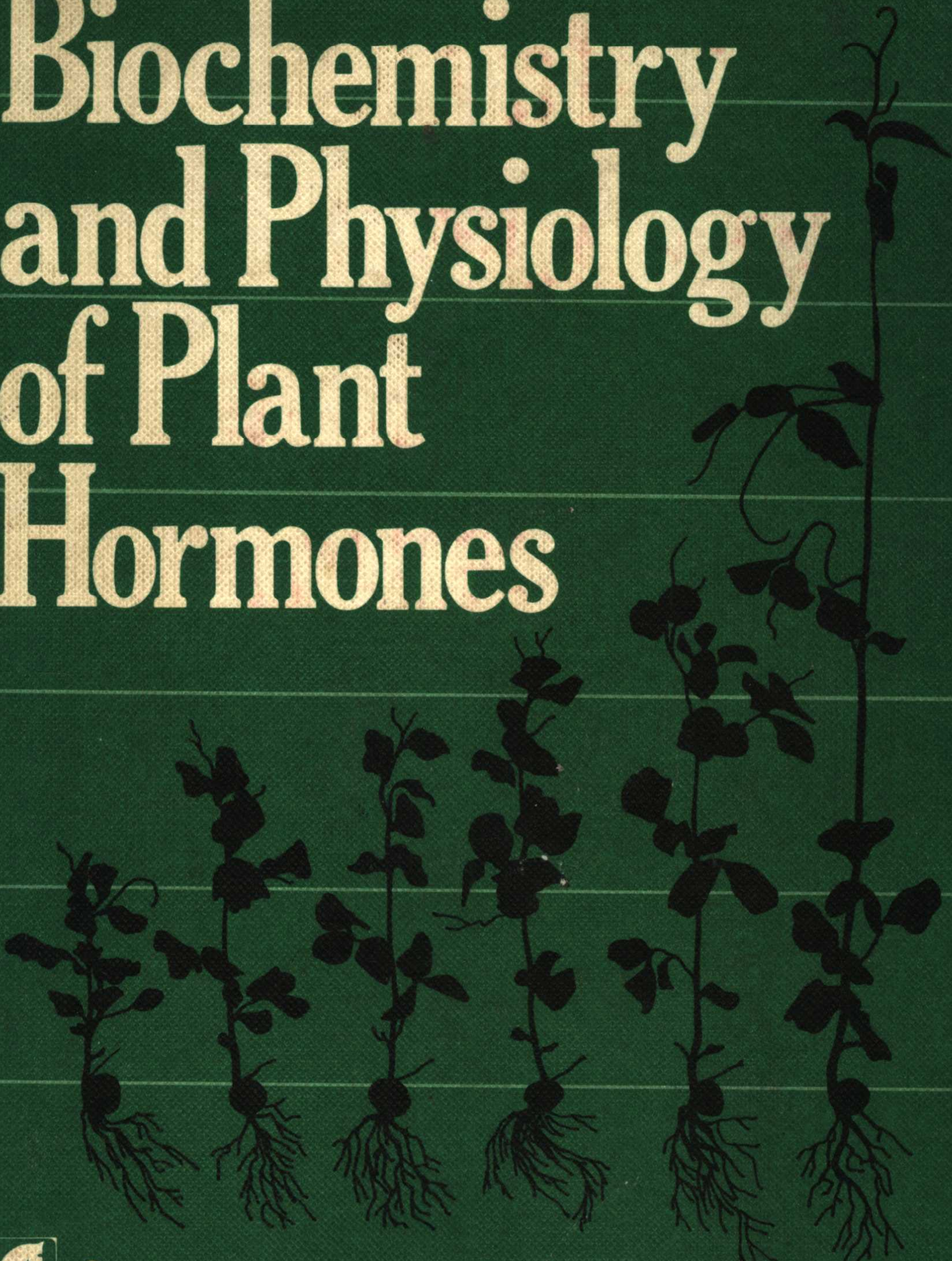
Thomas C. Moore

Biochemistry and Physiology of Plant Hormones



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With 164 Figures

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Preface

Biochemistry and Physiology of Plant Hormones is intended primarily as a textbook or major reference for a one-term intermediate-level or advanced course dealing with hormonal regulation of growth and development of seed plants for students majoring in biology, botany, and applied botany fields such as agronomy, forestry, and horticulture. Additionally, it should be useful to others who wish to become familiar with the topic in relation to their principal student or professional interests in related fields. It is assumed that readers will have a background in fundamental biology, plant physiology, and biochemistry.

