plants, chemicals and growth

F. C. Steward
and
A. D. Krikorian

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F. C. STEWARD and A. D. KRIKORIAN

Cornell University

State University of New York at Stony Brook

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Preface

This work was conceived as a concise, technical essay on the general theme covered by its original working title, "Plant Growth Regulators." However, perhaps because our aim was to present a philosophy of the subject rather than yet another compendium describing those chemicals which regulate the growth of plants and detailing the facts of the growth as regulated, the work outgrew its original format. In this, its more extended form, we hope it will be of interest to a wide audience of students, teachers, research workers, and agriculturalists.

Nevertheless, determined attempts were made to restrict its size. We did this because our view is that one will not necessarily learn all about plant growth regulators in general by attempting to know everything about each of them in particular. This is so because it is in the interactions of growth regulators with all other essential features of the responsive system that the truth about them seems to lie.

Therefore, we make no apology for approaching the subject in our own way, for we believe that too much has often been made of the supposed analogy between the plant growth regulators and the hormones of the animal body. Similarly, too little has been made of the special features of the plants, for assuredly they are not animals. No one who studies organisms closely can fail to be impressed by the very different ways in which higher plants and animals are organized and grow. Consequently, contrasts in the way their growth may be regulated (whether endogenously or exogenously) are to be expected and should not be surprising.

Deliberate interventions to modify the way plants grow by the use of chemical agents (whether these are naturally occurring or synthetic) have recently given to biologists new and powerful means to elucidate the many problems of growth and development, even as they have also been exploited for useful, as well as some illicit, ends. For all these reasons, students of biology, or agriculturalists, or even the lay public, should know more about the role of chemical growth regulatory substances in plants; this applies above all to those who advocate their synthesis and application. If this concise treatment contributes to a fresh approach to a most formidable problem, then our efforts will have been rewarded.

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F. C. STEWARD
A. D. KRIKORIAN

Introduction

This book is about chemicals and plants; it is also about growth. Since it concerns plants, it should be of interest to people. In a Western industrialized society, man is more remote than ever from problems of seedtime and harvest, of sowing and of growing crops; nevertheless, he is as dependent as ever on plants for food. He is ever more obtrusively dependent on plants for cleansing the air, which is not only "rendered noxious by animals breathing in it" in the normal balance of nature, but is now unnaturally polluted by industrial wastes and the fossil fuels plundered for energy.

In any work about growth, the fundamental biological questions of our time are encountered. No growth originates *de novo,* despite the recurring furor about the imminence of new life to be created in a test tube. Biochemists may skillfully create intricate molecules and substances, as in the synthesis of the substance that is called a gene, but life requires a degree of organization within which such molecules function far beyond any foreseeable fabrication. There is, as yet, no simple chemical alternative to the ability of cells as they grow to make such complexity out of simple random molecules in their environment. Although we may not yet know why cells, organs, and organisms grow, we do know increasingly how they inherit the details of this propensity. We can also readily observe how they grow as they translate the random molecules of earth and air into form and function.

In the "division of labor" among the parts of complex plants, we know that growth is internally regulated by natural "growth regulatory substances." These substances are not part of the plant's makeup, but are set apart for a more regulatory role. We can also intervene in the normal course of growth with a vast array of chemicals never before encountered by plants to change their behavior, control their pests, and greatly modify their yields of products useful to man. As this occurs in an ever more standardized way and in a mass-produced agriculture, one needs constantly to reflect upon the individual cells and organs to know how a single plant responds and, even more so, to trace the active molecules to their ultimate sites of action.

Whether in the miracle of the natural, regulated control of growth and development, or in the menace of the abuse of fertilizers, herbicides, and pesticides, the chemical controls of plant growth are of absorbing interest and of great importance to man.

Contents

CHAPTER 4. The Induction of Growth in Quiescent Cells

CHAPTER 5. Some Growth Regulatory Systems

CHAPTER 6. Growth-Regulating Effects in Free Cell Systems: Morphogenesis

CHAPTER 7. The Range of Biologically Active Compounds

CHAPTER 8. What Do the Growth-Regulating Substances Do?

