

HANDBOOK of PLANT CELL CULTURE

VOLUME 3

Crop Species



Edited by

**P.V. Ammirato, D.A. Evans,
W.R. Sharp, Y. Yamada**

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Volume 3

Crop Species

Editors

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HANDBOOK OF PLANT CELL CULTURE

Volume 3

Crop Species

This third volume in a new multi-volume treatise applies the state-of-the-art plant cell culture techniques described in Volume 1 to a wide range of crops. It continues the work of Volume 2. In 22 authoritative chapters, the world's foremost scientists cover forage grasses, millets, rice, alfalfa, peanut, cole crops, tomato, potato, yams, citrus, pineapple, blueberry, stone fruits, strawberry, cotton, hardwoods, cacao, coffee, and oil palm.

As in Volumes 1 and 2, the contributors emphasize practical methodology. Every chapter contains 1) detailed protocols which serve as the foundation for current research; 2) a critical review of the literature, including key contributions and summary tables that highlight valuable information; and 3) in-depth evaluations of the tremendous potential this field shows for crop improvement. In addition, the history and economic importance of each crop is discussed. This standard format ensures a clear and continuous presentation.

Special features include an important essay by the distinguished scientist E.C. Cocking on the history of plant hybridization and introductory chapters that concisely explore plant germplasm resources, underexploited crops, and the development of new varieties via anther

(continued on back flap)

culture. The definitive references on applying specific cell culture techniques to major crops, this volume and Volume 2 are an indispensable source of information for plant scientists and students as well as for researchers in agronomy, horticulture, phytopathology, molecular biology, and plant biology.

About the editors

PHILIP V. AMMIRATO is Professor of Biology and Chairman of the Department at Barnard College, Columbia University. **DAVID A. EVANS**, formerly of SUNY Binghamton, and **WILLIAM R. SHARP**, formerly Professor of Microbiology at Ohio State University, are the cofounders of the DNA Plant Technology Corporation, a leader in the development of new crops through bioengineering, based in Cinnaminson, New Jersey. **YASUYUKI YAMADA** is Professor of the Research Center for Cell and Tissue Culture, Faculty of Agriculture, Kyoto University, Japan.

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Preface

The tools of plant cell culture are increasingly being applied to a wide range of biotechnology ventures and in particular to the clonal propagation and genetic improvement of crop plants. For this, the approaches and methodologies must be specifically adapted to the differing problems and potentialities of each crop and to the differing responses of plants that may be herbaceous or woody, dicotyledonous or monocotyledonous, annual or perennial, inbred or highly heterozygous. It is the application of plant cell culture techniques to the improvement of specific crop plants that is the subject of this volume, as it was in Volume 2.

The list of plants that play an important part in agribusiness is longer than one might initially surmise. The selection of those to be included in these volumes reflects a necessary amalgam of several factors—the plants chosen must be of recognized economic importance, they need to have been successfully employed in cell culture research, and a key investigator had to be available and willing to contribute. Some important crops, then, are not here because these elements did not come together. And, it is to be expected in any area where technology is only just being applied that there will be varying degrees of experience and success. This can be seen in the varying lengths of the presentations. The plants finally selected do represent major crop plants where cell culture technology has been demonstrably applied.

In addition, in each volume, several general chapters provide overviews of topics that are particularly relevant to the subject at hand. In this volume, we have included a discussion of plant germplasm re-

sources, emphasizing the problems of rapidly diminishing natural and cultivated populations, and the requirements for germplasm collection, maintenance, evaluation, and distribution. These resources serve as both source material for introduction into cell culture programs and as a repository for the plants these programs generate. A second chapter discusses a number of crop plants that are not now fully exploited but offer the potential for increased production of food, oil, fiber, and other plant products, especially with the utilization of cell culture techniques. The last overview summarizes the application of anther culture techniques to the development of new varieties in China, a country where this technology has been advanced and applied with notable success.

As in our previous volumes, we are pleased to have an introductory essay by a distinguished scientist. E. C. Cocking is a pioneer in the development and application of protoplast technology and was recently elected to the Royal Society of London, joining a long list of distinguished scholars and scientists past and present, including F. C. Steward, who contributed the introductory chapter for the first volume of this treatise. In his essay, Dr. Cocking discusses aspects of the history of plant hybridization and in particular the contributions of Luther Burbank, a pioneer in the development of hybrids between distantly related species. Dr. Cocking's essay serves to illustrate the essential relationship between traditional sexual hybridization and the newer techniques of somatic hybridization.

The centerpiece for this volume, as for the entire series, is practical methodology, and we have again included for each chapter a major section with actual protocols, whether as recipes, tables, charts, or narratives. To introduce the specific crop, the history and economic importance are presented, culminating in a discussion of important breeding and propagation problems, areas in which cell culture methods may be particularly applied. A critical review of the literature summarizes past and current cell culture work, and a discussion of future prospects details where we may expect the technology to go. Again, key references have been highlighted, and references are given with full citation.