The dominant objective of *Biochemistry and Physiology of Plant Hormones* is to summarize, in a reasonably balanced and comprehensive way, the current state of our fundamental knowledge regarding the major kinds of hormones and the phytochrome pigment system. Written primarily for students rather than researchers, the book is purposely brief. Biochemical aspects have been given priority intentionally, somewhat at the expense of physiological considerations. There are extensive citations of the literature—both old and recent—but, it is hoped, not so much documentation as to make the book difficult to read. The specific choices of publications to cite and illustrations to present were made for different reasons, often to illustrate historical development, sometimes to illustrate ideas that later proved invalid, occasionally to exemplify conflicting hypotheses, and most often to illustrate the current state of our knowledge about hormonal phenomena. The lists of references at the ends of the chapters, containing some references which are cited and others that are not, are not intended as comprehensive bibliographies of the most recent, or even exclusively the most important, publications on each subject. Each list is intended both to document the text and provide other examples of the extensive literature on each topic.

An explanation should be given for inclusion of the subject matter comprising Chapter 1, since it is acknowledged that many readers will regard Chapter 1 as quite elementary information with which they already are familiar. That is fully to be expected. But for those readers whose background may be deficient, as has been found to be true of a fair percentage of students, Chapter 1 will provide a reasonable overall introduction to and perspective about growth and development of whole plants throughout ontogeny and set the stage for consideration of hormonal regulation.

Books such as this invariably disappoint some readers, which is to say that they cannot be—perhaps should not even purport to be—all things that all readers might wish or expect. In my judgment, *Biochemistry and Physiology of Plant Hormones* most likely might disappoint some readers in each of two ways. First, the book does not contain as lengthy and integrated a discussion either of the physiological roles of the different kinds of hormones or of hormonal interactions as some readers will wish, although, of course, these topics definitely are covered. To the extent that this is true it is by design. For in my ten years of experience teaching a graduate course in hormonal regulation of plant growth and development, I personally have found that it is more effective to guide students from an information base such as this book provides to a more integrated understanding of regulation of growth and development than to undertake the converse approach. Another way this book might disappoint some prospective users is that it lacks detailed and comprehensive coverage of practical uses of synthetic plant growth regulators, except for synthetic auxins and auxin-type herbicides. Such information is largely beyond the scope of this small volume. Moreover, practical uses of plant growth regulators are covered in many specialized books in agronomy, forestry, and horticulture.

It seems to be a good time in some ways, and not so good a time in other ways, for a new book on the biochemistry and physiology of plant hormones. On the negative side, so far during the decade of the 1970s there seems to be a relative lull in the field as regards dramatic new developments—the "acid growth theory" and other important advancements notwithstanding—compared, let us say, to either of the previous two decades. In view of the relative scarcity of "big news," it could be argued that it is not a particularly good time. But, on the other hand, there is really good and highly significant research going on, and there is a steady output of important new knowledge. The literature—the state of the science—probably is in the best shape ever as far as unequivocal validation of facts and concepts is concerned. It is a time of separation of fact from fiction and devising new approaches to old problems, as well as asking new, important, exciting questions. For these reasons, it seems, therefore, timely for a new book to call attention to this healthy state of the science. In any case, it is an excellent time to be a student at any level of the fascinating subject discussed in *Biochemistry and Physiology of Plant Hormones*.

Acknowledgments

The real credit for *Biochemistry and Physiology of Plant Hormones* ultimately should go to the many Plant Physiologists whose research during the last half century disclosed the information comprising the book. While too numerous to mention individually, the names of many of these scientists are contained in the literature lists at the ends of the chapters. Certain specific contributions by particular authors, of course, are acknowledged also in the forms of citations in the text and notations in legends to figures and tables.

