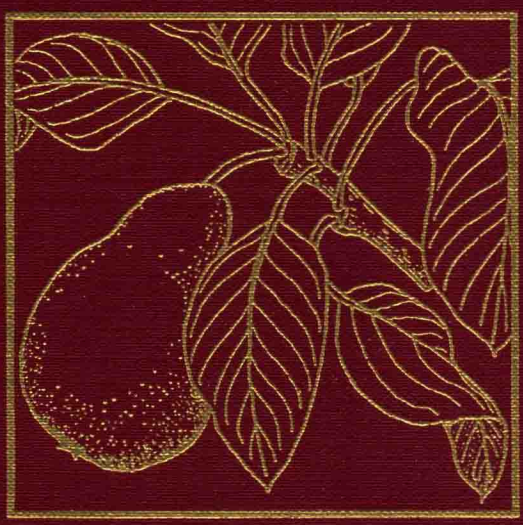
FRUIT BREEDING

Volume I.
Tree *and* Tropical Fruits



Edited by
Jules Janick • James N. Moore

FRUIT BREEDING

VOLUME I
TREE AND TROPICAL FRUITS

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FRUIT BREEDING

Donald H. Scott

DEDICATION

We proudly dedicate this book to Donald Hyde Scott, outstanding fruit breeder and horticulturist. His research accomplishments during a 38-year career with the United States Department of Agriculture (USDA) have had a lasting impact on the small fruit industry of the United States and the world.

Don Scott was born 3 December, 1911 at Buxton, North Dakota, and grew up on the family farm. After graduation from high school, he entered North Dakota Agricultural College (now North Dakota State University) at Fargo and graduated in 1937 with a B.S. degree in agriculture. Don majored in horticulture under the tutelage of famed horticultural plant breeder A. F. Yeager, worked as a horticultural aide in research, and taught the *Introduction to Horticulture* course during his senior year.

Immediately upon graduation, Don was employed by the Agricultural Research Service of the USDA to conduct research in the Stone Fruit Section at the Plant Industry Station, Beltsville, Maryland, under the supervision of F. P. Cullinan. While in Maryland, Don pursued graduate studies on a part-time basis at nearby University of Maryland, and was awarded a Ph.D. degree in Horticulture with a minor in Botany and Genetics in 1949.

In 1942, Dr. Scott was transferred from Beltsville to the USDA field station at Cheyenne, Wyoming, to conduct research on vegetable and small fruit breeding. There he developed a love for small fruits that he was to retain through the remainder of his career. In 1946, he returned to Beltsville to join George M. Darrow's Small Fruit Research Unit. In 1957, upon Dr. Darrow's retirement, Dr. Scott was promoted to Investigations Leader of the Small Fruit and Grape Section, a position that he held until his retirement in 1975.

Dr. Scott's professional career was marked by many notable achievements. He authored 160 scientific papers and a number of book chapters on his research on the breeding and culture of strawberry, blueberry, and blackberry. Especially noteworthy are his papers on inheritance studies, interspecific hybridization, and origination of new disease resistant cultivars with wide area adaptation.

Dr. Scott's prolificacy in developing outstanding fruit cultivars is legend in the fruit-breeding profession. During his career, he developed 27 disease-resistant, high-quality strawberry cultivars, 16 superior blueberry cultivars, and the first two winter-hardy, thornless blackberries ('Thornfree' and 'Smoothstem') adapted to the eastern United States. In his breeding programs he enlisted the aid of others,

especially plant pathologists, in the evaluation process, and was quick to credit their contributions. However, everyone recognized that Don Scott was the leader of the team.

Most of Dr. Scott's fruit cultivars found success in the commercial industry, and it is difficult to select the most important. Among the strawberries, 'Surecrop' (1956), 'Midway' (1959), 'Redchief' (1968), and 'Earliglow' (1975) stand out for their importance to the industry and are still being grown. Among blueberries, 'Bluecrop' (1952) is the leading highbush cultivar in the United States today and is still increasing in importance. 'Blueray' (1955), 'Lateblue' (1967), and 'Elliott' (1973) are also important cultivars, the latter two being noted for late ripening and suitability for machine harvest. 'Thornfree' and 'Smoothstem' blackberries are still widely grown in the eastern United States and have served as progenitors of a new generation of thornless blackberries.

