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# Weed Physiology

Volume 2: Herbicide Physiology

*Edited by*  
**Stephen O. Duke**

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# Weed Physiology

Volume II

## Herbicide Physiology

Editor

**Stephen O. Duke, Ph.D.**

Plant Physiologist

Weed Biology and Mechanisms  
of Control Research

Southern Weed Science Laboratory

Delta States Research Center

Agricultural Research Service

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## PREFACE

Weeds are plants existing at places and/or times at which they are considered undesirable by man. Thus, man's primary interest in weeds is in finding methods for eliminating their presence. Understanding the physiology of weeds and how it differs from that of crop plants is becoming increasingly important in discovering new chemical, genetic, and cultural methods of controlling weeds. The areas of highest interest and most promise in accomplishing this goal are (1) the physiology of weed reproduction, (2) the ecophysiology of weeds, (3) the mechanisms of herbicide action, and (4) the mechanisms of herbicide resistance and tolerance. Volume I deals with the first two of these areas and Volume II discusses the latter two. In these two volumes we have tried to cover each of the above areas at a level that will be useful to weed scientists, plant physiologists, agricultural chemists, and agricultural ecologists. Also, we have tried to provide enough background information for advanced weed science students to effectively utilize these reviews.

In Chapter 1 of Volume I Professor Gutterman discusses flowering, seed development, and influences during seed maturation on seed germination of annual weeds. The emphasis is on how the mother plant and its environment influences seed development and germination characteristics of weed seed. Chapter 2, by Dr. Egley and me, deals with weed seed germination and dormancy. This is an area of tremendous volumes of data, but of little actual biochemical or physiological information at the tissue or cellular level. Where possible, we have tried to discuss the ecological implications of what is known of the physiology. In Chapter 3, by Professors Kigel and Koller, asexual reproduction of weeds is reviewed. This is increasingly becoming an important area of research because annual and perennial weeds with primarily asexual means of reproduction are becoming more troublesome in many agricultural ecosystems. The next two chapters fall into the realm of weed ecophysiology. Dr. Patterson discusses the comparative ecophysiology of weeds and crops and Professor Putnam covers the area of allelopathy as it pertains to weed physiology. Improving our basic understanding of weed physiology in the context of the biotic and abiotic environments within which weeds exist is important in developing a practical knowledge of physiological factors involved in weed competition, weed population dynamics, and other important weed-related processes of agricultural ecosystems.

Volume II deals with the mechanisms of herbicide action and of resistance and tolerance to herbicides. The first five chapters of this volume cover the effects of herbicides and adjuvants on the physiology of plants. Professor Black's chapter begins by covering the effects of herbicides on photosynthesis, including photosynthetic assimilation of nitrogen, sulfur, and phosphorus. This is followed by Dr. Moreland's chapter on herbicide interactions with plant respiration. The third chapter by Professor Bartels deals with the effects of herbicides on chloroplast and cellular development with emphasis on correlating physiological information with ultrastructural effects. My chapter covers herbicidal effects on non-photosynthetic, biosynthetic processes. Nonorganelle membrane functions as affected by herbicides are discussed in Chapter 5 by Professor Balke. In field situations, herbicides are almost always applied with adjuvants. Thus, inclusion of the chapter by Dr. McWhorter on the physiological effects of adjuvants on plants compliments the coverage of herbicides. The last three chapters of the second volume concern the mechanisms of plant resistance and tolerance to herbicides. Professor Gressel's chapter summarizes resistance due to alteration at the site of action of the herbicide. His chapter deals mainly with resistance to herbicides that inhibit photosystem II, since this is the most studied and best understood mechanism of resistance. How absorption and translocation affect tolerance and susceptibility of plants to herbicides is reviewed by Professor Hess (Chapter 8). In the final chapter, Dr. Shimabukuro discusses detoxication of herbicides as a mechanism of tolerance of plants to herbicides.

