CRC

HANDBOOK *of* FRUIT SET *and* DEVELOPMENT

Shaul P. Monselise

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CRC Handbook of Fruit Set and Development

Editor

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To my dear Rachel,

To my Children and Grandchildren,

To my Students

PREFACE

Different phases of fruit development and utilization have been treated in many textbooks, reviews, and a host of scientific and professional papers. This seems, however, to be the first attempt to bring together case histories of so many different fruits and to present a balanced account of the whole period from set to harvest. Postharvest physiology, which has been in the center of the picture in many former books, is at the borderline of the subject matter of this book, and has not been fully covered, except in a few cases. For this reason, two separate chapters deal with physiological and pathological aspects of fruit life after harvest.

It was difficult to decide which fruits should be represented, and which aspects should be emphasized or subdued. The final picture is the result of both planning and compromise. For various reasons, several interesting fruits have not been presented. The Editor is well aware of the omission and still the treatment presented here tends to rend this book rather voluminous.

The Editor had suggested a unified outline for all chapters dealing with different fruit crops. Some of the authors followed this outline, but several preferred their own arrangement. One of the advantages of a multiauthored book is the diversity of approaches and interests. It is easy to feel, unless the writer has used a great deal of self-control, where his real, lively interests lie.

Another reason for diversity and a certain lack of balance among chapters is due to the different degree of depth and detail achieved by research devoted to different fruits. This depends in part from their commercial importance and their physiological peculiarities, but also from the amount of research facilities available in the countries where they attained importance. A very important factor also is the period of time (one, two, or three generations of scientists) elapsed since research started on a particular crop. It is therefore not unexpected that apples and strawberries should have provided material for longer chapters than many tropical or subtropical fruits. This handbook can therefore also be used to assess the sections where knowledge is still wanting with regard to each horticultural crop, and help specialists to plan additional research contributions in the missing areas. It would be wrong, however, to infer directly, from the length or the depth of the chapter devoted to a certain fruit, about the importance or the significance of the crop.

The last chapter of this book is an attempt by the Editor to sum up certain common features as well as obvious dissimilarities, according to his own tendencies and interests.

The Editor wishes to thank the numerous Contributors for their invaluable and thoughtful work. He is grateful to the Members of the Advisory Board, S. Gazit and R. Goren for their cooperation. A great part of the editorial work was carried out during a sabbatical leave from the Hebrew University of Jerusalem. Some support was obtained from the James de Rothschild Chair of Horticulture, of which the Editor is actually the incumbent. Last but not least, the Editor wishes to express his sincere appreciation to Members of the Editorial and Production Staff of CRC, and particularly to Mrs. A. G. Skallerup and Mrs. B. J. Caras for their patient and skillful editorial work.

Comments and criticism are welcome. We shall also appreciate if readers would bring to the attention of the Editor errors or omissions in this Handbook.

Shaul P. Monselise

THE EDITOR

Dr. Shaul P. Monselise is a James de Rothschild Professor of Horticulture at the Department of Horticulture, Faculty of Agriculture, Hebrew University of Jerusalem, Rehovot, Israel. He received both his M.Sc. and Ph.D. degrees from the Hebrew University, where he has served since 1945. In 1968, he became the Dean of Agriculture and served in that position until 1971. Since 1972 he has been the Head of the Department of Horticulture. He currently teaches undergraduate courses on the principles of horticulture and on citriculture and a graduate course on fruit set and development.

Dr. Monselise has spent several short sabbatical periods abroad — the University of California, Riverside and CalTech, Pasadena (1955 to 1956); Cornell University (1972); the East Malling and the Long Ashton Research Stations in England (1964 and 1973); the Agricultural University, Wageningen, The Netherlands (1977 to 1978); the University of Turin (1978); and the University of Naples (1983).

In 1964, Dr. Monselise was corecipient of the Alex Laurie Award of the American Society for Horticultural Science. In 1972, he was an FAO Consultant to the University of Montevideo, Uruguay and since 1978 has been a Member of the Executive Committee of the International Society of Citriculture.

