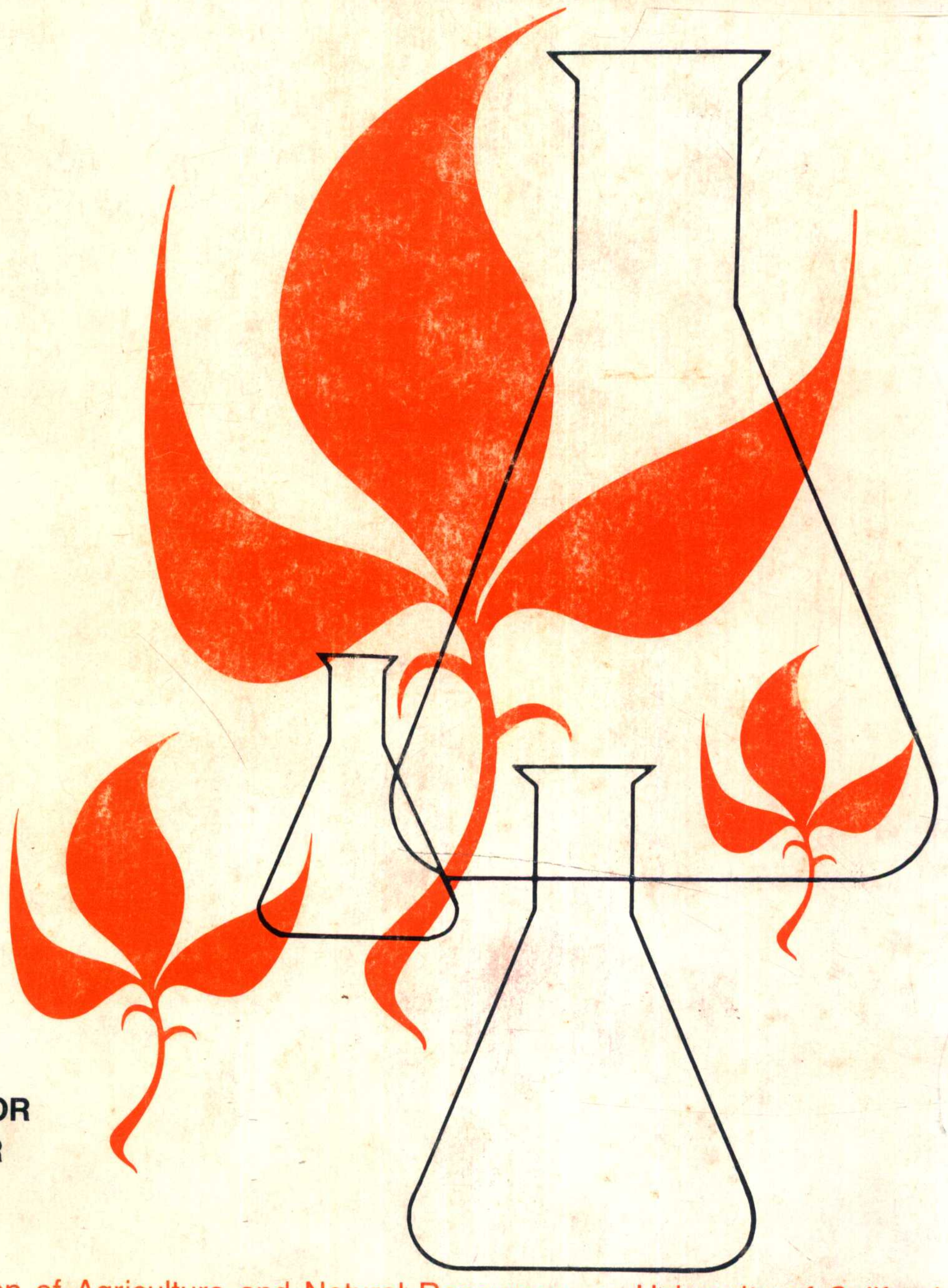
The Citrus Industry

VOLUME II

ANATOMY, PHYSIOLOGY, MINERAL NUTRITION, SEED REPRODUCTION, GENETICS, GROWTH REGULATORS



Edited by
WALTER REUTHER
LEON DEXTER BATCHELOR
HERBERT JOHN WEBBER

Revised Edition • Division of Agriculture and Natural Resources • University of California

THE CITRUS INDUSTRY

VOLUME II

Anatomy, Physiology, Genetics, and Reproduction

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DEDICATED TO

ROBERT WILLARD HODGSON

and

HOWARD BRETT FROST

both of whom possessed the ability to look far ahead and whose talents in divergent ways were reflected in substantial achievements for the citrus industry.

ROBERT WILLARD HODGSON
(1893-1966)

"The direct influence of his teaching can be measured by the enrichment and enhancement of many subtropical fruit industries and the improvement of teaching in agricultural colleges throughout the subtropical regions of the world."

—C. A. SCHROEDER

The impact of Robert Willard Hodgson—teacher, administrator, researcher, and consultant—on the citrus industries and other subtropical horticulture of the world still cannot be fully assessed. For almost fifty years—until his death on May 17, 1966—Dean Hodgson served as an unofficial horticultural ambassador to numerous citrus-growing nations. Many of Hodgson's former students, representing twenty-eight countries from six continents, are just now beginning to exert agricultural leadership in their homelands. The last product of his voluminous research and writings—a monumental work on citrus varieties of the world—was published posthumously in 1967 in Volume I of the new edition of *The Citrus Industry*.

Somewhat reserved by nature, Hodgson's underlying ardor was always evident when he spoke on the agricultural potential of developing nations. Even the characteristic pipe-tamping ritual that focused the listener's attention on the pipe while Hodgson found time during the pause to judiciously order his thoughts, was less drawn out when he touched upon this subject. He possessed the breadth of vision shared by many of the pioneer citrus investigators—men such as Swingle, Webber, Hume, Coit, and Chandler. Some of his missionary-like proselytyzing for agricultural research and education can probably be traced to the rigid influences of a Methodist upbringing in a clerical family accustomed to

HOWARD BRETT FROST

"Frost's genius lay in a total immersion in research, a gift for meticulous observation, and a rigorous objectivity sustained through decades of citrus experimentation. Few colleagues of the early Citrus Experiment Station days grasped the implications of Frost's solitary and unheralded quest or foresaw the revolutionary impact it would have on today's citrus industry."