CHAPTER 9. Concepts and Interpretations of Growth Regulation

CHAPTER 10. Prospects and Problems

CHAPTER 1 Some Chemical Regulators: Some Biological Responses

Many chemical substances are now applied to affect the growth of flowering plants. The angiosperms are the most highly organized, the most conspicuous plants of the earth's cover, and the most important ones to man in agriculture. Some of the substances used are now so familiar that their names have become household words, e.g., 2,4-D, 2,4-dichlorophenoxyacetic acid, and 2,4,5-T, 2,4,5-trichlorophenoxyacetic acid (Audus, 1964; Barth and Mitchell, 1969; King, 1966). In one way or another all these various regulatory substances intervene and exert recognizable effects upon the overall course of plant growth and development, but they do so in a characteristically nonnutrient way. They act not as substances which are built into the "stuff" of which the plants are made, although they may greatly modify the demand which plants make upon their environment for nutrient substances or for water by their effects.

Among the many regulatory substances in use we have controllable and selective herbicides, as well as some substances, e.g., CMU, 3-[*p*-chlorophenyl]-1,1-dimethylurea, and Ammate, ammonium sulfamate, which cause a total kill; we also have substances that stimulate the rooting of cuttings, e.g., indole-3-butyric acid, IBA (see Fig. 1-1), or that cause leaf (Osborne, 1968) or fruit abscission, e.g., Endothal, disodium 3,6-endoxohexahydrophthalate, or that prevent it (see Fig. 1-2); or those associated with fruit setting and artificial parthenocarpy, e.g., α-naphthaleneacetic acid, NAA (see Fig. 1-3), with stem elongation, e.g., Gibrel, gibberellic acid, or with stem retardation (see Fig. 1-4), e.g., Alar, B-9, or 1,1-dimethylaminosuccinamic acid or Cycocel, 2-chloroethyltrimethylammonium chloride (Cathey, 1964); substances affecting the subtle interactions in nature,

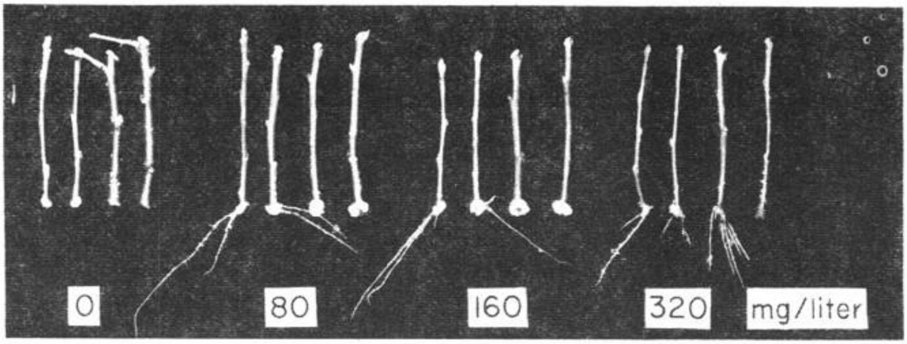

Fig. 1-1. Effects of indolebutyric acid on rooting of apple cuttings after 38 days. In each set of four, the first cuttings retained the shoot tip, the others were taken below the tips. The cuttings were planted in moist peat moss after treatment with the stated concentration for 4 hours. [Photograph supplied by the Boyce Thompson Institute for Plant Research, Inc. (Hitchcock and Zimmerman, 1937/8).]

as between different species (allelopathic substances) (Evenari, 1961; Grümmer, 1961; Muller, 1966; Rice, 1967). There are substances or conditions (temperature, light, etc.) necessary either to promote (e.g., –SH, nitrate) or even inhibit (e.g., coumarin, parasorbic acid, ferulic acid, etc.) germination of seeds in particular instances (Evenari, 1949; Toole *et al.*, 1956), as well as those (e.g., CO_2) to depress (Smock, 1970) or stimulate fruit setting, ripening (e.g., C_2H_4), or respiration (Hansen, 1966). Many useful compilations have been made of these various chemical compounds that have been studied, and of their practical applications (Audus, 1963, 1964; Cathey, 1964; King, 1966; Tukey, 1954).

One can, therefore, approach the problems of growth and growth regulation through the understanding of the roles of chemical substances, natural and synthetic, which intervene to modulate the behavior of the cells of flowering plants, within limits otherwise set by their genetic constitution and after their nutritional demands have been met.

But, inevitably, the observer of growth is impressed with the variety of responses that are involved, such as those to external stimuli and to internally regulated growth correlations. Students of morphology presented adequate descriptions of the regularities and abnormalities of "growth and form" long before their causal explanation could be comprehended in modern terms. One need only look at the transition from the formal descriptive morphology of Goethe (1952) through the attempted causality of Sachs' in terms of the physics and chemistry of his day (Sachs, 1887) which led to the still impressive, experimental approach of Goebel to problems of development [see his *Einleitung in die Experimentelle Morphologie der Pflanzen* (1908)] to see the march of events. But despite the care in ob-

Fig. 1-2. The prevention of apple drop with naphthaleneacetic acid. Left, unsprayed tree; right, sprayed tree. (Photograph courtesy of the U. S. Department of Agriculture.)

servation and the oftentimes definitive descriptions of morphogenetic events in these older works, they lacked the chemical techniques which have produced the present wealth of detailed, but often uncoordinated, observations in the modern period.

