Handbook of
Fruit Breeding

Scientific Methodologies and Technologies

Stuart Smith
Editor

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KOROS PRESS LIMITED
London, UK

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Revised Edition 2014

Published by
Koros Press Limited
3 The Pines, Rubery B45 9FF, Rednal,
Birmingham, United Kingdom

Tel.: +44-7826-930152
Email: info@korospress.com
www.korospress.com

ISBN: 978-1-78163-334-2

Editor: Dr Stuart Smith

Printed in UK

10 9 8 7 6 5 4 3 2 1

British Library Cataloguing in Publication Data
A CIP record for this book is available from the British Library

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Preface

Much of the world fruit industry is still based on grower selection from chance seedlings as well as mutations (sports) and as a result many fruit species are characterized by a narrow germplasm base. These elite seedlings have unique attributes such as outstanding flavour and texture, high fruitfulness and productivity, but also special problems associated with limited adaptation, and pest and disease susceptibility. Deficiencies in many cases have been ameliorated through ultural practices to prop them up including the use of rootstocks, insect and disease control practices, growth regulators, and special handling and storage technology. While some fruit and nut crops—fig, date, and almond, for example—are little changed from antiquity. Some fruits, such as peach, have been so transformed by continuous selection and genetic recombination that they are far removed from their wild progenitors. Not until the beginning of the 19th century was selection purposely imposed through cycles of hybridizations and selection. Current progress has been achieved through intensification of the same forces that have occurred naturally with emphasis on increased adaptability through hardiness, reducing chill requirements, and photoperiod insensitivity, plus resistance to biotic stress. Because many of our fruits are essentially little changed from wild types continued progress can be expected. Molecular techniques hold out the promise of increasing the efficiency of selection through molecular markers and the direct transfer of useful genes into adapted genotypes through recombinant DNA (transgene) technology.

Fruit breeding as an organized activity is a 19th century innovation. Current progress was achieved through intensification of the same forces that have occurred during domestication with increasing emphasis on increased adaptability through hardiness, lowered chill requirement, photoperiod insensitivity, resistance to biotic stress, plant architectural modifications, and selection of colour mutations.

Molecular techniques hold out the promise of increasing the efficiency of selection through molecular markers and insertion of individual genes through transgene technology. Early beginnings of fruit breeding technology can be demonstrated in strawberry and pear. The modern strawberry is derived from hybrids between two octoploid (2n=56) native American species, both usually dioecious: Fragaria virginiana indigenous to the East coast of the North America but reaching Europe in the 17th century, and F. chiloensis, native from Alaska to Chile. Hybrids between these two species were produced naturally in Brest, France early in the 18th century when a pistillate clone of the large-fruited F. chiloensis, introduced by Amédee François Frézier, a French army officer (and spy) whose family name curiously derives from the French word (fraise) for strawberry, was inter-planted with staminate plants of F. virginiana. The new hybrids (now known as F. ×ananassa or pineapple strawberry, after their shape and aromatic flavour, initiated the modern strawberry industry. Selection through the years has resulted in tremendous changes as the plant evolved from a predominantly dioecious species with male and female plants into a hermaphroditic species, in which flowers contained both stamens and pistils. The development of the day neutral character from interspecific crosses has resulted in continuous fruit production and has transformed the industry. Modern breeding has greatly increased fruit size and firmness.

This book presents information on the latest scientific information in applied fruit breeding using the current advances in the field, from an efficient use of genetic resources to the impact of biotechnology in fruit breeding.

—Editor

Contents

Chapter 1

Introduction

A fruit is a part of a flowering plant that derives from specific tissues of the flower, one or more ovaries, and in some cases accessory tissues. Fruits are the means by which these plants disseminate seeds. Many of them that bear edible fruits, in particular, have propagated with the movements of humans and animals in a symbiotic relationship as a means for seed dispersal and nutrition, respectively; in fact, humans and many animals have become dependent on fruits as a source of food. Fruits account for a substantial fraction of the world's agricultural output, and some (such as the apple and the pomegranate) have acquired extensive cultural and symbolic meanings.