—WALTON B. SINCLAIR

When Howard Brett Frost began his citrus studies in 1914 on plantings set out beneath the slopes of Mount Rubidoux in Riverside, California, nucellar embryony in citrus had already been studied by Strasburger and Biermann in Europe and the pioneer hybridizing experiments of Webber and Swingle in Florida had provided a rudimentary framework of citrus genetics. Frost built upon this framework: when he retired in 1948, he left behind a sound structure of knowledge which his colleagues were extending through further basic insights and the development of applications of far-reaching value to citrus horticulture.

The Frost legend persists at the Citrus Research Center and Agricultural Experiment Station in a multitude of stories—both true and apocryphal—about his complete absorption in the subject at hand. During an extended field trip one November, Frost is said to have asked: "What day is it? I promised my wife I'd be home for Thanksgiving." There are anecdotes relating to the thoroughness of Frost's field notebooks, still used by a new generation of geneticists. Riding up the Central Valley with a friend in the 1950's, Frost suddenly produced a notebook enabling him to compare precisely the traveling time from city to city with a trip made twenty years earlier. Such attentiveness to detail made it possible for Frost by persistent and devoted effort to wrest genetic-related information from a plant group in which changes of parish.

Robert Willard Hodgson was born on April 3, 1893, in Dallas, Texas, the son of Mark and Olivia Hodgson. His father, an Englishman, emigrated to America at an early age, entered the ministry, and served in parishes in Texas and New Mexico prior to accepting a post as a supervisor of Methodist church affairs in northern California in 1904. In 1906, after retiring from the ministry, the elder Hodgson purchased an orange grove of questionable varietal value at Thermolita near Oroville.

Mark Hodgson had always been a domineering parent, expecting his six children to mirror his views. His opinions on orange-growing were particularly hard for Robert to accept, conscious as the youth was of his father's mistaken assessment of the orchard. The son's rebellion to parental authority took the form of proving that he had the sounder grasp of agricultural principles. After much study, Robert persuaded his father to let him topwork the trees of variable character to a single variety. The boy's success led to many offers for topworking and propagation from other ranchers, and he was soon helping to manage his father's orchards as well.

Upon entering the University of California at Berkeley, Hodgson inevitably registered in the College of Agriculture. In 1916, he graduated with highest honors in biology and agriculture. He also became the first agricultural student at the University ever elected to Phi Beta Kappa. His talent was recognized by Dr. J. E. Coit who recruited Hodgson as his assistant in citriculture and became a major influence on the student's professional development.

In 1917, Coit was sent to Los Angeles by the College of Agriculture to found the Agricultural Extension Service there and organize the first chapter of the Farm Bureau in southern California. Hodgson, who received his M.S. degree that year, joined Coit as his assistant. Seven years of experience as a farm adviser or "county agent" instilled in Hodgson a lifelong concern for the problems of the farmer, reflected both in the direction of his later research and his approach to education. During this period, Hodgson carried out pioneering research on the adaptation and tolerance of citrus trees and on problems concerned with productivity.

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marker genes and simple inheritance patterns are almost nonexistent.

Howard Brett Frost, descended from French Huguenot and English ancestry, was born on September 28, 1881, in Dairyland, New York. One year prior to his birth, his father George Todd Frost, a former school principal, left teaching because of poor health and purchased a snow-covered farm near the Catskill Mountains. After the spring thaw, it became evident that the terrain was quite rocky. As a child, Frost recalls that "every time we planted new crops our main occupation was picking up stones," which were added to the rock fences between fields. It was on this small farm with its apple orchard that Frost acquired an interest in the growing of fruits.

Frost graduated from Dairyland's elementary school and continued studies on his own until he qualified for a teacher-training course that equipped him to teach children in the one-room schoolhouses of this rural region. Meanwhile, he became interested in several agricultural subjects from articles in *The Rural New Yorker,* a farm magazine. In 1904, after four years of teaching, Frost entered Cornell University, where he registered in the College of Agriculture.

Dr. John Craig, a professor of horticulture who had carried out considerable research on snapdragons, encouraged Frost in plant breeding experiments. In Frost's senior year, he conducted growth studies of Matthiola, the garden stock, and snapdragons in three separate greenhouses, discovering a number of peculiar variations in stocks which he later followed up in graduate work. Frost received his Bachelor of Science degree in 1908. He began graduate school, worked as a graduate assistant at Cornell, and interrupted his studies for about a year to take a Civil Service Commission post in Washington, D.C. He then returned to complete his Master of Science degree, followed by the Ph.D. in 1913.

Frost's work as a graduate student attracted the attention of Dr. Herbert John Webber, head of the department of plant breeding at Cornell, who with Walter T. Swingle had carried out citrus breeding experiments in Florida

In 1924, Hodgson was appointed associate professor of subtropical horticulture at the University of California, Berkeley. In that same year, the Regents adopted a resolution to transfer the Division of Subtropical Horticulture to the Los Angeles campus. When Hodgson was named head of the division in 1925, he immediately became involved in the intensive planning that resulted in the actual move to Los Angeles in 1932. Among his tasks was responsibility for planning and collecting materials for the variety and experimental orchard on the Los Angeles campus, which ultimately became an outstanding facility for research and teaching in the field of subtropical horticulture.

In 1932, Hodgson was promoted to assistant director of the Los Angeles section of the College of Agriculture. In 1935, he received the title of professor of subtropical horticulture. He became assistant dean in 1943, and advanced to the post of dean of the College of Agriculture at Los Angeles in 1952. He retained this position until retiring as dean emeritus in 1961. In 1965, Hodgson was awarded the honorary Doctor of Laws degree by the University of California, Los Angeles, for his outstanding service to the University and his advancement of agricultural science. In conferring this distinction, Chancellor Franklin D. Murphy of the Los Angeles campus praised Hodgson as "one of the pioneers who helped build UCLA into a great institution."