A modern student is faced with a seemingly overwhelming array of responses. These include various tropisms (photo- and geotropisms, Curry, 1969; Audus, 1969) and chemotropisms; nastic responses (Ball, 1969); rhythmic phenomena in growth and development (Bünning, 1967; Cumming and Wagner, 1968; Hamner, 1963; Wilkins, 1969); growth of organs by cell division and enlargement; initiation of lateral organs and problems of phyllotaxy (Richards and Schwabe, 1969); the induction of flowering (Lang, 1965) and the formation of such vegetative organs of perennation as buds, tubers, bulbs, etc. (Gregory, 1965; Vegis, 1964; Wareing, 1969a); periodicities in growth as in cambial activity; the regulatory effects of light (Hillman, 1967, 1969; Mohr, 1969) and temperature on growth and form (Chouard, 1960; Hartsema, 1961; Picard, 1968); and the many factors that impinge upon the balance between vegetative growth, flowering (Evans, 1969a), sexuality (see Dzhaparidze, 1967; Heslop-Harrison, 1956, 1964), and fruiting, followed by the formation, dormancy, and germination of seeds (Mayer and Poljakoff-Mayber, 1963; Nikolaeva, 1969). Over and above the problems presented by the more usual forms of develop-

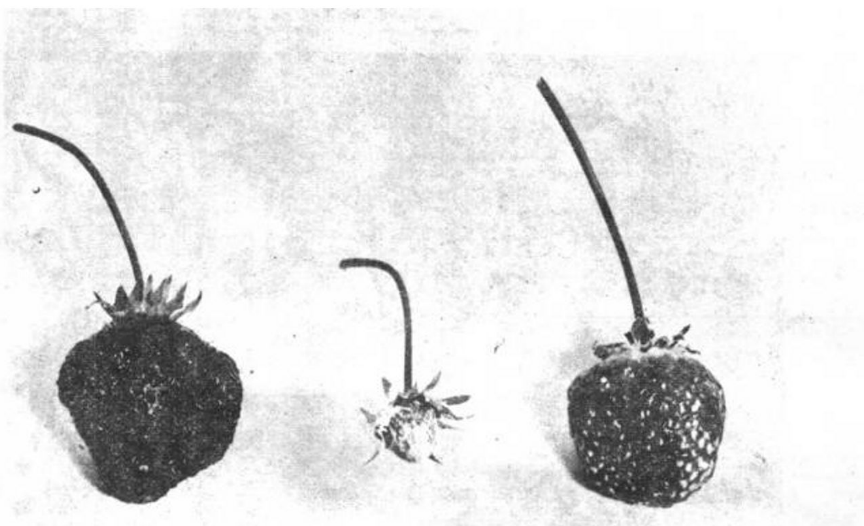

Fig. 1-3. The induction of parthenocarpic strawberry fruits by naphthaleneacetic acid. Left, normal control; center, strawberry which had its achenes removed, treated with lanolin paste; right, strawberry which had its achenes removed, treated with lanolin paste plus naphthaleneacetic acid (100 ppm). [Photograph supplied by Dr. J. P. Nitsch, C.N.R.S., Gif-sur-Yvette (Nitsch, 1950).]

ment enumerated above, there are others presented by abnormal or unusual ones such as the root nodules associated with symbiotic nitrogen fixation (Raggio and Raggio, 1962); the unusual growth of shoot apices which may lead to regular but anomalous phyllotaxy, and the equally anomalous growth of some flowers (for example, of bulb plants) in response to inappropriate exposures to temperature (Hartsema, 1961; Luyten *et al.*, 1926) (Fig. 1-5); and finally such pathological expressions of growth as those seen in teratomas, galls, "witches brooms," and tumors, whether induced by bacteria, insects, mycoplasma, viruses, or even those due to genetic imbalances, as in certain hybrids (see Braun, 1969a). Chemical causation is implicit in all these morphogenetic responses (see Fig. 1-6).