Dr. Scott carried out pioneer research to combat red stele root rot in strawberry, a disease that occurred widely and was devastating in much of eastern U.S. strawberry regions. He determined that the best control was to breed genetic resistance into strawberry cultivars, and he was very successful in this endeavor. He established that races of the red stele fungus (*Phytophthora fragariae* Hickman) exist and developed methods to screen young seedlings for resistance to multiple races of the pathogen without the risk of creating new races. Dr. Scott also recognized the wide occurrence and damaging effects of viruses in strawberries, and established the feasibility of using screenhouses to propagate virus-free foundation plants and isolated nursery fields for large-scale propagation of clean stocks. He was a leader in the organization of a strawberry certification program for nurserymen. For this achievement, his unit at Beltsville was awarded the Wilder Silver Medal of the American Pomological Society in 1962.

In 1972 and 1973, for 3 months each year, Dr. Scott was granted leave by the USDA to advise the Italian Ministry of Agriculture on small fruit production problems in Italy. Following retirement, he continued from 1976 to 1985 as a technical consultant for the Zanzi Fruit Nursery in Ferrara. His recommendations led to the establishment of the virus-indexed certification program for strawberries currently in use in Italy.

For his research accomplishments, Don Scott has been recognized with many honors and awards, including the Wilder Silver Medal, Blueberry Pioneer Award, Silver Medal of the Massachusetts Horticultural Society, Gold Medals from the Italian Strawberry Growers Association and the Po Valley Strawberry Growers Association, Honorary Life Membership of the North American Strawberry Growers Association, and Outstanding Cultivar Award (for 'Earliglow' strawberry) from the American Society for Horticultural Science. He is a Fellow of both the American Society for Horticultural Science and the American Association for the Advancement of Science.

Don Scott is kind and soft-spoken. While a serious person, he is a warm and gentle man. Throughout his career he has been exceedingly generous and helpful in assisting other researchers with suggestions and germplasm to further their work. Although his appointment with the USDA carries no teaching duties, he was

the role model for a generation of students and practitioners of small fruit breeding. On his frequent visits to cooperating universities across the United States, he derived special pleasure from counseling colleagues and students on the fine points of successful plant breeding. He remains an inspiration to the fruit-breeding profession.

James N. Moore
Jules Janick

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PREFACE

Advances in *Fruit Breeding*, published in 1975, updated fruit breeding in a single volume, the first to do so since the 1937 *USDA Yearbook of Agriculture*. Thirty-eight years was a long time to wait, but the compilation was well received with almost 3800 copies sold. It was translated into Russian, Spanish, and Chinese and, in various forms, can be found on the bookshelves of fruit breeders worldwide. It is now out of print. Royalties from the book were donated to the fruit-breeding working group of the American Society for Horticultural Science. Now, twenty years later, we are pleased to present an update on the general field of fruit breeding entitled simply *Fruit Breeding*. We have followed the outline of *Advances in Fruit Breeding* and have retained much of the original information, but have augmented breeding techniques with advances in biotechnology, a term little used in 1975. We have eliminated the chapters on Minor Temperate Fruits and Figs because there has essentially been no progress to report but we have added Bananas and Plantains, Kiwifruit and Pineapples. Kiwifruit has achieved remarkable success as a new world fruit crop in the past twenty years, and Banana, Plantain, and Pineapple are among the major fruit crops of commerce.

In most crops, progress had been achieved in the past twenty years due to the continuous efforts of various fruit breeders and in many cases their efforts have established what can be considered as new industries. These include new seedless grapes, day-neutral strawberries, and new raspberry–blackberry hybrids. Most of the improvements have come about from conventional breeding but we anticipate that the impact of biotechnology will become apparent in the next twenty years.

In no case is any chapter written by the original author(s) alone. In some cases the chapters were completely revised by new authors and in others the original authors have added new coauthors. Of the original authors, five (A. G. Brown, John Einset, George Darrow, Claron Hesse, and L. F. Hough) as well as the dedicatee (John Magness) have died since 1975. We miss them but they shall remain in our memory as mentors and good friends; they will be always remembered for the improved germplasm that is their legacy to all of us.