Hodgson's research on orchard efficiency analysis and pruning practices and characteristics of nucellar clones of lemons in California drew attention to many problems of the citrus industry, resulting in improved clones and better cultural and handling methods. His study of exotic citrus varieties in various parts of the world led to numerous introductions of value in breeding, rootstock-scion studies, and other applications. He also stimulated improvement of the avocado and had an influence on the walnut, date, persimmon, pomegranate, and fig industries of California.

Because of his abilities in organization and administration and his skill in appraising problems, Hodgson was sought frequently as a consultant in the fields of agricultural research and education. He was a participant in the United States Technical Assistance Program in Chile in 1957; he was a representative under sponsorship

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from 1892 to 1897. In late 1912, Webber accepted the post of first director of the University of California Citrus Experiment station (now the Citrus Research Center and Agricultural Experiment Station) at Riverside, California. On Webber's recommendation, the Regents of the University hired Frost as a plant breeder. The young scientist followed Webber to California, arriving at the Mount Rubidoux quarters of the experiment station in October, 1913.

In embarking on a career in citrus breeding and genetics, Frost was aware that long years of perseverance would be needed to secure meaningful results. Unlike fruit flies that complete a life cycle in three weeks or tomatoes which require four or five months, the period from seed to fruiting in citrus ranges from five to ten years. This protractedness is compounded by the scarcity of sexually-produced plants obtainable from the seed of many citrus species. Requisite to research that might extend over several generations of trees was a high degree of patience and dedication. Frost had chosen a harsh, lonely outpost of research, and more than three decades were to elapse before the enduring significance of his genetic studies was widely recognized and he was to see some of his hybrids and nucellar budlines attain commercial importance.

Frost's studies advanced the knowledge of genetic structure and crossing behavior in citrus. He was the first to report accurately the normal chromosome number of citrus, he was one of the discoverers of polyploidy in citrus, and was the first American to describe citrus tetraploids. Following up W. T. Swingle's discovery that young trees originating as nucellar-seedling lines from old citrus varieties displayed juvenile characters and thus differed from their parent lines, Frost and others, including pathologists, carried out studies showing that both temporary juvenility and elimination of disease viruses in seed reproduction were involved, as well as occasional genetic variation. Such basic scientific knowledge enabled Frost and his colleagues to develop commercial applications of great benefit to the citrus industry. Today more than half of all lemon and of The Rockefeller Foundation at the Indian Agricultural Research Institute in 1959, 1960, 1961, and 1962; he held a Food and Agriculture Organization consultantship in Cyprus during 1960; and in 1965 was a consultant to the Ministry of Agriculture in Libya. He spent 1951 to 1952 in Egypt as a Fulbright research scholar, and from 1955 to 1959 served as a member of the Administrative Committee of the Inter-American Institute for Agricultural Sciences at Turrialba, Costa Rica. In 1965, he was a consultant to the Faculty of Agriculture at Khartoum University in the Sudan.

His technical reports on horticultural missions in Tunisia, Morocco, India, Egypt, Chile, Palestine, Sudan, Libya, and Tripolitania resulted in substantial horticultural improvements in many of these nations. Among honors bestowed upon him for such services were the Order of Nichan Iftikhar, conferred by the Bey of Tunisia in 1931; the Order of Ouissam Alouite Cherifien presented by the Sultan of Morocco; and the Croix d'Officier du Merite Agricole of the Republic of France.

On the national and local level in this country, Hodgson was also professionally active in a number of organizations associated with agriculture. From 1960 to 1965, he served as chairman of the Walnut Control Board. He was also a member of the California Orange Administrative Board for many years. He was a recipient of the California Avocado Society Award of Honor in 1940, the Los Angeles County Farm Bureau Annual Award of Merit, and the Wilder Silver Medal Award of the American Pomological Society. He was elected a fellow in the American Association for the Advancement of Science, an active member of the New York Academy of Science, and served as president of the Western Section, American Society for Horticultural Science.

Hodgson's prolific publications record includes numerous papers on subtropical fruits and their culture and on agricultural problems in general, many of which were translated into foreign languages. Shortly before his death, he completed an exhaustive monograph on citrus varieties which appears in Volume I of *The Citrus Industry*. While this work is destined to become a classic of citrus literature, Hodgson's greatest legacy lies in the impress of his vigorous mind and ideas on the lives and careers of students and associates who will shape the role of agriculture in the world of tomorrow.

orange varieties propagated in California are vigorous nucellar selections, some of which were originated by Frost. He produced several high-quality mandarin hybrids, including the Kara and Kinnow. Because of their influence throughout the citrus world, however, Frost's greatest contributions are undoubtedly the two fundamental chapters on citrus genetics and reproduction which he wrote for the first edition of *The Citrus Industry* and the results of his research on nucellar-seedling lines.

Throughout his active career, Frost remained associated with the institution at which he began his studies on citrus. Even after achieving emeritus status, he continued work on citrus and on *Matthiola incana*. In the latter area of research, Frost in collaboration with Margaret Mann Lesley discovered a gene entirely new to genetics that controlled chromosome elongation in *Matthiola*. The Frost-Lesley studies included other significant contributions leading to the present methods for commercial production and selection of double-flowered stocks. For many years, Frost was also interested in Esperanto, a form of international language, and he presented an exhibit on the possibilities of international auxiliary languages at the International Congress of Genetics in 1932. The names of three citrus varieties produced by Frost are taken from Esperanto: Trovita (an orange) means "found"; Frua (a mandarin) means "early"; and Sukega (a grapefruit hybrid) means "very juicy."

Frost's membership in scholarly societies has included the American Genetics Association, the American Association for the Advancement of Science, the American Society for Horticultural Science, and the Genetics Society of America. In 1957, he was honored by the California Lemon Men's Club for his distinguished service to the lemon industry. His highest recognition came in 1966 when he was awarded the Wilder Medal of the American Pomological Society, the oldest and one of the most highly prized awards in American horticulture.