In common language usage, "fruit" normally means the fleshy seed-associated structures of a plant that are sweet or sour and edible in the raw state, such as apples, oranges, grapes, strawberries, bananas, and lemons. On the other hand, the botanical sense of "fruit" includes many structures that are not commonly called "fruits", such as bean pods, corn kernels, wheat grains, and tomatoes.

Botanic Fruit and Culinary Fruit

In the culinary sense of these words, a fruit is usually any sweet-tasting plant product, especially those associated with seeds; a vegetable is any savoury or less sweet plant product; and a nut is any hard, oily, and shelled plant product.

These culinary vegetables that are botanically fruit include cucurbits (e.g., squash, pumpkin, and cucumber), tomatoes, peas, beans, corn, eggplant, and sweet pepper. In addition, some spices, such as allspice and chilies, are fruits, botanically speaking. In contrast, rhubarb is often referred to as a fruit, because it is used to make sweet

desserts such as pies, though only the petiole (leaf stalk) of the rhubarb plant is edible. Edible gymnosperm seeds are often given fruit names, e.g., pine nuts, ginkgo nuts.

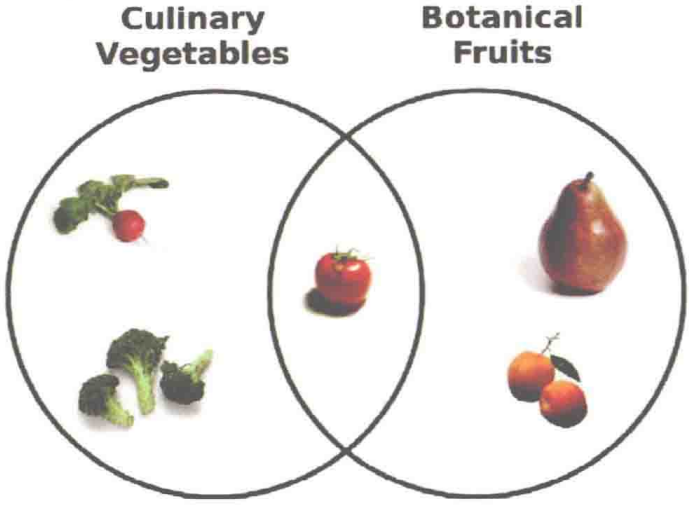

Figure: *Venn diagram representing the relationship between (culinary) vegetables and botanical fruits*

Botanically, a cereal grain, such as corn, wheat or rice, is also a kind of fruit, termed a caryopsis. However, the fruit wall is very thin, and is fused to the seed coat, so almost all of the edible grain is actually a seed.

Many common terms for seeds and fruit do not correspond to the botanical classifications. In botany, seeds are ripened ovules; fruits are the ripened ovaries or carpels that contain the seeds and a nut is a type of fruit and not a seed.

Fruit Development

A fruit results from maturation of one or more flowers, and the gynoecium of the flower(s) forms all or part of the fruit.

Inside the ovary/ovaries are one or more ovules where the megagametophyte contains the egg cell. After double fertilization, these ovules will become seeds. The ovules are fertilized in a process that starts with pollination, which involves the movement of pollen from the stamens to the stigma of flowers. After pollination, a tube grows from the pollen through the stigma into the ovary to the ovule and two sperm are transferred from the pollen to the megagametophyte. Within the megagametophyte one of the two sperm unites with the egg, forming a zygote, and the second sperm enters the central cell

forming the endosperm mother cell, which completes the double fertilization process. Later the zygote will give rise to the embryo of the seed, and the endosperm mother cell will give rise to endosperm, a nutritive tissue used by the embryo.

Figure: *The development sequence of a typical drupe, the nectarine (*Prunus persica*) over a 7.5 month period, from bud formation in early winter to fruit ripening in midsummer*

As the ovules develop into seeds, the ovary begins to ripen and the ovary wall, the *pericarp*, may become fleshy (as in berries or drupes), or form a hard outer covering (as in nuts). In some multiseeded fruits, the extent to which the flesh develops is proportional to the number of fertilized ovules. The pericarp is often differentiated into two or three distinct layers called the *exocarp* (outer layer, also called epicarp), *mesocarp* (middle layer), and *endocarp* (inner layer). In some fruits, especially simple fruits derived from an inferior ovary, other parts of the flower (such as the floral tube, including the petals, sepals, and stamens), fuse with the ovary and ripen with it. In other cases, the sepals, petals and/or stamens and style of the flower fall off. When such other floral parts are a significant part of the fruit, it is called an *accessory fruit*. Since other parts of the flower may

contribute to the structure of the fruit, it is important to study flower structure to understand how a particular fruit forms.