Jules Janick
James N. Moore

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CHAPTER 1

APPLES

Jules Janick, James N. Cummins, Susan K. Brown, and Minou Hemmat

The apple is the most ubiquitous of temperate fruits and has been cultivated in Europe and Asia from antiquity. It was known to the Greeks and Romans and mentioned by Theophrastus in the third century B.C. Since then the apple has been distributed into almost all parts of the world. The genetic variability found in the apple has allowed adapted types to be selected for different environments, and selection continues for new types to extend apple culture into both colder and warmer regions. Orchards are now found in Siberia and northern China where winter temperatures fall to –40°C and in high elevations in Colombia and Indonesia straddling the equator where two crops can be produced in a single year (Janick 1974). Present world production of apples (FAO 1995) is close to 49 million tonnes. Apples are the fourth fruit crop in importance after all citrus (85 million t), grapes (56 million t), and banana (53 million t). The leading countries for apple production are presented by continent in Table 1.

Apples are popular because of the many ways that they can be consumed and because of their convenience and durability. Apples may be eaten off the tree or stored for up to a full year. Apples can be processed into sauce, slices, or juice and are favored for pastries, cakes, tarts, and pies (Downing 1989). The pulp has been processed into candies (fruit leathers) and used as a source of pectin. The juice can be consumed fresh, either natural or filtered, fermented into alcoholic beverages such as cider or wine, distilled into brandy, or transformed into vinegar. Apples have become the symbol of wholesomeness: "An apple a day keeps the doctor away" is a favorite aphorism, and apple pie has become a symbol of goodness along with motherhood. Finally, crabapples, grown for their attractive flowers, foliage, and fruit, are among the most popular of ornamental trees.

At one time each country and area had its own local cultivars. This is still the case in some areas, but with expanding production and transport networks, and the

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TABLE 1. World Production of Apples, 1994

Principal apple producing country	Production (million tonnes)	Principal apple producing country	Production (million tonnes)
Asia	**20.4**	**North America**	**6.0**
China	12.0	United States	4.9
Iran	1.6	Mexico	0.5
India	1.2	Canada	0.5
Japan	1.0		
		South America	**2.7**
Europe	**13.2**	Argentina	1.0
France	2.2	Brazil	0.8
Italy	2.1		
Russian Federation	1.7	**Africa**	**1.3**
Romania	1.4	South Africa	0.6
Poland	1.4	Egypt	0.3
Germany	0.9	Morocco	0.3
Spain	0.7		
Hungary	0.7	**Oceania**	**0.9**
Netherlands	0.7	New Zealand	0.5
		Australia	0.3

Source: FAO (1995).

requirements for high yield of commercial quality, a few cultivars dominate all the major apple growing areas. For example, the most widely grown cultivars by far are 'Golden Delicious' and 'Delicious' and its red sports, both chance seedlings of American origin. 'Golden Delicious' has been widely and successfully used in breeding, and its seedlings, which make up a high proportion of the new cultivars, are rapidly changing the apple industry. Since the apple is a long-lived tree and vegetatively propagated, cultivars known hundreds of years ago still exist. Apples that date to antiquity have been collected in Italy (S. Sansavini, personal communication). The large world collections and germplasm repositories are living museums that show the development and improvement of the apple and contain a vast reservoir of desirable genes. Old cultivars are little used by breeders because their seedlings generally produce fruit inferior to that of the cultivars being grown today, but they represent a living gene bank. Most breeding in recent years has been among the best commercial cultivars. Interspecific hybridization to introduce new genes to scion cultivars as well as rootstocks is being used, but this requires a lengthy breeding process. To overcome these limitations of time and space, recent advances in biotechnology involving gene transformation now make it possible to introduce genes from almost any source into apple.