PREFACE

Since each of the four volumes of this revised and new edition of *The Citrus Industry* is complete in itself, the general plan of the work must necessarily be restated in each volume. The first volume of the revised edition, *History, World Distribution, Botany,* and *Varieties,* was published by the University of California Division of Agricultural Sciences in 1967. The present volume, *Anatomy, Physiology, Genetics,* and *Reproduction,* encompasses morphology, anatomy, physiology, mineral nutrition, genetics, breeding, seed reproduction, and growth regulators. The remaining two volumes, *Production Technology* and *Biology and Control of Pests and Diseases,* are in course of preparation; the dates of publication, however, cannot yet be announced.

The first edition of *The Citrus Industry,* published in two volumes, served for more than two decades as the classic reference work on the biology and culture of citrus throughout the world. The first volume, *History, Botany and Breeding,* edited by H. J. Webber and L. D. Batchelor, was published by the University of California Press in 1943, followed by two later reprintings. A larger printing of the second volume, *Production of the Crop,* edited by L. D. Batchelor and H. J. Webber, was published in 1948 by the University of California Press. By the 1960's, it had become apparent that many sections of the original volumes had been rendered obsolete by technological advances and the acquisition of new basic knowledge merely touched upon or not considered in the original edition.

Prompted by Dean A. M. Boyce and other colleagues, I agreed to serve as editor for a new, revised edition. Revision of *The Citrus Industry* was initiated on July 21, 1961, as Citrus Research Center and Agricultural Experiment Station Project 2015. Because of substantial expansion of coverage, it became necessary to divide the subjects originally covered in Volume I of the first edition into two volumes. Thus, the present volume includes much of the subject matter that appeared in the first volume of the original work. At the same time, most chapters in this volume represent new treatments of their subjects, reflecting the broader base of experience and information available to the authors as a result of the increased tempo of citrus research in the decades since World War II.

All of the authors of chapters in this volume are members of the staff of the University of California, Riverside, closely affiliated with the Citrus Research Center and Agricultural Experiment Station at Riverside. Their treatment of subjects therefore tends occasionally to exhibit a regional perspective, although improved communications and transportation in the past few decades has made it possible for citrus researchers to be more cognizant of developments in other countries than for contributors to the original volumes.

This new edition of *The Citrus Industry* is intended to present a comprehensive view of all phases of the industry to a broad readership of researchers, administrators, teachers, students, and knowledgeable growers. An effort was made to present material clearly, yet scientifically, so that it might be understood by an intelligent readership. The editor, however, considered it essential that scientific principles on which various practices are based should be explained. Some parts of this volume, therefore, may present material of a highly technical nature best followed by specialists. Literature reviews for most chapters in the volume were completed with 1966 citations, although some authors were permitted to add significant new material during the proofreading of page proofs.

In the first edition, general morphology, histology, and physiology of citrus were treated in a single chapter. In this volume, anatomy and physiology are presented separately in the first two chapters.

Chapter 1, "The Anatomy of Citrus" by Henry Schneider, provides greatly expanded coverage on anatomy. The author has carried out a number of original studies and developed entirely new illustrative material to present as detailed a treatment as possible of the morphology and developmental anatomy of each plant organ.

Chapter 2, "The General Physiology of Citrus" by Louis C. Erickson, concentrates primarily on a discussion of those factors that influence the physiology and metabolism of leaves and fruit. Special attention is also given to some of the physiological disorders of citrus, including such recent problems as those arising from toxic airborne pollutants.

Chapter 3, "The Mineral Nutrition of Citrus," represents a greatly extended treatment of the topic as originally handled by Homer D. Chapman in the first edition. Chapman's new treatment reflects a critical examination of the vast body of recent literature that has enhanced our understanding of the effects of certain mineral deficiencies and excesses on citrus physiology and fruit quality. In addition, methods of controlling nutrient disorders are outlined briefly.

Chapter 4 represents a revision of Howard B. Frost's original chapter on seed reproduction. Robert K. Soost has incorporated much new knowledge on flower biology, embryo development, cytology, and seed germination into this review of the basic biology of seed reproduction in the genus *Citrus*.

Two chapters in the original edition have been synthesized by James W. Cameron into Chapter 5, "Genetics, Breeding, and Nucellar Embryony." Genetics and breeding and bud variation and selection were covered separately in the first edition. Integration of bud variation into the genetics chapter has produced a more unified treatment of disciplines relating to variety improvement. Cameron has also traced the history and progress of citrus breeding activities beginning with the early work of the U. S. Department of Agriculture and indicated the impact of nucellar embryony research on citrus variety improvement.

In Chapter 6, C. W. Coggins, Jr., and H. Z. Hield examine "Plant-Growth Regulators." Although much remains to be learned about these substances and their role in citrus physiology, the authors review the status of knowledge and research and discuss some of the current applications of plant-growth regulators and their potential for the future.

The editor wishes to express his deep appreciation to the authors of the various chapters for their wholehearted cooperation and patience during preparation of this volume. A number of authors also found time despite their busy schedules to assist in the review of chapters by their colleagues.

Gratitude must also be expressed to those who assisted in reviewing parts of the text dealing with their particular specialties and fields of research. Reviewers were as follows: Chapter 1, Katherine Esau, W. W. Thomson, L. C. Erickson, E. S. Ford, and Shirley C. Tucker; Chapter 2, W. W. Jones, Walton B. Sinclair, and Franklin C. Turrell; Chapter 3, Paul Smith and T. W. Embleton; Chapter 4, James W. Cameron, Henry Schneider, and Philip C. Reece; Chapter 5, J. R. Furr, William C. Cooper, Philip C. Reece, and Robert K. Soost; and Chapter 6, William C. Cooper, L. N. Lewis, L. P. Batjer, and C. H. Hendershott.

The photograph of Robert W. Hodgson for the dedicatory page was provided by Evelyn Hodgson, who was also helpful in reviewing the biographical material on her late husband. C. A. Schroeder assisted in providing information for the biographical section.

The dedicatory photograph of Howard B. Frost was generously furnished by his daughter, Mrs. L. W. Towner. Biographical assistance on Dr. Frost was provided by his son, Robert H. Frost, and his brother, Henry Frost.

I wish also to express my thanks for their assistance on editorial and publication problems to William W. Paul, manager of Agricultural Publications, and Lucy G. Lawrence of his editing staff.

