who took up the challenge of breeding barley for unfavorable conditions. For over 25 years, ICARDA could rely on a man who was competent, innovative, communicative, outspoken, open



Fig. 1.5. Salvatore showing barley plots at a farmers' field day (Stefania Grando).
Source: Stefania Grando.

mindful, and friendly to scientists, students, trainees, and most of all, to farmers all over the world. His outstanding credibility and availability have been often acknowledged and recognized.

His thoughts have always been for disadvantaged farmers and their families, and he never refused a request to travel, visit, listen, and support farmers, whether in Syria, other countries of the Middle East, in Africa, South and East Asia, Central Asia, the Caucasus and Latin America.

Abderrazek Jilal, barley breeder in Morocco and former PhD student at ICARDA, adds:

During my training on participatory barley breeding at ICARDA in 2001, I accompanied Dr. Ceccarelli in a tour visit to many farmers in Syria. I witnessed a smiley and humble man esteemed by all farmers. His willingness to provide them with advices on barley by making efforts of speaking their own language demonstrates his unlimited generosity in contributing to improve the welfare of smallholder farmers. He was always friendly with all of them. I still remember a Syrian farmer who once composed a poem dedicated to him featuring his quality as a human being.