The rate of increase in the number of publications in the area of weed physiology is

growing yearly — a trend seen in many other scientific disciplines. In the case of weed physiology, the increase can be related, at least partially, to the more than 20 billion dollar annual economic loss due to weeds in the U.S. alone and the growing realization that physiological information will be necessary to substantially reduce this loss. For instance, much new research effort is being expended on production of herbicide resistance in crop plants with the techniques of molecular biology. This work can not be intelligently conducted without adequate physiological knowledge of the mechanism of action of the herbicide for which resistance is being sought. Thus, mechanism of herbicide action research is being conducted at a previously unparalleled rate and many of the existing gaps in our knowledge that have been pointed out in these volumes may soon be filled. We hope these reviews will be stimulating and useful to those engaged in this effort and to those interested in plant physiology as it relates to weeds and herbicides.

Stephen O. Duke  
February, 1984

## THE EDITOR

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Dr. Duke has authored more than 50 research and review papers and has given more than 25 invited lectures at symposia and seminars. His current research interests include herbicide mechanisms of action, plastid development, seed dormancy, plant secondary metabolism, and naturally-occurring compounds as herbicides.

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The support of my family, particularly that of my wife Barbara, is gratefully acknowledged. Finally, I would like to recognize the many fine teachers that I have had, especially my parents and Professors Adelpia Basford, James Wickliff, and Aubrey Naylor.

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## TABLE OF CONTENTS

### Volume I

#### Reproduction and Ecophysiology

Chapter 1 Flowering, Seed Development, and the Influences During Seed Maturation on Seed Germination of Annual Weeds.....	1
<b>Yitzchak Gutterman</b>	
Chapter 2 Physiology of Weed Seed Dormancy and Germination.....	27
<b>Grant H. Egley and Stephen O. Duke</b>	
Chapter 3 Asexual Reproduction of Weeds .....	65
<b>Jaime Kigel and Dov Koller</b>	
Chapter 4 Comparative Ecophysiology of Weeds and Crops .....	101
<b>David T. Patterson</b>	
Chapter 5 Weed Allelopathy .....	131
<b>Alan R. Putnam</b>	
Index .....	157

### Volume II

#### Herbicide Physiology

Chapter 1 Effects of Herbicides on Photosynthesis.....	1
<b>Clanton C. Black, Jr.</b>	
Chapter 2 Effects of Herbicides on Respiration .....	37
<b>Donald E. Moreland</b>	
Chapter 3 Effects of Herbicides on Chloroplast and Cellular Development.....	63
<b>Paul G. Bartels</b>	
Chapter 4 Effects of Herbicides on Nonphotosynthetic Biosynthetic Processes.....	91
<b>Stephen O. Duke</b>	

Chapter 5	
Herbicide Effects on Membrane Functions .....	113
<b>Nelson E. Balke</b>	
Chapter 6	
The Physiological Effects of Adjuvants on Plants .....	141
<b>C. G. McWhorter</b>	
Chapter 7	
Herbicide Tolerance and Resistance: Alteration of Site of Activity .....	159
<b>Jonathan Gressel</b>	
Chapter 8	
Herbicide Absorption and Translocation and Their Relationship to Plant Tolerances and Susceptibility .....	191
<b>F. Dan Hess</b>	
Chapter 9	
Detoxication of Herbicides .....	215
<b>Richard H. Shimabukuro</b>	
Appendix	
Common and Chemical Names of Herbicides, Insecticides, and Plant Growth Regulators Used in Text .....	241
Index .....	245

Chapter 1

EFFECTS OF HERBICIDES ON PHOTOSYNTHESIS

Clanton C. Black, Jr.