WALTER REUTHER
Riverside, California
July, 1968

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James W. Cameron and *Howard B. Frost*

CHAPTER 6. Plant-Growth Regulators

C. W. Coggins, Jr., and *H. Z. Hield*

CHAPTER 1

The Anatomy of Citrus

HENRY SCHNEIDER

THE MATURE CITRUS TREE is a living, changing entity. Leafy twigs, roots, and the vascular tissues connecting the two are periodically extended, added to, or replaced. After newly formed tissues reach maturity, processes of aging, modification, and degeneration ensue. In typical subtropical climates, flowering and fruit formation occur annually in most citrus species. In tropical areas, flowering and fruit formation is more or less continual, depending on rainfall distribution and other factors. The anatomical aspects of development and senescence of tissues described in this chapter are based primarily on plant materials collected in subtropical California.

Most modern commercial citrus trees have a single trunk. The main branches usually diverge from the trunk at 60 to 120 cm above the ground. The trunk is cylindrical, except in older trees where ridges may form on the trunk above large roots and below large branches. Such ridges are more often found in the lemon than in other citrus species.

The general branching system of cultivated varieties of citrus gives the top or crown of the tree a more or less spherical shape. The form of trees under cultivation varies somewhat with the pruning method. Orange and grapefruit trees produce a dense growth with numerous small branches, whereas the lemon tree has a more open growth with fewer and larger branches. The larger lateral branches of lemon trees grow in a characteristic, eccentric way that results in a flattened limb. Cambial activity is decidedly greater on the lower side of the branch (geotropic growth); consequently, growth rings are distinctly eccentric. Eccentric growth is exhibited also by the lateral limbs of the orange, grapefruit, and other citrus trees, although not commonly so marked as in the lemon. The ability to heal wounds is much stronger on the lower side of such limbs than on the upper. Geotropic growth is shown most clearly by limbs that are approximately horizontal.

Citrus plants in the seedbed have a single primary or taproot. The two or more taproots often observed on older, uprooted citrus trees result from cutting or breaking the original taproot during transplanting from the seedbed or nursery.

Under the influence of a Mediterranean-type, subtropical climate such as California's, citrus species of commerce (except for the lemon) become dormant in winter, but do not shed their leaves. Axillary buds begin to break during warm spells in January and February, but the new shoots do not actively grow until late February or March. A large proportion of the axillary buds grow, particularly those at the extremities of shoots (fig. 1–1, *C*).[1] The resulting spring-cycle shoots are predominantly flower-bearing and vary in composition (Reece, 1945). They may resemble

[1] For the reader's convenience, all figures are presented together at the end of this chapter. Since all details shown by a particular figure are not discussed in any single section of text, there are repeated references to many of the figures throughout the chapter in the course of discussing various organs and tissues.

cymose inflorescences and have flowers and aborted leaves (fig. 1–1, *C*, shoots 3 and 6) or have some fully formed leaves, some aborted leaves, and flowers (fig. 1–1, *C*, shoots 4 and 5). Other shoots are leafy with terminal flowers and a few or many axillary flowers (fig. 1–1, *B*), and still others are sterile, vegetative shoots (fig. 1–1, *A*). Flower-bearing shoots predominate on mature trees, and sterile shoots predominate on young trees.

Flower-bearing shoots tend to be about eight nodes in length. The internodes of leafy, flower-bearing shoots and of sterile shoots are long and triangular in cross-section, whereas the internodes of shoots with aborted leaves are short, circular in cross-section, and may have fewer than eight internodes. In some instances, especially with lemons, the vegetative nature of flower-bearing shoots may be so modified that they appear to be flower stalks with solitary, terminal flowers. Such shoots are short and round, and their aborted leaves are inconspicuous. Flowering of orange trees is profuse in the spring, but most flowers abort and abscise, as do also rudimentary leaves. Twigs usually die if all of their leaves and fruits abscise.

Cambial activity begins during the spring growth cycle and spreads basipetally in the tree, reaching the trunk about a month after it is initiated beneath the buds (Cameron and Schroeder, 1945; Schneider, 1952).

Root elongation like shoot growth occurs in flushes, and some researchers have suggested that shoot growth triggers root growth (Reed and MacDougal, 1937; Schneider, 1952).

In subtropical citrus-growing regions, the summer and fall growth flushes of oranges differ from the spring flush. Usually no flowers form, larger leaves are produced, shoots are longer, sometimes becoming several feet long, and the number of new shoots that grow is small.

This chapter briefly considers the morphology of each organ and describes its developmental anatomy. Since many published anatomical studies do not describe organs in their entirety, several original studies were made by the author to fill in such gaps. Many anatomical studies have been concerned with the sweet orange (*Citrus sinensis* [L.] Osbeck), and most statements about it apply to all commonly grown citrus species, and vice versa. Unless other species are mentioned, it is implied that the author knows from unpublished research that the descriptions also apply to the sweet orange. Some general anatomical considerations of citrus only incidentally related to ontogeny and normal anatomy are reviewed at the end of this chapter. Since literature on citrus anatomy has been reviewed by Hayward and Long (1942), Ford (1942), Scott, Schroeder, and Turrell (1948), and Bartholomew and Reed (1948), a comprehensive survey was not undertaken for this chapter.

THE SHOOT

Leaves, axillary buds, thorns, flowers, and fruits are produced on the citrus stem. Leaves are arranged spirally around the stem, and, in the sweet orange, after the stem is spiraled three times the eighth leaf is directly above the leaf referred to as *n* in figure 1–1, *A*. In other words, the phyllotaxy is 3/8. Direction of spirality, either to the right or left, is determined by counting leaves acropetally. The direction of spirality is reversed with each growth flush (Schroeder, 1953).

Schroeder (1953) reported that in the University of California orchard at Los Angeles the phyllotactic pattern is 3/8 for the following *Citrus* species: *C. medica* L., *C. limon* (L.) Burm. f., *C. reticulata* Blanco, *C. grandis* (L.) Osbeck, *C. paradisi* Macf., *C. aurantifolia* (Christm.) Swing., *C. sinensis* (L.) Osbeck, *C. aurantium* L., *C. ichangensis* Swing., and *C. hystrix* DC. Schroeder also found the phyllotaxy to be 3/8 for *Poncirus trifoliata* (L.) Raf. and *Fortunella margarita* (Lour.) Swing. On the other hand, Banerji (1952) reported a phyllotaxy of 2/5 for *C. grandis*. At the University of California Citrus Research Center, Riverside, the author has observed the phyllotaxy of *C. grandis* and *C. paradisi* to be 2/5.

