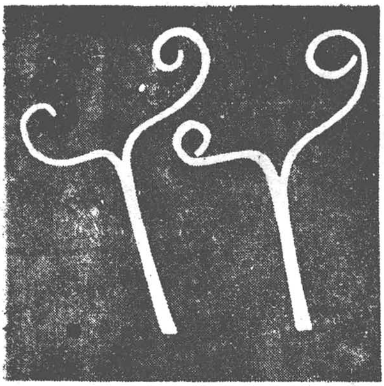
A. CARL LEOPOLD

AUXINS AND PLANT GROWTH



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AUXINS AND PLANT GROWTH

AUXINS

Dedicated to Kenneth V. Thimann

PREFACE

It is my strong conviction that the technology or the applied science in a field of knowledge can make efficient progress only when pursued with sound understanding of the fundamental science upon which that technology is based. Progress in technology without a foundation of fundamental science can take only two forms, I believe. First, minor improvements of applications or treatments which are already essentially known can be made by technology alone; and second, occasional (though rare) accidental discoveries of new applications or treatments may be made. Practically every *major* advance in agricultural technology in the past half century has stemmed from fundamental scientific information.

In view of this strong conviction, it is with considerable alarm that I have become more and more aware that a large proportion of research work, dealing with auxins and growth regulators, is being done without cognizance of what auxins do in plants, how they are formed or destroyed there, or even how one tests for them. This book is written in the hope of providing the agricultural research worker with a brief review of the physiological basis, so far as it is known, upon which the applied technologies rest.

Although several books are currently available in the area of auxin physiology it is my feeling that none of them provide the research man with as complete a general integration of the field as is needed. Especially lacking has been an organized description of the various techniques for obtaining, measuring and identifying auxins, as well as an integration of the fundamental and technological aspects of auxin physiology.

It is my intention to present the general status of knowledge of auxins in plant physiology, and to integrate this fundamental information with each of the applied phases of auxin technology. I have written for the graduate student and the professional research man.

This book does not attempt to review in detail the development of knowledge of auxin physiology, for that is a function of the annual and quarterly reviews. On the other hand, it is not intended that the book should become a manual for the practical applications of auxins.

It is hoped that the book will help to reverse the present tendency to design and carry out research programs involving auxin applications without taking advantage of the great progress that has been made in fundamental physiology. By utilizing the footholds which fundamental discoveries have established, agricultural technology will not be restricted to small consolidations of already known phenomena. Nor will it be restricted only to occasional and accidental discoveries of really new applications. Instead technology may advance in a rapid and orderly manner toward greater and greater efficiency in agriculture at a time, now, when greater agricultural productivity is vital to the peaceful progress of our overpopulated world.

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The literature review for this book was concluded in June, 1954.

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July 14, 1954

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FUNDAMENTALS OF AUXIN ACTION

CHAPTER I

Development of Knowledge of Auxins

The development of the knowledge of auxins, as in the case of nearly all major scientific advances, originated in experimental inquiries by scientists seeking answers to fundamental questions. If any one worker could be identified as first in the field, perhaps it would be Charles Darwin, who in 1881 published his book *The Power of Movement in Plants*. His investigations of fundamental questions about plant tropisms opened a minute gate in the dike of the unknown which ultimately led to the flood of information concerning not only tropisms, but the whole general field of plant growth and the growth hormone as well. In the seventy years following this modest beginning, the role of the growth hormone in plants has been clarified to an almost startling degree. The revealed capacity of many chemical compounds to exploit the same mechanisms in plants has led to a situation nearly approaching an agricultural revolution. Auxins and growth regulators promise to have an impact on agriculture as great as the advent of the windmill or perhaps even of the mechanical harvester. At the same time the impact on the science of plant physiology is as great as that of any other single development since the turn of the century.

DEFINITIONS

There has been a considerable confusion among physiologists and agriculturists concerning the terminology of auxins and growth hormones. Before entering into an extensive discussion of these compounds, it will be well to define our terms.

A *hormone* has been accepted for many years as being "a substance which, produced in any one part of an organism, is transferred to another part and there influences a specific physiological process" (Went and Thimann, 1937, p. 3). It may be advisable to emphasize that hormones are *produced in the organism,* and have the property of serving as chemical messengers, i.e., they are *transported* from a site of formation to a site of action. In contrast to some compounds which act as substrates for general physiological processes, hormones influence "a specific physiological process," and in each case minute amounts produce a large physiological effect. It is evident that, by this definition, the word hormone cannot apply to chemicals produced exclusively in a laboratory, nor to such indigenous compounds as sugars, amino acids or other substrates for growth. Although these latter types of compounds may be transported, none of them are specific in their control of physiological process, as far as is known. The status of vitamins in this nomenclature is not clear. They are considered to be phytohormones by some (Bonner and Bonner, 1948) in cases where they are transported in the plant.

A *phytohormone,* or plant hormone, by simple projection of the preceding definition, is a hormone produced specifically in plants. Within this category lie the growth hormone, the still-theoretical flowering hormone, and possibly some vitamins. A few other phytohormones have been proposed from time to time, but these first two are the only ones generally recognized at present. Thimann (1948) has defined a phytohormone as "an organic substance produced naturally in higher plants, controlling growth or other physiological function at a site remote from its place of production, and active in minute amounts."