His research interests are in the field of citrus biology and physiology, with a strong accent on native and applied growth regulators. He has published about 170 research papers on these topics and one book on citrus fruit.

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APPLE

Lat. *Malus domestica* L. Borkh., Rosaceae; Fr. Pomme; Ger. Apfel; It. Mela; Sp. Manzana

Frank G. Dennis, Jr.

INTRODUCTION

Numerous review articles have been written on fruit set and/or development. Several have dealt chiefly or exclusively with apple[1-3] or apple and pear,[4,5] including several on fruit thinning.[6-10] Computer modeling of physiological processes is currently under investigation as a means of better understanding the effects of environmental parameters on them. The ultimate goal of these efforts is the prediction of crop size based upon flowering intensity, fruit set, fruit size, etc. Landsberg and co-workers[11-13] have been the leaders in such studies with apple, and several of their publications provide overviews of the subject.

This review will be confined to fruit set and development per se of apple, omitting postharvest physiology in all but a few cases. Conditions and cultural treatments applied prior to, during, and after anthesis which influence set and/or development will be discussed, emphasizing physiological aspects and omitting conditions which affect pollen transfer only. Following a brief review of the subject from flower initiation to fruit senescence, the factors which control the processes of fruit set and development will be discussed, emphasizing recent literature and assuming that control of insects and diseases is adequate. Heavy emphasis will be placed on hormonal control. This topic is a difficult one to review, given the plethora of papers published on apple. In Vol. 51 of *Horticultural Abstracts*, for example, 18 papers are cited dealing with apple fruit set alone. Next in numerical order are grape — 9, pear — 8, peach — 3, cherry — 2, and plum — 1. I apologize to those readers who may feel that I have failed to see the orchard for the trees.

FLOWER AND FRUIT MORPHOLOGY AND FLOWERING HABIT

As in many other temperate zone fruits, apple flowers are initiated the year prior to anthesis. In the north temperate zone induction occurs from shortly after bloom until mid-summer, depending upon cultivar and other conditions (see Buban and Faust[15]). Initiation of the flower parts occurs in a centripetal direction, sepals being initiated first, pistils last. By autumn, all parts are microscopically visible except for ovules.[16,17]

The inflorescence is a cyme consisting of up to eight flowers and occurs in both apical and axillary buds on spurs and shoots. Flower buds on spurs are generally confined to the apex; those on shoots can occur at the apex or in the leaf axils. Some cultivars (e.g., McIntosh) seldom, if ever, produce flower buds at the apices of shoots; others (e.g., Rome Beauty) bear most of the flowers in this position, leading to a "weeping" growth habit as a result of the bending of branches under the weight of the fruits. The flower is epigynous and normally consists of 5 sepals, petals, and pistils and up to 20 stamens (Figure 1). The ovary is enclosed in the receptacle (or fused base of the sepals, petals, and stamens) and all flower parts except the petals remain attached to the fruit, which is a pome (Figure 2). The fruit contains five carpels, each with two or four ovules, depending upon cultivar.

OVERVIEW OF FRUIT SET AND DEVELOPMENT

Fruit Set

Although several facultatively parthenocarpic apple cultivars exist (see Dennis[18]), none