An axillary bud covered by several prophylls (bud scales) occurs in the axil of each citrus leaf (fig. 1–2, *B*). An axillary bud consists of an apical meristem with leaf primordia as in the apex of a growing stem. Accessory buds develop in the axils of the prophylls; thus, multiple buds are present in the axils of leaves (fig. 1–2, *B*). Axillary thorns may subtend the buds, occurring opposite the first prophyll as shown in figure 1–3, *F* (West and Barnard, 1935). Thorns occur to the left of the axillary bud if spirality is to the left, and to the right if spirality is to the right (Schroeder, 1953).

Individual growth flushes may be distinguished from each other by short, swollen internodes at the beginnings and end of each flush. Moreover, each flush is at a slight angle to the previous one because each new flush originates from an axillary bud. As the stem increases in diameter, the slight zig-zag pattern is obscured (Schroeder, 1953).

The Stem

The newly forming stem is green and tender, with a prominent ridge extending for several centimeters below the base of each petiole (fig. 1-1, *A*). The ridges cause the young stem to be triangular in cross-section, but this form is not maintained when secondary growth appears. Within the ridge at each node, there is a large median leaf trace and two smaller lateral ones (fig. 1-1, *E*). There are also axillary bud and thorn traces (fig. 1–3, *A–F*). Proceeding basipetally down the vascular cylinder, the median leaf trace passes between a lateral leaf trace and a portion of the axillary bud traces of the eighth leaf below. Thus, the arrangement of traces appears related to the 3/8 phyllotaxy (see leaf trace 5 in fig. 1–3, *A–F*).

Below each leaf, within the stem, the various vascular traces to a leaf and its axillary bud and thorn are in a **U**-shaped configuration as seen in transsection, and in the form of a vertical trough as viewed three dimensionally (fig. 1–3, *F*, trace 13). This **U**-shaped configuration also contains the complex of traces associated with the median trace from the eighth leaf above (fig. 1–3, *A*, primordium 5; and its trace in fig. 1–3, *B–E*). The median leaf trace and its lateral traces diverge from the vascular cylinder at a lower level than do the bud and thorn traces (fig. 1–3, *E*, leaf 13). Each of the leaf traces forms a small cylinder after divergence. The lateral leaf bundles unite with the median bundle in the upper portion of the leaf base to form a single cylinder in the petiole (fig. 1–3, *C* and *D*, leaf 13). Above where the leaf bundles diverge, portions of each of the two remaining arms of the **U** become semicircular as seen in transsection, and these unite end to end to form the cylinder of the axillary bud and thorn (fig. 1–3, *C* and *D*).

The Shoot Apex.—At the tip of the elongating shoot is the domelike apical meristem (fig. 1–2, *A*). The single-layered tunica sheathes the corpus, which consists of what appears to be a mass of randomly dividing cells, but in which Frost and Krug (1942) found evidence of two genetically distinct layers. Leaf primordia occur in a spiral around the apical dome and are, of course, successively younger toward the top of the dome (figs. 1–2, *A*; and 1–3). The primordia form as outgrowths from the apical dome and include both tunica and corpus cells.

Leaf primordia are an integral part of the stem tip, but as leaf blades, petioles, and abscission layers differentiate, the leaves become more clearly defined as appendages. Even so, the continuity of leaf and stem should be kept in mind when considering leaf anatomy on subsequent pages (figs. 1–1, *E*; and 1–2, *A*).

The Stem During Procambial Strand Formation.—Procambial strands arise in conjunction with (1) leaf primordia, (2) axillary buds, and (3) either the thorn or primordial floral parts, if one or the other is present. Each strand is a continuous, discrete entity from within the primordial structure it serves to far down into the provascular cylinder (fig. 1–2, *A*). As shown earlier, the median leaf trace, which develops from a procambial strand, remains distinct for more than eight internodes basipetally. Whether each procambial strand forms (1) simultaneously throughout its length, (2) develops basipetally from newly forming primordium into the vascular cylinder, or (3) differentiates from some point in the stem upward into the newly forming primordial structure has not been investigated with regard to citrus. Xylem elements with annular thickenings may appear in the base of the third youngest leaf primordium (Scott *et al.*, 1948; fig. 1–2, *A*), and from there xylem differentiation progresses both basipetally and acropetally. But apparently maturation occurs acropetally (fig. 1–2, *C* and *D*). Sieve tubes, on the other hand, are initiated and mature acropetally. Thus, several growth and development phenomena occur in the provascular cylinder simultaneously, both basipetally and acropetally.

In cross-section, the provascular cylinder of the elongating stem is more or less triangular, and median traces of three leaves form the triangle corner (fig. 1–3, *B* and *C*). Each of the traces at any particular level in the young stem is in a different developmental stage. Degree of development of each trace depends upon the degree of differentiation of the leaf it serves.

The ground meristem is located between the protoderm and the provascular cylinder; the cortex eventually differentiates from it (fig. 1–4, *A*). Cells of the ground meristem are large compared to those of the adjacent meristems, and oil glands differentiate in the outer part. Surrounding the ground meristem is the protoderm (figs.

1–3, *B*; and 1–4, *A*), which is continuous with the tunica of the apical dome (fig. 1–2, *A*). The protoderm cuticle is a thin, continuous film. Where it covers the depression between adjoining cells, the cuticle is thickened and intrudes between the cells (fig. 1–4, *A*). It apparently is not cutinized at this stage, for it does not stain with Sudan IV and does not fluoresce with light having a peak wavelength of 350 mμ. Cells derived from the protoderm differentiate into the epidermis (fig. 1–4, *B–D*). The epidermis is covered by a thick waxy cuticle and contains stomata (fig. 1–5, *D–G*).