Faced with all this, the trend has been to invent classes of substances that correspond with biological responses, and we now have a plethora of these which include the historically important auxins, the gibberellins, the cytokinins, florigen(s) and anthesin(s), vernalin(s), dormin(s), or abscisin(s), and the recent and even more diffuse class of morphactins. Added to the already formidable array of naturally occurring growth substances are the innumerable products of synthetic chemistry which may also intervene to regulate the growth and behavior of plants. All this has emerged

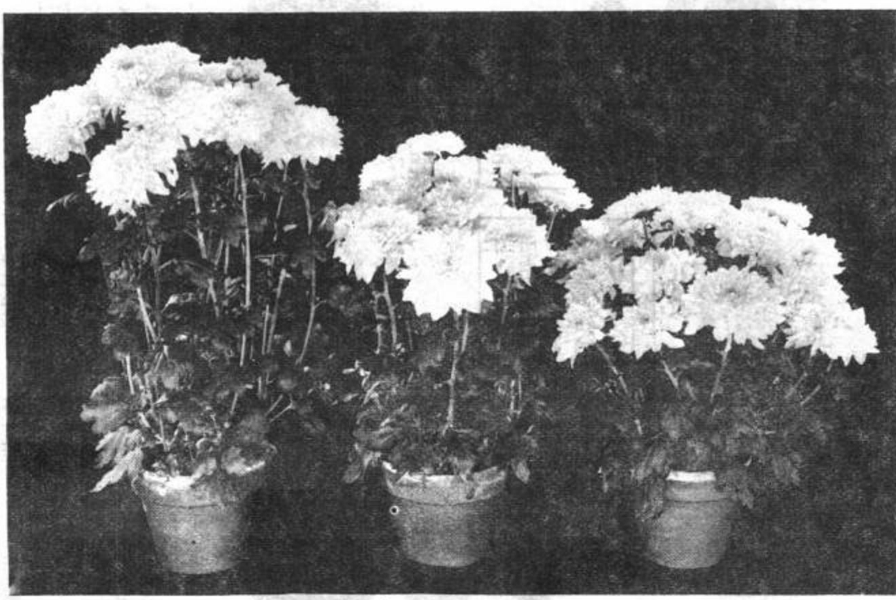

Fig. 1-4. The retardation of stem length in *Chrysanthemum* by B-9 or Alar. Left, control plants; center, plants sprayed with 2500 ppm B-9; right, plants sprayed with 5000 ppm B-9. (Photograph courtesy of the U. S. Department of Agriculture.)