ORIGIN AND EARLY DEVELOPMENT

The apple, in company with most of the important temperate fruits-pear, plum, peach, apricot, cherry strawberry, raspberry, and blackberry-belongs to the

Rosaceae or rose family. Apple, pear, quince, medlar, and some less well-known genera have been classified into the subfamily Pomoideae, the pome fruits. These are characterized by fruits consisting of two to five carpels enclosed in a fleshy covering. The genus *Malus* has, according to most authorities, 25 to 30 species and several subspecies of so-called crabapples, many of which are cultivated as ornamental trees for their profuse blossom and attractive fruits (Table 2). Most of the species intercross and, since self-incompatibility is common, trees produced from seed obtained from a botanic garden or arboretum where collections of *Malus* are grown are almost always interspecific or intercultivar hybrids. It is therefore very difficult to be certain of the authenticity of specific names.

The cultivated apple is likely the result of interspecific hybridization and at present the binomial *Malus* ×*domestica* has been generally accepted as the appropriate scientific name (Korban and Skirvin 1984). The main ancestor of apple is now considered to be *Malus sieversii*, which is wild from the Heavenly Mountains (Tien Shan) at the boundary between western China and the former Soviet Union, to the edge of the Caspian Sea (Morgan and Richards 1993). This species is diverse and wild trees bearing the full range of forms, colors, and tastes are found in Kazakhstan and other independent countries of Central Asia formed from the breakup of the Soviet Union and especially around Alma Ata (Father of Apples). This is the area of greatest diversity and the center of origin. Recent collection trips to central Asia have verified that *M. sieversii* is very diverse and has all the qualities present in *M.* ×*domestica* (Forsline et al. 1994; Forsline 1995). Vavilov (1930) in his explorations found many wild apples in woods in the Caucasus and Turkestan bearing fruits within a wide range of sizes, some of quite good quality. Species that have contributed to the genetic makeup of the apple include *M. orientalis*, which bears late-keeping bitter fruit; *M. sylvestris*, the European crab, bearing small astringent, greenish-yellow fruits, native to an area that extends from Britain across Europe to the Balkans and northern Turkey; and a number of species from eastern Asia, including *M. baccata*, the hardy but small Siberian crab, *M. mandshurica*, the Manchurian crab; and *M prunifolia*, the larger Chinese crab. A list of *Malus* sections, primary species, and species hybrids is presented in Table 2.

Cultivation of the apple seems to have been practiced by the Greeks and Romans and, as a result of their travels and invasions, to have been spread by them throughout Europe and Asia. Later cultivation was concentrated around the medieval monasteries. Cultivars were selected and propagated in very early times, for grafting was known at least 2000 years ago. By the end of the thirteenth century, many named cultivars were known, and from this time we get the names 'Pearmain' and 'Costard'. The history and romance of the apple has recently been summarized in *The Book of Apples* by Morgan and Richards (1993).

Until the latter half of the twentieth century most of the world's apple cultivars were chance seedlings selected by fruit growers. More than 10,000 cultivars are documented, yet only a few dozen are grown on a commercial scale worldwide (Way et al. 1990). In 1983, the best known cultivars in the world were all chance seedlings found in the eighteenth or nineteenth centuries, of which many were derived in North America: 'Golden Delicious' (6.3 million t, origin US),