The actual writing and production of the book naturally has involved several forms of assistance by many persons, to all of whom I express my sincere gratitude. For directly supplying or assisting to make available certain illustrations, I thank Douglas O. Adams, James D. Anderson, Gerard W. M. Barendse, Michael L. Evans, Peter Hedden, Hans Kende, Anton Lang, A. Carl Leopold, Morris Lieberman, Bernard O. Phinney, Folke Skoog, Nobutaka Takahashi and Jan A. D. Zeevaart. Donald J. Armstrong and Ralph S. Quatrano are thanked for the advice and technical assistance that they provided regarding various topics. I thank Ellen Witt and Leona Nicholson for typing and clerical assistance, and E. Kay Fernald for photographic service. Mark Licker, Science Editor, and Judi Allen, Production Editor, at Springer-Verlag Inc., New York, and their staff were very helpful throughout the review and production processes. Finally, I wish to acknowledge the financial support provided by the National Science Foundation for those of my own investigations during the past fifteen years which are cited in the book.

Corvallis, Oregon
January, 1979

Thomas C. Moore

Contents

Chapter 1
Introduction

Fundamental Terms and Concepts

The term "development," as it applies to whole seed plants arising by sexual reproduction, denotes the gradual and progressive changes in size, structure, and function which collectively comprise the transformation of a zygote into a mature, reproductive plant. It is also a correct and common practice to speak of the development of particular organs from initials or primordia, and to refer to development of a whole plant from any single cell. Whatever the specific case, development is a gradual process that takes time to be fully realized, generally is accompanied by increases in size and weight, involves the appearance of new structures and functions and the loss of former ones, is characterized by temporal and spatial discontinuities and changes in rate, and eventually slows down or ceases when mature dimensions are reached.

Unfortunately, but perhaps not surprisingly, there is no rigorously standardized terminology applied to the phenomena of plant growth and development. Some physiologists, the author included, consider that there are three interrelated processes that together comprise development, namely, "growth," "cellular differentiation," and "morphogenesis." "Growth" is defined as an irreversible increase in size which is commonly, but not necessarily (e.g., the growth of an etiolated seedling), accompanied by an increase in dry weight and in the amount of protoplasm. Alternatively, it may be viewed as an increase in volume or in length of a plant or plant part. In any case, it must be emphasized that growth can occur only by an increase in volume of the individual cells. Some authors consider cell division as a separate process which accompanies growth in meristems, but a more generally held view is that growth includes cell division as well as cell enlargement.

"Cellular differentiation" is the transformation of apparently genetically identical cells of common derivation from a zygote or other single cell into diversified cells with various biochemical, physiological, and structural specializations. It is the sum of the processes by which specific metabolic competences are acquired or lost and distinguish daughter cells from each other or from the progenitor cell.

"Morphogenesis" is the integration and coordination of growth and differentiative events occurring at the cellular level and is the process which accounts for the origin of morphological characters and gross form.

Other authors have used the terminology somewhat differently. For example, E. W. Sinnott (1960) in a book entitled *Plant Morphogenesis* wrote, "The process of organic *development,* in which are posed the chief problems for the science of morphogenesis, occurs in the great majority of cases as an accompaniment of the process of growth. The association between these two activities (growth and development) is not an invariable one, for there are a few organisms in which growth is completed before development and differentiation are finished, but far more commonly the form and structure of a living thing change while it grows." One example of an exception is the development of the female gametophyte from an 8-nucleate stage in embryo sac development in angiosperms.

Some have employed the term "morphogenesis" in a strictly descriptive sense, essentially as synonymous with classical developmental morphology. More generally and properly, however, it includes, besides descriptive facts as to the origin of form, a study of the results of experimentally controlled development and an analysis of the effects of factors, external and internal, that determine how the development of form proceeds. In other words, it attempts to get at the underlying formativeness in the development of organisms and especially to reach an understanding of the basic fact of which form is the most obvious manifestation, namely, biological organization itself. According to morphogeneticists like Sinnott, "The organism may thus be said to make the cells rather than the cells to make the organism."

F. B. Salisbury and Cleon Ross (1978) used the term "development" (or "morphogenesis") as an inclusive term and regard the phenomenon as consisting of two primary functions: growth and differentiation. They consider growth primarily as an increase in size, and differentiation as the process by which cells become specialized. P. F. Wareing and I. D. J. Phillips (1970) likewise adopted the view that development should be applied in its broadest sense to the whole series of changes which an organism goes through during its life cycle, while noting that it may also be applied to individual organs, to tissues, or even to cells. According to these authors, "plant development" involves both "growth" and "differentiation." "Growth" is used to denote quantitative changes occurring during development and is defined as an irreversible change in the size of a cell, organ, or whole plant. "Differentiation" is applied to qualitative changes. Thus, in their view growth and differentiation are the two major developmental processes. They reserve the term "morphogenesis" as one used by experimental morphologists (morphogeneticists) to denote origin of form. F. C. Steward (1968) employed a quite inclusive connotation of growth. Essentially he used the term "growth" in a very general way to include what others consider more explicitly to be growth, differentiation, and morphogenesis.