There are three general modes of fruit development:

- Apocarpous fruits develop from a single flower having one or more separate carpels, and they are the simplest fruits.
- Syncarpous fruits develop from a single gynoecium having two or more carpels fused together.
- Multiple fruits form from many different flowers.

Plant scientists have grouped fruits into three main groups, simple fruits, aggregate fruits, and composite or multiple fruits. The groupings are not evolutionarily relevant, since many diverse plant taxa may be in the same group, but reflect how the flower organs are arranged and how the fruits develop.

Simple Fruit

Figure: *Epigynous berries are simple fleshy fruit. Clockwise from top right: cranberries, lingonberries, blueberries red huckleberries*

Simple fruits can be either dry or fleshy, and result from the ripening of a simple or compound ovary in a flower with only one pistil. Dry fruits may be either dehiscent (opening to discharge seeds), or indehiscent (not opening to discharge seeds). Types of dry, simple fruits, with examples of each, are:

- achene - Most commonly seen in aggregate fruits (e.g. strawberry)
- capsule – (Brazil nut)

- caryopsis – (wheat)
- Cypsela - An achene-like fruit derived from the individual florets in a capitulum (e.g. dandelion).
- fibrous drupe – (coconut, walnut)
- follicle – is formed from a single carpel, and opens by one suture (e.g. milkweed). More commonly seen in aggregate fruits (e.g. magnolia)
- legume – (pea, bean, peanut)
- loment - a type of indehiscent legume
- nut – (hazelnut, beech, oak acorn)
- samara – (elm, ash, maple key)
- schizocarp – (carrot seed)
- silique – (radish seed)
- silicle – (shepherd's purse)
- utricle – (beet)

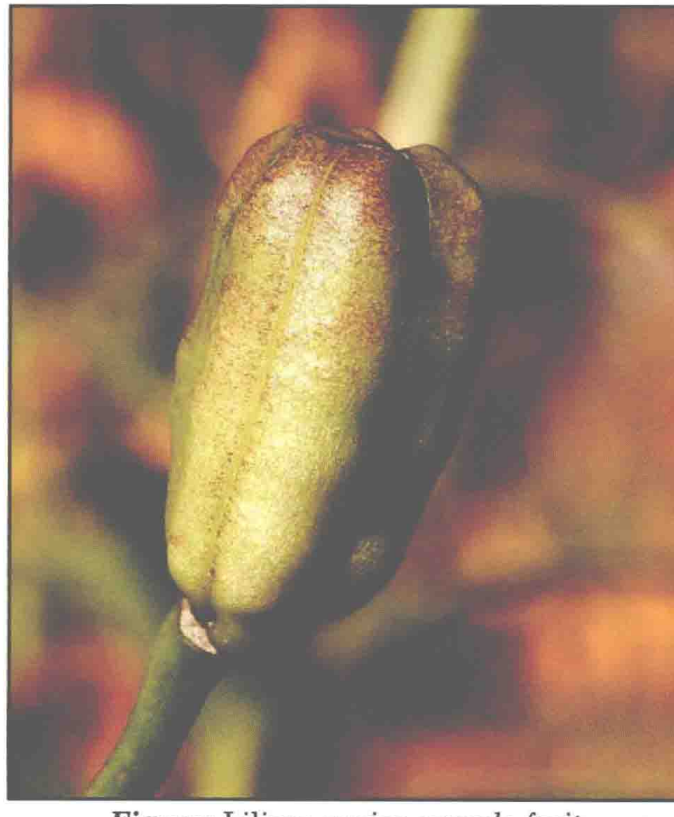

Figure: Lilium *unripe capsule fruit*

Fruits in which part or all of the *pericarp* (fruit wall) is fleshy at maturity are *simple fleshy fruits.* Types of fleshy, simple fruits (with examples) are:

- berry – (redcurrant, gooseberry, tomato, cranberry)
- stone fruit or drupe (plum, cherry, peach, apricot, olive)

Figure: *Dewberry flowers. Note the multiple pistils, each of which will produce a drupelet. Each flower will become a blackberry-like aggregate fruit.*

An aggregate fruit, or *etaerio*, develops from a single flower with numerous simple pistils.