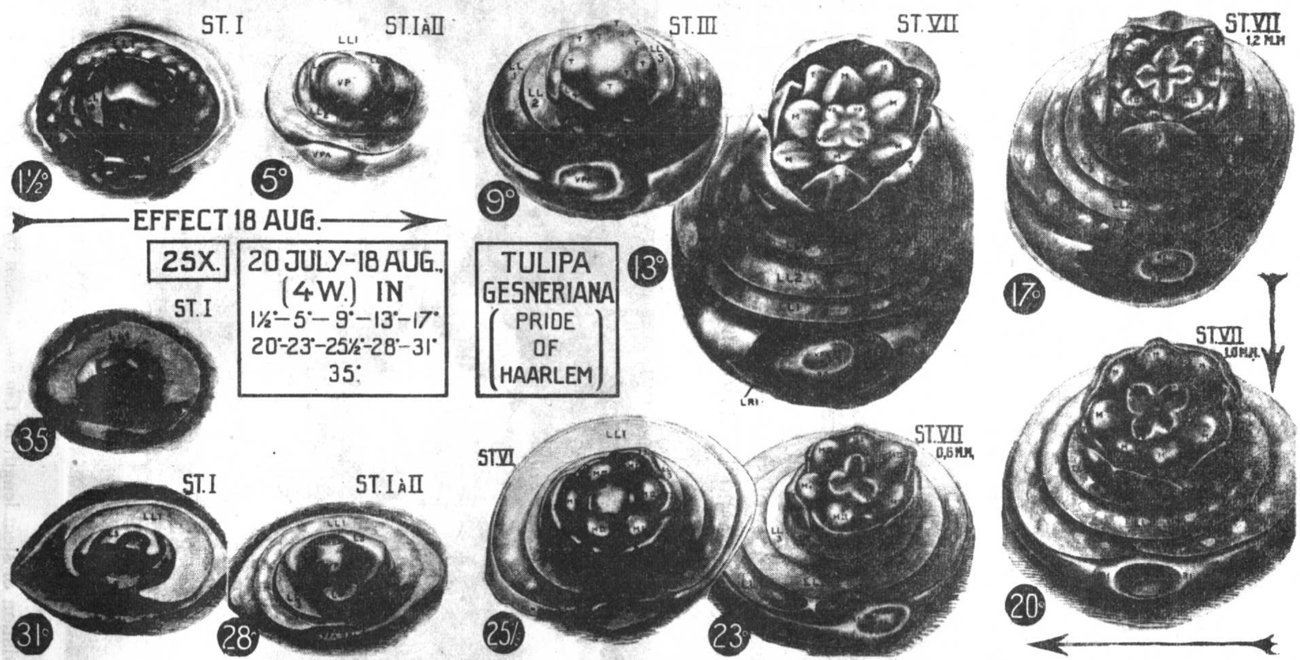

Fig. 1-5. Effects of temperature on the development of flowers in *Tulipa*. The figure shows the apex after 4 weeks of storage at temperatures from 1.5 to 35°C. Normal flowers developed at 23°–25°C; abnormal tetramerous flowers were initiated at 9°–13°C; at 17° to 20°C intermediate numbers of flower parts were formed; at low, i.e., 1.5°C and at high, i.e., 31° and 35°C, the growing point remained vegetative; at 5° and 28°C the growing point was about to initiate flowers; at 9°C only petals had been initiated. This series emphasizes the need for a succession of distinct temperature-dependent morphogenetic stimuli. [Photograph supplied by the Agricultural University. Wageningen (Luyten *et al.*, 1926).]

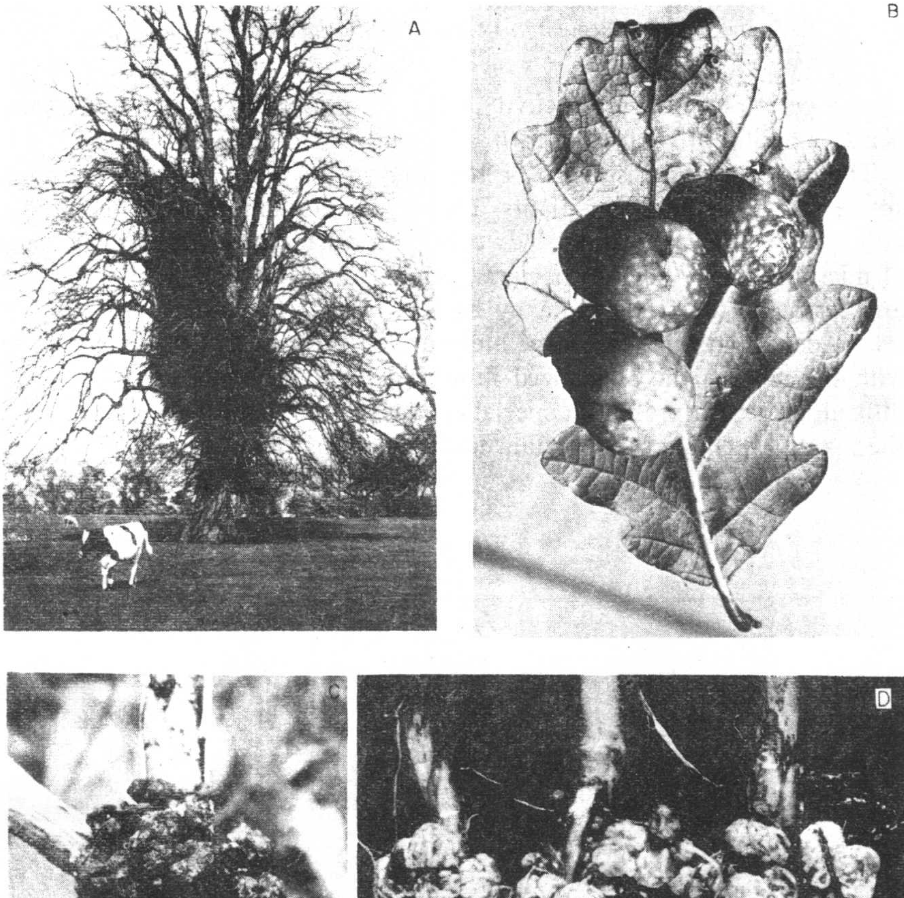

Fig. 1-6. Some anomalous expressions of growth. A, "Witches' broom" on *Tilia*; B, "Cherry gall," due to a cynipid, on veins of *Quercus* leaf; C, galls on bramble (*Rubus*) induced by gall midges; D, root nodules of soybean (*Glycine max*). [Photograph A–C courtesy of M. J. D. Hirons (Darlington, 1968); D, courtesy of the Nitragin Company, Milwaukee.]