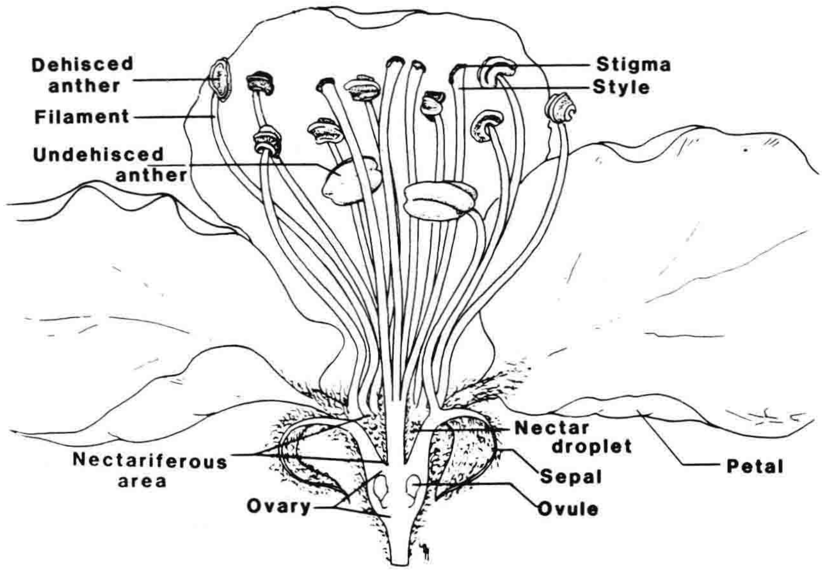

FIGURE 1. Longitudinal section of Delicious apple flower. From McGregor, S. E., *USDA Agric. Handb.*, 496, 81—88, 1976.

is of commercial importance. True parthenocarpy is rare in commercial cultivars,[19] although seedless fruits may develop following embryo abortion as a result of frost injury, climatic conditions, or chemical treatment (see below).

Most cultivars are self-unfruitful, cross-pollination being necessary for commercial crops. The pollen is heavy, hence, insects, primarily bees, are essential to ensure adequate cross-pollination. Wind pollination can occur, but usually has little impact on cropping.[19] The diploid number of chromosomes is 34; some commercial cultivars are triploids, e.g., Rhode Island Greening, Mutsu (=Crispin), and, therefore, of no value as pollinizers. Incompatibility is a problem with several combinations, including Cortland × Early McIntosh. There is considerable interest at present in producing fruit in orchards of a single cultivar, and ornamental crabapples are being evaluated for their possible use as pollen sources (e.g., see References 21 to 24).

The percentage of flowers which develop into fruitlets normally ranges from 10 to 30, depending upon cultivar, blossom density, weather conditions, etc. The remaining flowers abscise within 1 to 2 weeks after petal fall. Small fruitlets continue to abscise for several more weeks; this may occur in waves or almost continually. A "June" drop generally occurs 4 to 6 weeks after bloom, reducing the crop to 5 to 15% of the original number of flowers. The smaller fruits are much more likely to abscise than the larger ones (Figure 3), as is the case with other fruits (see chapters on Citrus and Peach). Little abscission occurs thereafter until shortly before harvest, when the preharvest drop begins. Its intensity varies with cultivar, climatic conditions, and cultural practices.

Excessive fruit set results in small fruit size and can reduce or completely inhibit flower initiation, leading to biennial bearing.[15,25] Flower or fruit removal in early summer ("thinning") promotes flowering and increases fruit size. The increase in size usually does not compensate for the reduction in yield,[27] but *cumulative* yields are generally increased and marketability of the fruits is greatly improved. Naphthaleneacetic acid (NAA), which *promotes* abscission during the "June" drop, can be used to *delay* abscission when applied prior to harvest.

A.

B.

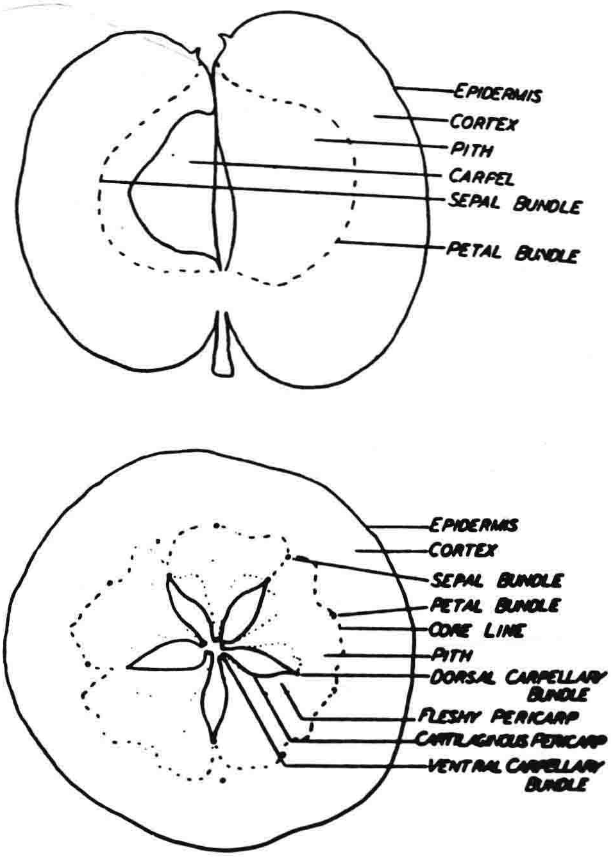

FIGURE 2. Longitudinal (A) and transverse (B) sections of Twenty Ounce fruits 4 weeks prior to harvest.[31]