- Magnolia and Peony, collection of follicles developing from one flower.
- Sweet gum, collection of capsules.
- Sycamore, collection of achenes.
- Teasel, collection of cypsellas
- Tuliptree, collection of samaras.

The pome fruits of the family Rosaceae, (including apples, pears, rosehips, and saskatoon berry) are a syncarpous fleshy fruit, a simple

fruit, developing from a half-inferior ovary. Schizocarp fruits form from a syncarpous ovary and do not really dehisce, but split into segments with one or more seeds; they include a number of different forms from a wide range of families. Carrot seed is an example.

Aggregate Fruit

Aggregate fruits form from single flowers that have multiple carpels which are not joined together, i.e. each pistil contains one carpel. Each pistil forms a fruitlet, and collectively the fruitlets are called an etaerio. Four types of aggregate fruits include etaerios of achenes, follicles, drupelets, and berries. Ranunculaceae species, including *Clematis* and *Ranunculus* have an etaerio of achenes, *Calotropis* has an etaerio of follicles, and *Rubus* species like raspberry, have an etaerio of drupelets. *Annona* have Etaerio of berries.

The raspberry, whose pistils are termed *drupelets* because each is like a small drupe attached to the receptacle. In some bramble fruits (such as blackberry) the receptacle is elongated and part of the ripe fruit, making the blackberry an *aggregate-accessory* fruit. The strawberry is also an aggregate-accessory fruit, only one in which the seeds are contained in achenes. In all these examples, the fruit develops from a single flower with numerous pistils.

Multiple Fruits

A multiple fruit is one formed from a cluster of flowers (called an *inflorescence*). Each flower produces a fruit, but these mature into a single mass. Examples are the pineapple, fig, mulberry, osage-orange, and breadfruit.

Figure: *In some plants, such as this noni, flowers are produced regularly along the stem and it is possible to see together examples of flowering, fruit development, and fruit ripening.*

In the photograph on the right, stages of flowering and fruit development in the noni or Indian mulberry (*Morinda citrifolia*) can be observed on a single branch. First an inflorescence of white flowers called a head is produced. After fertilization, each flower develops into a drupe, and as the drupes expand, they become *connate* (merge) into a *multiple fleshy fruit* called a *syncarpet.*

Berries

Berries are another type of fleshy fruit; they are simple fruit created from a single ovary. The ovary may be compound, with several carpels. Type include (examples follow in the table below):

- Pepo – Berries where the skin is hardened, cucurbits
- Hesperidium – Berries with a rind and a juicy interior, like most citrus fruit

Accessory Fruit

Some or all of the edible part of accessory fruit is not generated by the ovary.

Table: *of fruit examples*

Types of fleshy fruits					
True berry	***Pepo***	***Hesperidium***	***Aggregate fruit***	***Multiple fruit***	***Accessory fruit***
Blackcurrant, Redcurrant, Gooseberry, Tomato, Eggplant, Guava, Lucuma, Chili pepper, Pomegranate, Kiwifruit, Grape, Cranberry, Blueberry	Pumpkin, Gourd, Cucumber, Melon	Orange, Lemon, Lime, Grapefruit	Blackberry, Raspberry, Boysenberry	Pineapple, Fig, Mulberry, Hedge apple	Apple, Rose hip, Strawberry

Seedless Fruits

Seedlessness is an important feature of some fruits of commerce. Commercial cultivars of bananas and pineapples are examples of seedless fruits. Some cultivars of citrus fruits (especially navel oranges), satsumas, mandarin oranges, table grapes, grapefruit, and watermelons are valued for their seedlessness. In some species, seedlessness is the result of *parthenocarpy*, where fruits set without fertilization. Parthenocarpic fruit set may or may not require pollination but most seedless citrus fruits require stimulus from pollination to produce fruit.

Seedless bananas and grapes are triploids, and seedlessness results from the abortion of the embryonic plant that is produced by fertilization, a phenomenon known as *stenospermocarpy* which requires normal pollination and fertilization.