The first protophloem sieve tubes differentiate in the outer portion of the procambial strands after the first protoxylem tracheary elements differentiate at the inner margins (fig. 1–2, *C* and *D*). Additional protophloem sieve tubes develop inward from the first-formed ones, whereas the xylem vessels develop outwardly from the first-formed protoxylem vessels. Meanwhile, the procambium, between the protoxylem and the protophloem, produces additional xylem and phloem mother cells. Once xylem and phloem have developed from a procambial strand, the combined tissues are referred to as a vascular bundle. A bundle may be a trace (leaf, bud, or flower trace) or a combination of these called a trace complex.

The Primary Phloem.—As previously mentioned, the protophloem sieve-tube members differentiate from procambial cells. The sieve-tube members are of the same shape and size as the protophloem parenchyma cells, but differ from them in having clear contents (Schneider, 1955). Sieve plates, which occur on the end walls, are more or less transversely oriented. Companion cells, if present, have not been distinguished from protophloem parenchyma cells.

As the internodes elongate, the protophloem sieve tubes are stretched and collapse, but they are replaced by metaphloem sieve tubes derived from the procambium. While the metaphloem is functional, protophloem fibers form from the protophloem parenchyma cells; they elongate by intrusive growth and then form secondary lignified walls (fig. 1–6, *B* and *C*). The primary phloem of the median leaf traces occurs in several bundles, which are elliptical in cross-section. The bundles are separated from each other by large parenchyma cells (fig. 1–6, *B*). The elliptical shape of the bundles seems to result from periclinal divisions of cells surrounding one or a few central cells (fig. 1–6 *D*). Eventually certain procambial cells differentiate into the parenchyma cells that separate the metaphloem from the metaxylem and its procambial cells (fig. 1–6, *B*).

The Primary Xylem.—As early as the third leaf primordium tracheary elements begin to differentiate on the inner side of the procambial strands (fig. 1–2, *A*). Differentiation begins at the base of the primordium and extends basipetally into the stem and acropetally into the leaf. Additional elements differentiate laterally and abaxially from the first ones (fig. 1–6, *D*). The first-formed tracheary elements in leaf primordia are short, fusiform in shape, and have conspicuous annular thickenings (fig. 1–6, *A*; Scott *et al.*, 1948). Later elements have spiral thickenings, are up to 500 microns long, and have tapered ends that overlap other elements. In still later formed elements, thickenings are scalariform. Parenchyma cells lie between the tracheary elements. As the stem elongates, the first-formed protoxylem elements are stretched vertically and collapse (fig. 1–6, *A*). The procambial derivatives from which the metaxylem differentiates occur in radial rows, with the procambium becoming cambium-like (fig. 1–6, *B*). The metaxylem vessels with scalariform thickenings occur in radially arranged rows, and their end walls are transverse and perforated. Each succeeding vessel in a radial row is larger in cross-section than the previously formed one. Parenchyma cells occur between the radial rows of vessels.

The transition from primary to secondary xylem is not readily discernible. Fewer vessels occur in radial rows in secondary xylem than in metaxylem, and fibers are a dominant part of the secondary xylem.

The Mature Primary Stem.—The transition from primary to secondary growth occurs with the beginning of cambial activity. As mentioned earlier, the metaxylem is formed from a cambium-like procambium (fig. 1–6, *B*) which later takes on the functions of the cambium. Therefore the exact time of onset of secondary-xylem formation is not clear. The primary phloem bundles, however, are clearly delimited from the secondary phloem by large parenchyma cells, and the onset of secondary growth occurs with the beginning of secondary-phloem formation.

At the completion of primary development, the cortex is composed of two distinct regions (fig. 1–4, *B*). The inner cortex is composed of large, highly vacuolated cells with thin layers of cytoplasm and thick walls. The cells in the outer cortex are small, thin-walled, and contain thick layers of cyotoplasm with chloroplasts (fig. 1–5, *F*). Cells containing calcium oxalate crystals are especially prominent among cortical cells immediately inside the epidermis. These cells become several times as large as adjacent cortical cells and intrude into the epidermis (fig. 1–5, *F*). As the crystal grows, the cell wall thickens, and eventually the protoplast degenerates.

At completion of primary growth, the epidermis contains unspecialized epidermal cells, stomatal guard cells, and oil-gland cover cells (fig. 1–5, *D–G*). The unspecialized, tabular epidermal cells are irregular in shape as seen in tangential section and for a time retain a capacity to stretch tangentially and to divide to accommodate the increase in stem circumference.

Origin of the Cambium.—As the primary stem grows, it has been noted that the metaxylem-forming portion of the procambium *(metaxylem procambium)* takes on characteristics of the cambium in that it cuts off the metaxylem initials in radially arranged rows. The *metaphloem procambium* is set off from the metaxylem procambium by large parenchyma cells. As metaphloem formation is completed, remnants of the metaphloem procambial cells differentiate into metaphloem cells. The metaxylem procambium, on the other hand, is transformed into the cambium. This is accomplished when secondary-phloem initials are cut off.

Cambial cells which add cells to the vertical system are called fusiform initials, although they are not precisely fusiform in shape. They are relatively small and rectangular as seen in cross-section. In tangential section, they are much elongated, with their radial walls parallel through most of their length; at either end they converge, thus forming a wedge. The radial walls are conspicuously pitted (fig. 1–7, *C*). The tangential walls are more or less long rectangles with triangular ends.

The ray initials and their recent derivatives differentiate into rays cells when the cambium is inactive. In contrast, fusiform initials and their immediate derivatives do not differentiate into xylem or phloem cells during periods of inactivity.