Fruit Growth

Bollard[28] discussed apple fruit growth in the course of a more general review. Growth in diameter continues until the fruit matures or is harvested (Figure 4).[29-31] Various portions of the fruit develop at different rates (Figure 4), resulting in changes in ratios of core (= ovary) to fruit diameter,[31] length to diameter,[32] etc. Almost all cell division in the flesh ceases 4 to 6 weeks after bloom, but cell enlargement continues until harvest (Figure 5).[29,31] As the cells enlarge, the proportion of intercellular space increases[28] and the specific gravity falls.[33] Growth is considerably more rapid at night than during the day,[34-34b] probably because of differences in relative humidity and thus in rates of evapotranspiration. Fruits often contract during the morning, but compensate by rapid expansion between 6 p.m. and 6 a.m.[34a,34b] Holding trees in growth chambers prevented this shrinkage,[34b] probably by reducing the rate of transpiration. Fruit shape varies with cultivar, climate, and other factors (see below). In commercial cultivars, seeds are usually essential both for retention on the tree and for continued growth. Fruit size and shape are often related to seed number and distribution; hormones produced by the seed may be responsible for these effects.

Yield in apple, as in many other species, is a function of planting density, flower density, final fruit set, and fruit size. Within trees, the percentage of flowers setting fruit declines as flower density increases, and fruit size is inversely related to fruit density (= fruit set × flower density). Although flower density can be important, particularly in biennial cultivars, fruit set is more closely correlated with yield than is either flower density or fruit

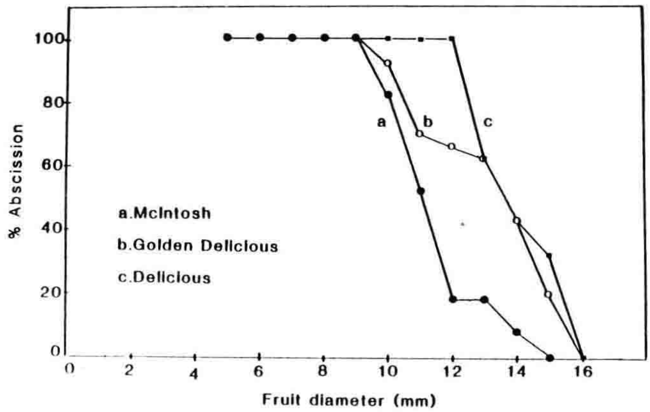

FIGURE 3. Relationship between fruit diameter at first sampling in early June and percentage of fruits abscising within the succeeding 12 days in three apple cultivars.[123]