With the variable usage of terminology, as has been illustrated, perhaps it is understandable why the coupled terms "growth and development" are used so prevalently. This couplet connotes the kind of concept that James Bonner and A. W. Galston (1952) had when they wrote, "The changing shape, form, degree of differentiation, and state of complexity of the organism constitute the process of development." They viewed "growth" as a quantitative matter concerned with the increasing amount of the organism. On the other hand, "development," in their view, refers to changes in the nature of the growth made by the organism.

Many biologists have emphasized the biological importance of organization and emphasize that the characteristics of life itself are characteristics of a system arising from, and associated with, the organization of materials and processes. It is of utmost importance to keep in mind the fact that there are unique emergent qualities associated with each successively higher level of biological organization—from molecular and subcellular to the levels of cells, tissues, organs, whole organisms, and beyond. In no instance is the cliché that the whole is more than the sum of its parts more vividly exemplified than when we observe the complicated changes which a seed plant manifests during the repeating cycle of development. We can arbitrarily conceive of this cycle as starting with the germination of a seed and continuing with the passage of a juvenile phase of growth and the graduation into maturity. With maturity the organism is capable of shifting from vegetative to reproductive development, with the development of flowers, the development of fruits, and the production again of a new generation of seed. Ultimately, the development of the individual plant ends with senescence and death. This book is concerned with the processes involved in and the mechanisms which control the growth and development of seed plants.

Patterns and Kinetics of Growth in Cells, Tissues, Organs, and Whole Plants

The curve which typically describes the changing size of a growing organism, organ, tissue, cell population, or individual cell is sigmoid in shape (Fig. 1-1a). The sigmoid growth curve can, for convenience, be considered in three parts. First, there is an accelerating phase in which growth starts slowly and gathers momentum. During this period of constantly ac-

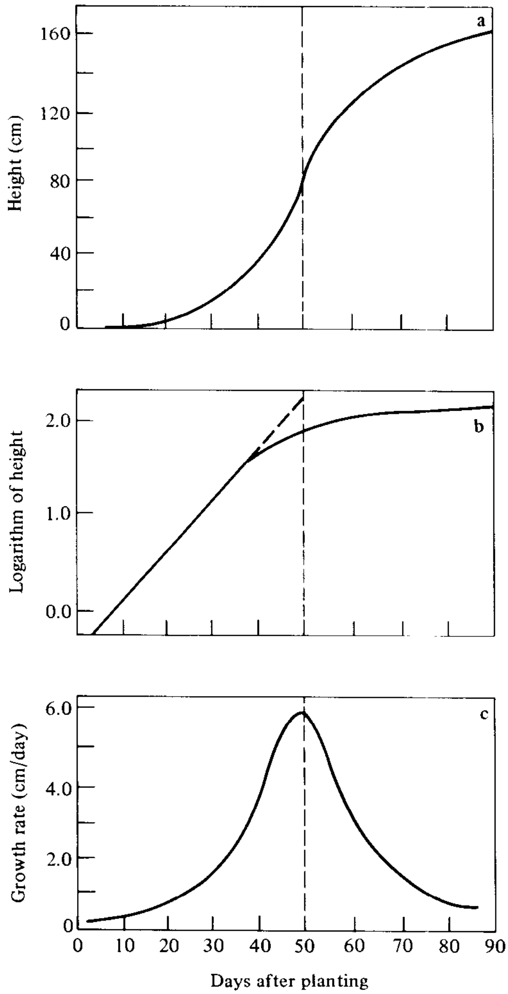

Figure 1-1. Generalized growth curves. **a**, Size-versus-time sigmoid growth curve; **b**, logarithmic growth curve; and **c**, growth rate curve. (Based on data for corn, *Zea mays*, in Whaley, 1961.)