The Secondary Phloem.—The functional or conductive portion of the phloem is a moist, soft, glistening, translucent layer of tissue 1 mm or less thick on the inner side of the bark. In addition to *functional phloem,* there are three other more or less distinct layers. These are the *developing phloem,* the *degenerating phloem,* and the *nonfunctional phloem.*

The *developing phloem* occurs adjacent to the cambium; it is transitory in nature, being present during periods of phloem production. In this tissue, phloem mother cells derived from the phloem initials of the cambial zone are transformed into sieve-tube members, companion cells, parenchyma cells, crystal idioblasts, and phloem fibers (fig. 1–7, *A–D*). The parenchyma cells are formed by transverse divisions of cambiform-phloem mother cells (fig. 1–7, *D*). In the formation of sieve-tube members and companion cells, the phloem mother cell divides by a longitudinal wall to form a long, narrow companion cell and a sieve-tube element (fig. 1–7, *D*). Companion cells are usually in contact with the rays. Sieve plates consisting of several sieve areas occur on one of the two converging radial walls at each end of the sieve element as may be seen in figure 1–7, *D* (Schneider, 1952). Nuclei and slime bodies occur in the differentiating sieve-tube members, but both disintegrate at maturity. The formation of fibers, at least in some instances, occurs during temporary stoppages of cambial activity. Bands of fibers form at the end of the grand period of growth and periodically during the remainder of the season (Schneider, 1952). Because fiber formation is erratic, and since several bands form during the season, these bands cannot be used for detecting annual rings. The oldest portion of the *functional phloem* is estimated to be two or more years old—approximately the same age as the oldest leaves. Dormancy callose is not deposited on sieve areas during the winter.

A ring of *degenerating phloem* occurs on the outer margin of the functional phloem. The first evidence that a sieve tube is beginning to degenerate is the appearance of copious callose deposits on the sieve areas, which may be demonstrated by staining the callose with lacmoid. After callose is deposited, sieve-tube contents undergo a lysis and the walls collapse. In some plants, relatively thick callose deposits are normally present on sieve plates of functional sieve tubes, but in citrus phloem callose is so thin it can only be demonstrated with fluorescent dyes.

The *nonfunctional phloem* occurs extensively in the trunk and older branches and consists of layers of fibers, living parenchyma cells, and the dead, collapsed sieve tubes and companion cells (fig. 1–5, *B*).

The Secondary Xylem.—The light-yellow wood of citrus is diffuse porous; in subtropical climates, at least, annual rings may be distinguished with some degree of certainty (fig. 1–8). In sweet orange, cambial activity begins in the twigs in connection with a new flush of growth and spreads basipetally into the scaffold branches, trunk, and roots. At Riverside, California, there is a grand period of cambial activity in the trunks of mature sweet orange trees lasting from about the first of May until middle July (Schneider, 1952). The xylem produced during this period is composed of rays, vessels, parenchyma cells, fibers, and crystal idioblasts (fig. 1–8; DeVilliers, 1939). The vessels are sheathed by living parenchyma cells; some are paratracheal cells and some are ray cells (figs. 1–7, *A*; and 1–8, *C*).

During the summer, cambial activity is erratic, and tangentially arranged bands of metatracheal parenchyma cells tend to form near or between vessels as shown in figure 1–8, *A* (Webber and Fawcett, 1935; Schnieder, 1952). When growth is terminated in the fall by cold weather, a band of small, terminal parenchyma cells forms, within which there may be a few small vessels (fig. 1–8, *A*). This band of terminal parenchyma cells, along with the differences in the character of early and late formed wood, are useful characteristics for distinguishing annual rings. However, in some specimens, bands of metatracheal parenchyma cells form which closely resemble terminal parenchyma. When such bands of parenchyma are followed by formation of thick rings of xylem resembling early wood, a false ring results.

Vessels normally remain free of tyloses and wound gum. However, they do become filled with wound gum as a result of poisoning and disease (Bitancourt, Fawcett, and Wallace, 1943).

Responses of the Cortex and Nonfunctional Phloem to Secondary Growth.—In response to secondary growth, primary tissues of the bark undergo drastic disruption and some degeneration, but they are not sloughed off (figs. 1–4, *B–D*; and 1–5, *A*; Schneider, 1955). When secondary growth first commences, some cells of the inner cortex collapse and die (fig. 1–4, *C*), while others are stretched tangentially. Parenchyma cells between bundles of primary phloem fibers and the cortical cells outwardly from them are stretched tangentially and divide by anticlinal walls (fig. 1–4, *D*). The cuticle and usually the epidermal walls become broken in such a way that vertical cracks appear on the stem (fig. 1–9, *A* and *B*). Periderm formation begins in the cortical cells under these cracks and spreads to the epidermis (fig. 1–9, *C* and *D*). In older stems, dilation of the cortex and phloem occurs entirely in radially arranged, meristematic sheets called dilation meristems, which extend from the secondary-phloem rays to the phellogen (fig. 1–5, *B*; Schneider, 1955). Parenchyma cells and sclereids differentiate from the derivatives of the dilation meristems (fig. 1–10, *A* and *B*).

The Periderm.—The *periderm* gradually replaces the epidermis after the onset of secondary growth. The periderm is composed of the *phellem* and the *phelloderm* (figs. 1–9, *F*; and 1–10, *C* and *D*), which are derived from the transitory *phellogen* (fig. 1–9, *D* and *E*). The phellem protects the bark from drying out, and is composed of layers of cork cells, parenchyma cells, and phelloids; the latter are cuboidal sclerenchyma cells (fig. 1–9, *D–G*). The phelloderm consists of thin-walled parenchyma cells similar to those of the outer cortex.

Phellogen activity occurs in conjunction with the activity of the dilation meristems (fig. 1–10, *C*), with new periderm formation localizing in vertical strips opposite the dilation meristems. The two meristems appear as a **T** in cross-section. Whether a period of phellogen formation over the entire bark occurs at any time during the season is not known. During each period of activity, a new phellogen is formed from the outer phelloderm parenchyma cells (fig. 1–9, *E*); when phellogen activity ceases, the phellogen cells differentiate into either parenchyma or cork cells.

The Leaf

The citrus leaf is unifoliately compound and pinnately reticulate in venation (fig. 1–11, *A*). Abscission zones occur between the leaflet and the petiole and between the petiole and stem (fig. 1–1, *D*). In most *Citrus* species, the petioles are winged. Grapefruit (*C. paradisi* Macf.) and pummelo (*C. grandis* [L.] Osbeck) petiole wings are large, those of sweet orange are smaller, and petioles of the lemon leaf are without wings. Abscission usually occurs at the abscission zone at the base of the petiole, although after certain types of injury, notably those caused by desiccating winds, separation occurs at the junction of the leaf blade and the petiole (fig. 1–1, *D*). Leaf blades of oranges and lemons are oval to oblong in form, dark green on the upper surface and light yellow-green on the lower surface when ma-