TABLE OF CONTENTS

I.	Introduction .....	2
II.	Plant Photosynthesis .....	2
III.	Assimilatory Activities of Photosynthesis .....	4
	A. The Photochemical Electron-Transport Portion of Photosynthetic Nutrient Assimilation .....	5
	B. Pathways for the Photoassimilation of CO <sub>2</sub> , NO <sub>3</sub> <sup>-</sup> , SO <sub>4</sub> <sup>2-</sup> , and PO <sub>4</sub> <sup>3-</sup> ...	7
	1. CO <sub>2</sub> Assimilation Pathways .....	7
	a. C <sub>4</sub> Photosynthesis .....	8
	b. CO <sub>2</sub> Assimilation During Crassulacean Acid Metabolism .....	12
	2. Nitrogen Assimilation .....	16
	3. Nitrate and Nitrite Photoreduction .....	16
	4. Ammonia Assimilation .....	17
	5. Sulfur Assimilation .....	19
	6. Sulfate Reduction Cycle in Chloroplasts .....	20
	7. Phosphorus Assimilation .....	21
	C. Chloroplast Communication with the Rest of the Plant Cell .....	22
	D. Summary of Photosynthetic Assimilating Activities .....	24
IV.	Herbicide Action in Photosynthesis .....	24
	A. Electron-Transport Inhibitors .....	24
	B. Electron-Transport Diversion .....	28
	C. Uncouplers and Inhibitors of ATP Synthesis .....	29
	D. Carbon Metabolism Inhibitors .....	30
	E. Nitrogen Assimilation Inhibitors .....	31
	F. Photosynthetic Pigment Synthesis Inhibitors .....	32
V.	Summary and Conclusions .....	32
	References .....	33

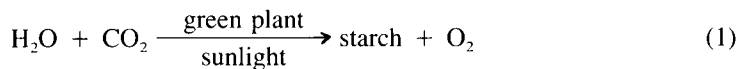
## I. INTRODUCTION

The autotrophic nature of plants due to the presence of photosynthesis is a unique biological feature of plants that also presents a natural site for the development of herbicides. Indeed, photosynthesis inhibitors are widely employed as herbicides today. In addition to being a specific and natural site of herbicide action, any quantitative assessment of physiological processes in green plants will quickly show that photosynthesis is the dominant metabolic process in plants based on measurements such as rates or amounts of product. Again, if one wished to influence adversely the growth of plants, one would correctly try to inhibit photosynthesis. Thus, an understanding of weed physiology and, in turn, the roles and usages of many herbicides must be buttressed by an understanding of photosynthesis.

Both crops and their associated weeds are dependent upon photosynthesis which also may be the common site of herbicide action. Solving the dilemma of how to selectively inhibit photosynthesis in the desired plant species, therefore, is a central topic in chemical weed control research. This chapter presents our understanding of plant photosynthesis primarily at the level of the chloroplast with initial emphasis upon the utilization of light to photoassimilate the essential elements carbon, nitrogen, sulfur, and phosphorus followed by a consideration of the chloroplast as it partitions assimilates with the rest of the plant. Finally, we will consider the action of herbicides and other inhibitors on the physiological and biochemical functions of photosynthesis.

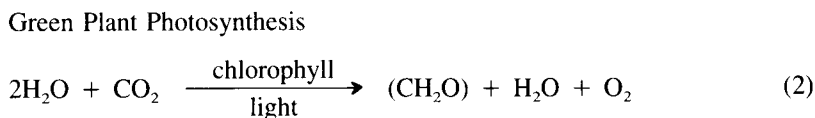
## II. PLANT PHOTOSYNTHESIS

For over a century plant photosynthesis has been understood in terms of involving the use of atmospheric CO<sub>2</sub> to form starch plus the release of O<sub>2</sub> in the aqueous milieu of green cells catalyzed by light and chlorophyll. This early understanding can be presented as:

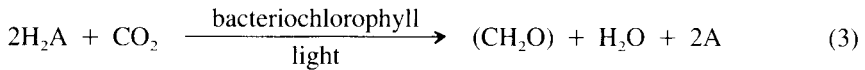


Even today this is a fairly adequate representation of overall photosynthesis which certainly serves to emphasize that much of photosynthesis is related to CO<sub>2</sub> assimilation. Though this fact is true, e.g., about 40% to 45% of a total plant is carbon, we also know that plants photoassimilate other essential elements such as N, S, and P through photosynthesis. Not only do plants utilize photosynthesis to assimilate their essential nutrients, we also know the overall pathways and mechanisms for utilizing light in chloroplasts and we know specific plants including important weeds and crops have developed several assimilatory pathways for the same essential element.