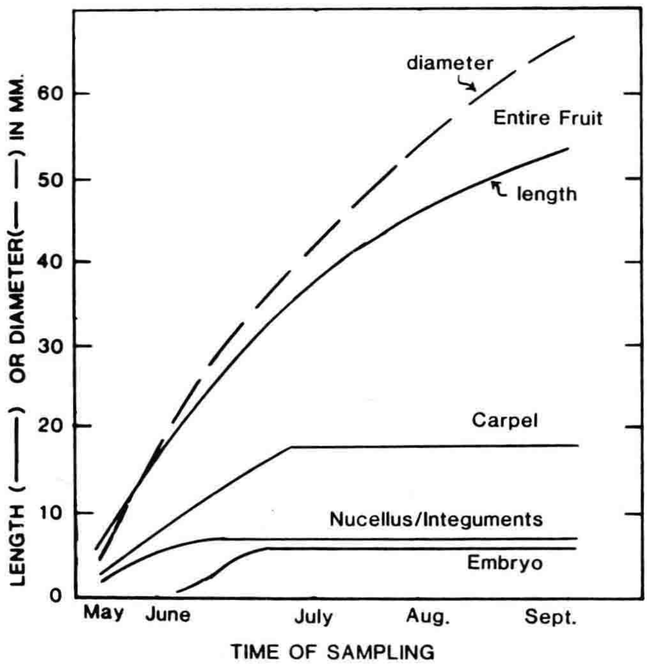

FIGURE 4. Growth of various portions of the McIntosh apple fruit and seed from full bloom until fruit ripening. (Adapted from Tukey, H. B. and Young, J. O., *Bot. Gaz.*, 104, 3—25, 1942.)

size.[4,27,35] Landsberg[36] calculated that the number of fruits per tree accounted for 70% of the variation in yield of apple in England. Surprisingly, Roversi et al.[37] found productivity over several years to be inversely related to stability of yield. However, they may have discounted the importance of fruit size in marketing.

Fruit Maturation, Ripening, and Senescence

To avoid confusion, one should distinguish between maturation, ripening, and senescence.

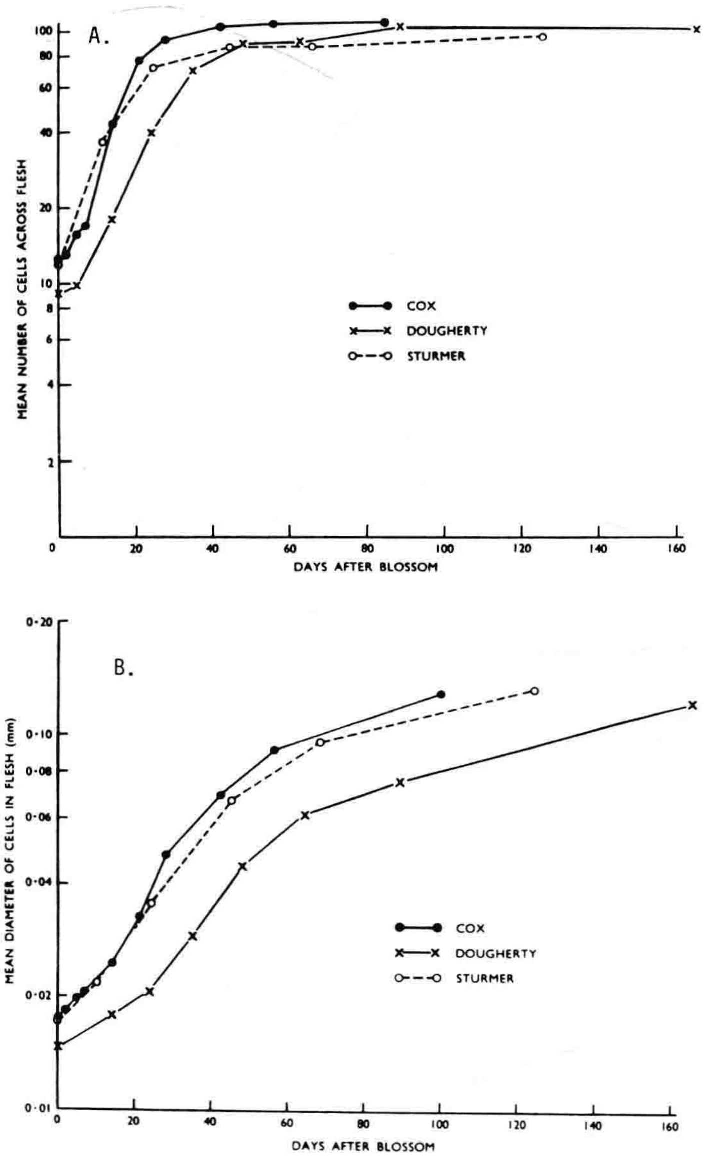

FIGURE 5. Increases in number of cells across flesh (A) and in cell diameter (B) during fruit development in three apple cultivars.[30]

In the case of apple, maturation is the process by which the fruit acquires the ability to ripen properly. A Delicious fruit is normally harvested in early October in Michigan. If harvested in late August, it will not ripen properly, even after chemical treatment, and is thus immature. Ripening is the process during which the mature fruit becomes fully edible and includes a number of physiological events (see below). Senescence of the fruit tissue follows ripening and is the process of deterioration leading eventually to death. Various storage techniques can postpone senescence but, like all living things, the fruit per se is "mortal", although the seed survives.