As before, our goal is to provide a comprehensive and practical compilation that students and scientists, academicians and businessmen alike will find useful in both understanding current strategies and in extending scientific frontiers.

The publication of Volume 3 completes the initial phase of this treatise. However, plant cell culture continues to progress at an astonishing pace, with the refinement of old techniques, the development of new ones, and their successful application to an ever greater number of economically important plants. We are delighted that this series is being continued and that additional volumes are already being readied to document and foster these advances.

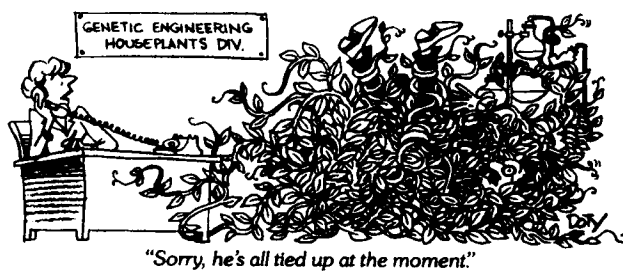
At this juncture, after having witnessed the metamorphosis of piles of manuscripts into three finished volumes, we again thank those that helped in this endeavor but do so with an extra measure of gratitude.

We are indebted to our editors at Macmillan, Sarah Greene and Frances Tindall, for the necessary support in bridging the gap from concept to book. Especial thanks go to Susan Dale, who saw to the translation of words into text with more than a full measure of care. Janis Bravo again served as editorial assistant, the crucial link from us to both authors and editors, for which she deserves our sincere appreciation. We also wish to thank our typists, Karen Selover, Flora Loose, Cheryl Baskin, and Joann Morrison, and Mary Ellen Curtin for preparation of the index. Lastly, we offer our deep thanks to our many authors who provided manuscripts on time and ushered them through the various publication stages with despatch and good cheer.

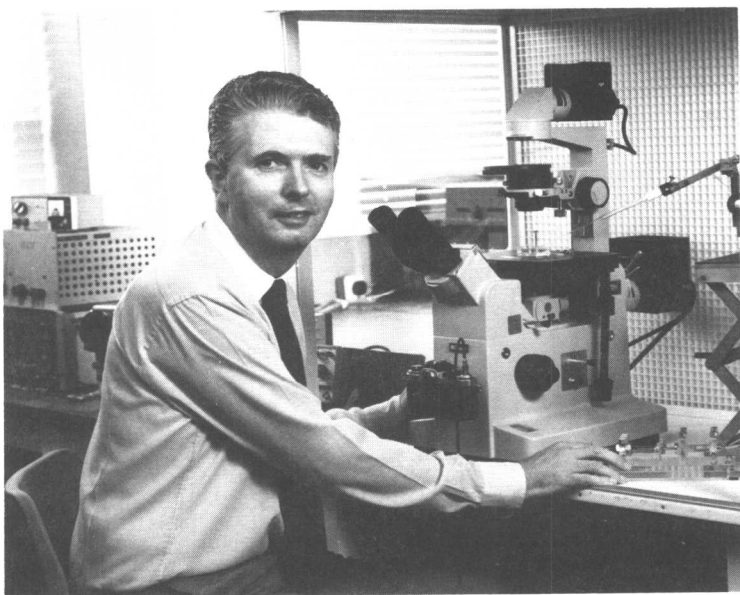
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SPECIAL ESSAY:

Hybridizations Past and Present

E. C. Cocking

It was through the demonstration of the possibility of hybridization that the sexuality of plants, for a long time doubted, was indisputably proven; it was with this objective in view that hybrids were raised in great numbers by Koelreuter as early as 1761. Occasionally the sexual cells of different varieties, species, or even genera were shown to be able to unite and produce descendants capable of development (for detailed references to this early work see Strasburger et al., 1908). As early as 1676 Nehemiah Grew in an address to the Royal Society in London suggested that the stamens are the male organs of the plant. In 1694 the German botanist Camerarius in his classic work *De Sexu Plantarum* provided experimental proof that pollen was necessary in a number of plants for seed development. In 1717 the English gardener Thomas Fairchild obtained the first sexual hybrid of which there is an authentic record, a cross between carnation (*Dianthus caryophyllus*) and the Sweet William (*D. barbatus*). He noted that the progeny of the cross resembled both parents (Dreyer, 1975).

These studies, of course, predated the enumeration of Mendel's laws in relation to intervarietal sexual crosses. They laid the foundation for ongoing work on hybridization, which found its expression in the extensive, but at present largely forgotten, work of Luther Burbank on plant improvement by sexual hybridization. Currently a reappraisal of Luther Burbank's work is required because the resurgence of interest in extending the range of hybridizations by somatic hybridization is highlighting the need for a comprehensive knowledge of the limitations of sexual procedures.