celerating growth rate, increase in size is exponential. When a plant is growing exponentially, it is said to be in the logarithmic phase of its growth. Second, there is either a point of inflection or a phase, more or less protracted, in which the course of growth is approximately linear with time. That is, equal increments of growth tend to occur in equal intervals of time. This is often termed the linear phase of growth. In some cases, however, there is no linear phase but merely a point of inflection in the curve, when the first rising rate of growth gives way to a decreasing rate of growth. Third, there is a phase of declining growth rate until, in fact, growth subsides and the organism may maintain only the size it has already achieved. In annual plants this is followed by senescence and death. In the case of woody perennials, each period of shoot growth is approximately sigmoidal and is followed by dormancy. Shoots of biennials, of course, exhibit two seasons of sigmoidal growth. Instead of plotting merely size versus time (Fig. 1-1a), it is often useful to plot the $\log_e$ of size versus time (Fig. 1-1b) or growth rate versus time (Fig. 1-1c) when analyzing growth. Examples of various specific growth curves and a brief discussion of each follow.

Even the growth of single cells has been demonstrated to be sigmoidal (Fig. 1-2). Organs such as leaves follow a sigmoidal pattern also on the basis of several parameters, including fresh weight, area of lamina, length of lamina, and cell number (Fig. 1-3).

Many fruits exhibit common sigmoid growth curves—e.g., apple (Fig. 1-4), pineapple, strawberry, pea, tomato, etc. However, fruits of many species exhibit more complicated growth curves, which are essentially double sigmoid growth curves. This type of curve is common to probably all the stone fruits such as cherry (Fig. 1-5), apricot, plum, and peach. Such curves are also typical of some nonstone fruits such as fig, grape, and currant. However, neither type of growth curve seems to be distinctive for a particular morphological type of fruit, because there are berries, pomes, and simple and accessory fruits which manifest each.

The double sigmoid growth curve can be explained on the basis of asynchrony of growth of the different parts of the fruit. Two general types of growth centers occur in fleshy fruits, the pericarp and ovule(s). The

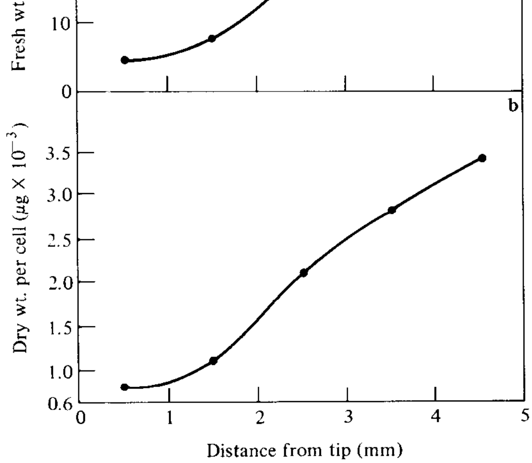

Figure 1-2. Growth curves of single cells in the corn (*Zea mays*) root tip. **a**, Fresh weight; **b**, dry weight. (Redrawn, with permission, from Boss, 1964.)