The apple is a climacteric fruit; endogenous ethylene levels remain low (<0.1 ppm) until maturity, then rise dramatically, leading to ripening. This process includes a rise in the respiratory rate (the climacteric), enzyme synthesis, flesh softening, conversion of starch to sugar, synthesis of volatiles, etc. Ripening can be induced in maturing fruits by treatment with ethylene, ethylene-releasing chemicals, or compounds which stimulate ethylene biosynthesis; it can be delayed by removal of endogenous ethylene, or by inhibiting ethylene production with chemicals. These facts suggest that ethylene is the key hormone controlling ripening in vivo.[38] As ripening continues, chlorophyll is degraded in both skin and flesh, leading to a change in "ground color" from green to yellow. Synthesis of idaein, a red pigment, occurs in the skin in some cultivars but not others. This is not associated with ripening per se, for the fruits of many cultivars develop considerable pigmentation long before maturation begins.

Preharvest fruit abscission is a problem in certain cultivars, e.g., McIntosh. Even in cultivars whose fruits remain relatively firmly attached, strong winds at the approach of harvest can remove many fruits from the trees. Chemical treatment can delay abscission.

Removal from the tree hastens ripening; storage at low temperature and/or low O_2 tension delays ripening and senescence, and many thousands of tons of fruit are cold stored for 1 to 10 months for subsequent commercial sale. Most fruits are stored in air, but many are now being kept under high CO_2 and low O_2 concentrations in gas-tight rooms ("controlled atmosphere" storage; see Smock[39]).

CONTROL OF FRUIT SET

Effects of Conditions or Treatments prior to Anthesis

A number of factors can affect the setting potential of flowers long before anthesis (Table 1). Probably the most important of these is cultivar, for certain cultivars produce heavy crops year after year while others set poorly.[1,40-42] Nitsch[43] suggested that fruit development actually begins with flower initiation. This is the basis for growers' comments concerning "strong" vs. "weak" flower buds or flowers. May[44] considered the term "floral strength" to be a "physiologically meaningless but horticulturally useful concept". Although documentation is often lacking for such differences in flower quality, a number of observations are relevant (Table 1). The position of the bud on the shoot definitely affects setting potential; flowers in the terminal bud are more productive than those in axillary buds.[45] However, this could result from differences in vascular connections. Several studies indicate that large buds are more productive than small ones (Table 1). Schwabe[47] reported that heavily cropping Cox's Orange Pippin (hereafter referred to as "Cox") trees formed smaller flower buds than did trees bearing light crops, and that initial fruit set the following year was greater on the latter, although final set was little affected. Flowers from large buds consistently set better (22%) than did those from small buds (14%). The relative size of flower buds may reflect spur size and leaf number per spur, both of which are associated with setting potential (see Table 1).

Flower size has also been correlated with setting ability. The terminal ("king") flower in the cluster consistently sets better than do the lateral flowers (Table 1), probably because it forms first, is larger, and has better vascular connections than do the laterals. An interesting exception to this rule is the better setting of nonpollinated lateral flowers of Cox following treatment with growth regulators.[48] Even when flowers are thinned to one per inflorescence, terminal blossoms set better than do laterals and the resulting fruits contain more seeds, suggesting innate differences in ovule viability.[49]

Dorsey[50] observed marked differences in vigor among blossoms of several cultivars. Although the criteria for classification were not defined, Goldwin[51] observed better set of "strong" flowers (16%) of Cox in comparison with "weak" ones (4%) on adjacent limbs following application of growth regulators.

A number of additional factors affect the fruit-setting ability ("quality") of apple flowers, including application of nitrogen fertilizer during the summer preceding anthesis, summer