The most recent comprehensive survey of interspecific hybridization in plant breeding (Sanchez-Monge and Garcia-Olmedo, 1977) does not mention the work of Luther Burbank. As pointed out by Lacadena (1977), what is considered as the first international congress of genetics was the International Conference on Hybridization held in London in 1899, and this intense interest in the possible usefulness of hybridization led to the postulation by Winge (1917) that hybridization and chromosome doubling could generate new species. The work of Karpechenko in the 1920s, which showed that it was indeed often possible to restore fertility in distant hybrids by doubling the chromosome number, was being undertaken at a time when Luther Burbank was approaching the end of his working life (he died in 1926). It was also Karpechenko (1927) who succeeded in developing an amphidiploid between radish and cabbage (*Raphanobrassica*), but as will be described later Luther Burbank was paralleling this with the development of crosses between various fruit species, including the cross between plum and apricot (the plumcot), and between a range of horticultural species, including the cross between *Nicotiana* and *Petunia* (the *Nicotunia*). Also paralleling this work was the production by others of experimental hybrids between wheat and rye (*Triticale*) in the early 1900s. Only in recent years however has this man-made cereal become adequately perfected (Caudeyron, 1977). As recently pointed out by Dreyer (1975) in his penetrating reassessment of the life of Luther Burbank, it was not until 1943 that Jones in a review in the *Journal of the New York Botanical Garden* observed that "Burbank's most valuable contribution to science, his *Rubus* hybrids that bred true, have been largely overlooked by geneticists. When they were first announced, Mendelian segregation was expected in all hybrids and his statements were not accepted. Now that amphidiploids are known to transmit without segregation, Burbank is not given the priority he deserves for producing and putting these on record." As pointed out by Dreyer, Burbank's priority lies in having produced such hybrids and clearly distinguishing them as "Another Mode of Species Forming" (Burbank, 1909).

Luther Burbank's name is associated with the Burbank potato, and it is interesting to recall that Burbank developed this variety when he was a young man of 24 in 1873. Even in 1906 the U.S. Department of Agriculture estimated that not less than 17 million dollars worth of Burbank potatoes had been grown in the United States. What Luther Burbank found in his Massachusetts garden was a seed ball on one of his Early Rose potato vines. It required an imaginative mind to conceive that there was importance in this exceptional phenomenon. There were 23 seeds in the cluster and these were planted the next spring, each one by itself; his plan was nearly frustrated by the loss of the seed ball which was broken off by the wind just as it ripened. As noted by his biographer (Williams, 1915), after patient search the treasure was recovered and carefully preserved over the winter. In the fall, when the potatoes were dug up it was obvious that they represented 23 different varieties. Two of these were of altogether exceptional size and quality and from these were developed the Burbank potato. Williams remarked that the remarkable Burbank potato

was thus developed in a single season merely by potato seeds that developed quite independently of human effort: "Forty years of subsequent effort in which vast numbers of hybridizing experiments have been performed have failed to produce another variety of potato superior to the one that was virtually a gift of Nature. In this field of endeavor as in so many others there is an element of uncertainty that adds to its charm."

Luther Burbank sold this new potato variety for \$150 to a practical gardener, who gave it the name of the Burbank potato. This sale helped him to migrate to the better climate of California and set up experimental work as a plant developer on 4 acres in Santa Rosa, together with a tract of 18 acres at Sebastopol 7 miles away. Within this relatively small area more than 100,000 distinct experiments were carried out.

Williams (1915) has emphasized that the fundamental principles of plant development through which Burbank sought to develop new and improved varieties were not in themselves novel or revolutionary. They consisted essentially of the careful selection among a mass of plants of any individual that showed exceptional qualities of a desirable type, the saving of seed of this exceptional individual, and the carrying out of the same process of selection of the progeny through successive generations. Couple this method of selection with the method of cross-pollination of different varieties of species, to produce hybrid forms showing a tendency to greater variation of desired characters, and we have, as so succinctly stated by Williams, the outline of the fundamental principles of plant breeding as known to horticulturalists for generations. What Luther Burbank did was to add the extra dimension of screening very large numbers, including a wide range of varieties and species. Through the astute use of his highly trained senses, backed by an amazing fund of practical knowledge, the entire procedure took on a mystifying aspect of wizardry (Williams, 1915).

As we have seen, while others have explored the theoretical reasons why an increase in the number of chromosome sets should play an important role in the processes of speciation in plants, Luther Burbank was par excellence an experimenter who saw a closer parallel between plant breeding and evolution; he was less interested in theories and more interested in producing better plants by extensive assessments of hybridizations, coupled with rigorous selection of the best. As his biographer (Williams, 1915) commented, his work was not conducted to prove or test any particular scientific theories or make scientific discoveries, but it had for its sole aim the production of more and better varieties of cultivated plants. "I shall be contented if because of me there shall be better fruits and fairer flowers," Burbank said.

The printed records of Burbank's life and work are found almost exclusively in newspapers, magazines, and books. Written under Burbank's immediate direction are twelve beautifully illustrated volumes entitled "Luther Burbank, His Methods and Discoveries and their Practical Application, prepared from his original notes covering more than 100,000 experiments made during forty years devoted to plant improvement" (Whitson et al., 1914-1915). As far as I can discover Burbank only published one or two scientific papers—somewhat refreshing for these