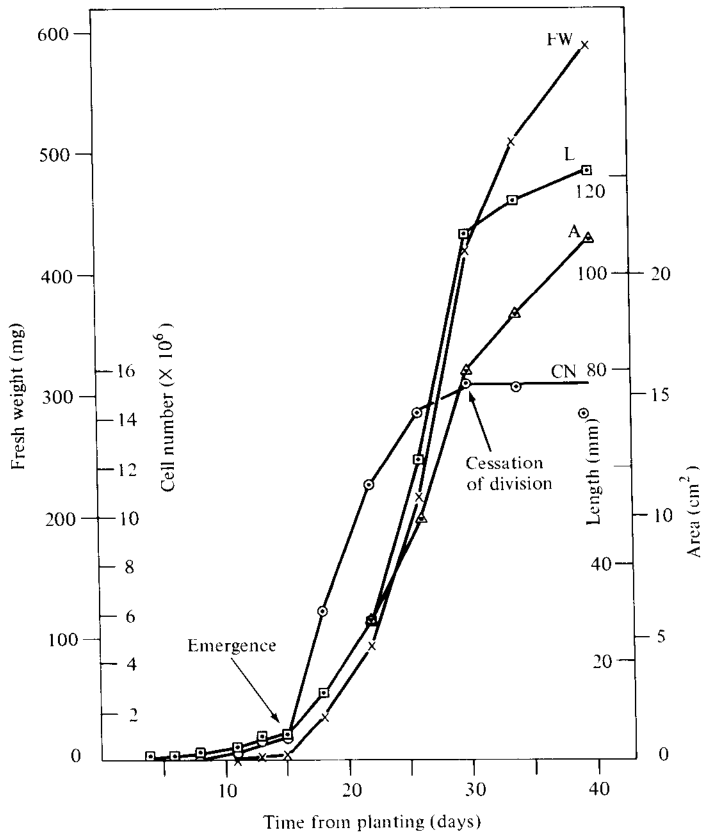

Figure 1-3. Growth curves for leaves of sunflower (*Helianthus annuus*). FW, fresh weight; A, leaf lamina area; L, length; CN, number of cells. (Redrawn, with permission, from Sunderland, 1960.)

growth of the pericarp commonly accounts for the initial enlargement. Growth in later stages generally is associated with seed development.

There is wide variation in the extent to which cell division participates in the growth of fruits, ranging from cases in which cell division (except in the developing seeds) has been completed at the time of pollination (*Ribes*, *Rubus*), to cases in which there is a brief period of cell division just following pollination (tomato, *Citrus*, cucurbits, apple, *Prunus*), or rather extended periods of cell division (strawberry).

The curve describing the kinetics of growth of whole plants also is typically sigmoidal. Herbaceous annual plants, such as garden pea (*Pisum sativum* L.), exhibit a single sigmoid growth curve throughout ontogeny from germination to senescence and death (Fig. 1-6). Size versus time plots of the shoot growth of woody perennials are sigmoidal throughout ontogeny (Fig. 1-7), although there is a gradual progression toward the

Figure 1-4. Growth curves for apple fruits. **a**, Cell number versus fruit weight; **b**, volume and weight versus time after pollination. (Redrawn from data of Bain and Robertson, 1951, in: *Plant Growth and Development*, 2nd ed., by A. C. Leopold and P. E. Kriedemann. Copyright © 1975 by McGraw-Hill Book Company. Used with permission of McGraw-Hill Book Company.)

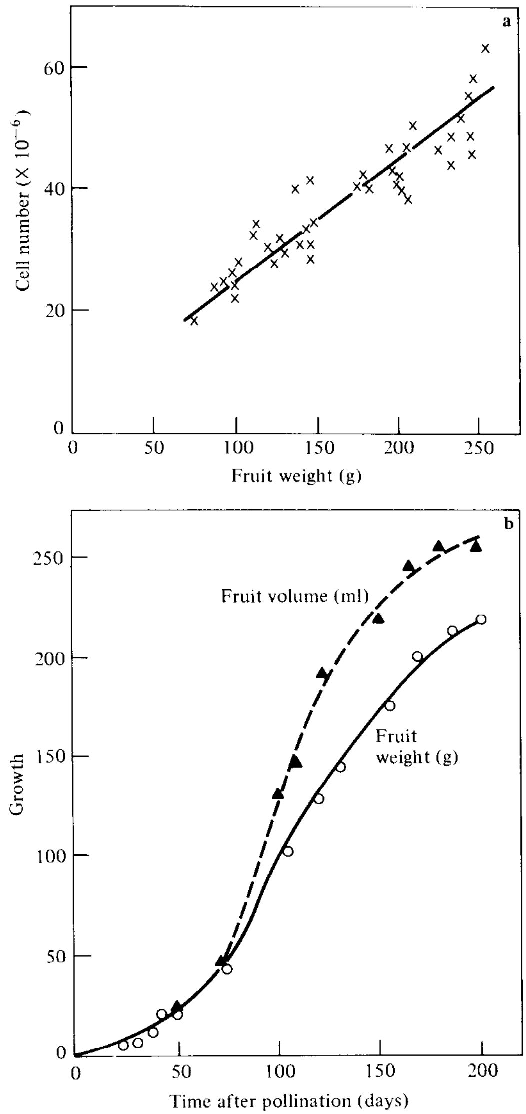

Figure 1-5. Generalized double sigmoid growth curve of cherry. (Redrawn from: *Plant Growth and Development*, 2nd ed., by A. C. Leopold and P. E. Kriedemann. Copyright © 1975 by McGraw-Hill Book Company. Used with permission of McGraw-Hill Book Company.)