The *growth hormone* is the phytohormone which is involved in growth. It is normally essential to growth by cellular enlargement, both in length and in width, and is essential to growth of organs—buds, stems, roots, fruits, and so on.

The term *auxin* was originally suggested to refer to substances which were capable of promoting growth in the manner of the growth hormone (Kögl & Haagen-Smit, 1931). The search for the actual growth hormone in plants led to the isolation of the first pure active compound, not as the indigenous active hormone, but instead as an ingredient of such miscellaneous biological materials as urine, corn oil, and malt extract. The first such compound was named auxin *a,* the second auxin *b.* In keeping with the original intent of the term, auxin will be used to refer to "an organic substance which promotes growth (i.e. irreversible increase in volume) along the longitudinal axis when applied in low concentrations to shoots of plants freed as far as practicable from their own inherent growth-promoting substances" (Thimann, 1948). This growth promotion may be conveniently measured by any of the standard auxin assay methods described in chapter II. The growth hormone itself is an auxin, and so are any other chemical compounds which can bring about the same growth effect.

The term *growth regulator* refers to organic compounds other than nutrients, small amounts of which are capable of modifying growth. Included in this category are substances which either stimulate, inhibit, or otherwise alter growth. It is presumed that growth regulators act upon growth by altering the net effect of the growth hormone, though this is speculative in many cases. Included as growth regulators are such substances as auxins, anti-auxins, epinastic agents and other types of materials as discussed in chapter VII.

In the early literature, the term *heteroauxin* was used to refer to indoleacetic acid (Kögl *et al,* 1934). Since the time when this term was suggested, a great quantity of evidence has accumulated indicating that indoleacetic acid is indeed the commonest growth hormone, and hence to classify it as an "outsider" or heteroauxin seems entirely misleading. In accord with the suggestion by Thimann (1948), we will not use the term in the present discussion.

Unfortunately there has been a considerable usage of the term *hormone* in referring to synthetic auxins or other growth regulators. This has been done largely to strike an appeal to potential buyers of commercial products containing auxins. Such a misuse of terms is definitely confusing and has no place in scientific writing. The term hormone will be used in the present discussion to refer only to substances identical with those known to be indigenous to the plant, and known to act as hormones in the plant.

TROPISMS AND THE EARLY WORKERS

When Charles Darwin turned his brilliant mind to the study of plant movement and tropisms, the first glimmering of the existence of the growth hormone was revealed. Darwin's simple and logical experiments, using canary-grass seedlings, a light source and a razor blade, told him that the tip of the shoot is involved in the overall tropic response. Removal of the tip was followed by loss of sensitivity to light in the coleoptile below. He concluded (1881) that "when seedlings are freely exposed to a lateral light, some influence is transmitted from the upper to the lower part, causing the latter to bend."

Darwin's work aroused much interest and discussion, and led eventually to the work of Boysen-Jensen (1913) in Germany, who found that although severing the oat coleoptile tip removed phototropic sensitivity, simply replacing the tip restored the sensitivity again. He concluded that "the transmission of the irritation is of a material nature produced by concentration changes in the coleoptile tip."

Careful repetition of Boysen-Jensen's work in turn by Paál (1919), a physiologist at Budapest, amply confirmed the earlier work and added one simple but crucial point. Paál found that replacement of the severed tip on one side of the coleoptile stump would produce curvatures away from the treated side. This in fact was a *replacement* of the effect of lateral light by the asymmetrical distribution of some stimulus being produced by the tip. Paál then came to the conclusion that "the tip is the seat of a growth regulating center. In it a substance (or mixture) is formed and internally secreted, and this substance, equally distributed on all sides moves downwards through the living tissue. If the movement of this correlation carrier is disturbed on one side, a growth decrease on that side results, giving rise to curvature of the organ."

By his careful research, Paál had come essentially to the explanation of phototropism, but more important still, he had demonstrated the existence of a "substance" or "correlation carrier," which could control growth processes.

The wider concept of Paál's "correlation carrier" as a growth hormone intimately involved in all plant growth was left for two other minds to grasp almost simultaneously.

EMERGENCE OF THE HORMONE CONCEPT

At the time that Darwin was studying the nature of the phototropic stimulus, Sachs (1880) launched the first theory of substances (which we would now call hormones) controlling plant growth. He envisaged the existence of organ-forming substances moving in various polar patterns, and controlling form and development. Fitting (1909) actually extracted substances from orchid pollen which could cause swelling of the ovary in a manner suggestive of fruit-set. He suggested that these substances were hormones. After Paál's (1919) deduction that specific substances produced in the coleoptile tip were responsible for phototropism, Söding (1923) established that these same substances were capable of stimulating straight growth as well.

The demonstrations of a correlation carrier in oat tips attracted many new workers to the field. Among these were Cholodny (1927) in Russia and F. W. Went (1928) at Utrecht, who independently extended the correlation carrier theory to both phototropism and geotropism. Each of them then came to the conclusion that all tropisms were mediated by a growth hormone system which was essential to all plant growth: "Ohne Wuchsstoff, kein Wachstum"; without auxin there is no growth.

In carrying out his exploration of the role of auxin in growth, Went did two things which opened the field of growth hormones to