TABLE 2. *Malus* Sections and Primary Species

Sections	2*n*	Apomixis	Fruit size (cm diam)	Calyx[a]	Carpel no.	Persistance ofripe fruit
SECTION 1. Malus						
Subsection A. Pumilae						
Series a. Pumilae						
M. asiatica Nakai	34	No	>2	P	5	No
M. domestica Borkh.	34, 51, 68	No	>2	P	5	No
M. micromalus Makino	34	No	1	D	—	—
M. orientalis Uglitzk. ex Juz.	—	—	—	—	—	—
M. prunifolia (Willd.) Borkh.	34	No	2	P	5	Yes
M. pumila Miller	34	No	>2	P	5	No
M. sieversii (Lodeb.) M. Roemer	—	—	>2	P	5	No
M. spectabilis (Aiton) Borkh.	34, 68	No	2	P	5	Yes
M. sylvestris Miller	34	No	>2	P	5	No
Series b. Baccatae						
M. baccata (L.) Borkh.	34, 68	No	1	D	4, 5	Yes
M. floribunda (Siebold) ex. Van Houte	34	No	1	D	4, 5	Yes
M. halliana Koehne	34	No	1	D	3, 4, 5	Yes
M. hupehensis (Pampan.) Rehder	51	Yes	1	D	3, 4	Yes
M. mandshurica (Maxim.) V. Komarov	34	No	1	D	5	Yes
M. sikkimensis (Wenzig) Koehne ex C. Schneider	51	Yes	1	D	4, 5	Yes
Subsection B. Sieboldianae						
M. sargentii Rehder	68	Yes	1	D	3, 4, 5	Yes
M. sieboldii (Regel) Rehder	34-85?	?	1	D	3, 4, 5	Yes
Subsection C. Kansuenses						
Series a. Kansuenses						
M. fusca (Raf.) C. Schneider	34	No	1	D	2, 3, 4	Yes
M. kansuensis (Batalin) C. Schneider	—	No	1	D	3, 4, 5	Yes
M. komarovii (Sarg.) Rehder	—	—	1	D	—	Yes
M. toringoides (Rehder) Hughes	51	Yes	1	D	4, 5	Yes
M. transitoria (Batalin) C. Schneider	—	—	1	D	5	Yes
Series b. Yunnanenses						
M. honanensis Rehder	—	—	1.5	P	4	Yes
M. ombrophila Hand.-Mazz.	—	—	>2	P	5	No?

TABLE 2. (Continued)

Sections	2*n*	Apomixis	Fruit size (cm diam)	Calyx[a]	Carpel no.	Persistance ofripe fruit
M. prattii (Hemsley) C. Schneider	34	No	1.5	P	5	Yes
M. yunnanensis (Franchet) C. Schneider	34	No	1.5	P	5	Yes
SECTION II. Sorbomalus						
M. florentina (Zuccagni) C. Schneider	34	No	1	P, D	3, 4, 5	Yes
SECTION III. Eriolobus						
M. trilobata (Poiret) C. Schneider	—	No	2	P	5	—
SECTION IV. Chloromeles						
M. angustifolia (Aiton) Michaux	34	No	>2	P	5	No
M. coronaria (L.) Miller	51(68)	Yes?	>2	P	5	No
M. ioensis (Alph. Wood) Britton	34	No	>2	P	5	No
SECTION V. Docyniopsis						
M. doumeri (Bois) A. Chev.	—	No	>2	P	5	No
M. melliana (Hand.-Mazz.) Rehder	—	—	>2	P	5	No
M. tschonoskii (Maxim.) C. Schneider	34	No	>2	P	5	No

Note. Malus species hybrids (secondary species) include

M. ×*adstringens* Zabel. (*baccata* × *pumila*
M. ×*arnoldiana* (Rehd.) Sarg. (*baccata* × *floribunda*)
M. ×*astracanica* Dum.-Cours. (*pumila* × *prunifolia*)
M. ×*atrosanguinea* (Spaeth) Schneid. (*halliana* × *sieboldia*)
M. ×*dawsonia* Rehd. (*fusca* × *pumila*)
M. ×*gloriosa* Lem. (*pumila niedzwetskyana* × *scheideckeri*)
M. ×*hartwiggii* Koehne (*halliana* × *baccata*)
M. ×*heterophylla* Spach (*coronaria* × *pumila*)
M. ×*magdeburgensis* Schoch. (*spectabilis* × *pumila*)
M. ×*platycarpa* Rehd. (*coronaria* × *domestica*)
M. ×*purpurea* (Barbier) Rehd. (*niedzwetzkyana* × *atrosanguinea*)
M. ×*robusta* (Carr.) Rehd. (*baccata* × *prunifoia*)
M. ×*scheideckeri* (Spaeth)Zab. (*floribunda* × *prunifolia*)
M. ×*soulardii* (Bailey) Brit. (*ioensis* × *pumila*)
M. ×*sublobata* (Dipp.) Rehd. (*prunifolia* × *sieboldiii*)
M. ×*zumi* (Mats.) Rehd. (*mandschurica* × *sieboldii*)

[a] P, persistent; D, deciduous.

Source: Adapted from Way et al. (1990).