Historically, the dominant model for photosynthesis research which lead to our current understanding of photosynthesis and its diversity come from the thinking of C.B. van Niel. About five decades ago, van Niel<sup>1</sup> reasoned that the overall ideas about green plant photosynthesis (Equation 1) could be modified by comparisons with bacterial photosynthesis. He knew these bacteria required a reduced substance for photosynthesis, e.g., H<sub>2</sub>S, H<sub>2</sub>, acetone, or a variety of oxidizable substances, which he abbreviated H<sub>2</sub>A. He also knew photosynthetic bacteria fixed CO<sub>2</sub>, but did not evolve O<sub>2</sub>. Thus from his comparative thinking he presented green plant and bacterial photosynthesis as:

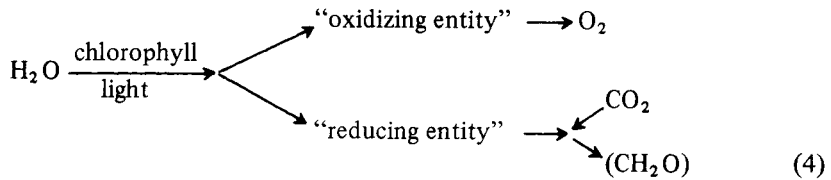


Bacterial Photosynthesis



(CH<sub>2</sub>O) represents a reduced carbon product such as starch.

Such comparisons allowed van Niel to propose that the O<sub>2</sub> evolved during plant photosynthesis originates from H<sub>2</sub>O (compare Equations 2 and 3). And he formulated a model for plant photosynthesis research as:



Though we would change this model somewhat today to show a charge separation as an initial event rather than the photolysis of H<sub>2</sub>O, this model guided photosynthesis research through the next five decades and led to the discovery and characterization of many of the “reducing” and “oxidizing” entities of Equation 4. In addition, the roles of photosynthetic pigments and learning that substances other than CO<sub>2</sub> also are reduced and assimilated during photosynthesis were determined.

We will soon consider these entities, pigments, and substances, but to more clearly grasp photosynthesis research in relationship to herbicide action and weed control research let us consider the times or speeds of the photosynthetic process. About two decades ago Kamen<sup>2</sup> presented an informative way to visualize photosynthesis based on the speed or time required for various steps in photosynthesis to occur. He divided photosynthesis into various processes and research areas based on the logarithm of time in seconds. An appropriately modified representation of his idea that has been discussed recently<sup>3</sup> is given in Figure 1. Think in temporal terms of orders of magnitude of time in seconds to understand Figure 1.

Photosynthesis begins with the absorption of light in about 10<sup>-15</sup> sec followed by photon stabilization as excitation energy in a pigment such as chlorophyll. The excitation energy must result in photochemical conversions into oxidizing and reducing components or the photon will be re-emitted as fluorescence usually by 10<sup>-9</sup> sec. The photochemical formation of oxidizing and reducing components results in photon energy conversion into components that are used in enzyme-catalyzed reactions.

The enzyme-catalyzed reactions of biochemistry require energy and transfer energy to ultimately result in the storage of energy in a variety of substances such as starch. During these biochemical conversions beginning near 10<sup>-7</sup> sec, we begin to find the products of photosynthesis that most of us recognize, such as O<sub>2</sub>, or we first observe the assimilation of CO<sub>2</sub>.

As biochemical processes proceed, other biological processes, such as physiology of cell growth and division or plant growth, interact with photosynthetic biochemistry. Environmental constraints and genetic information also influence the products of photosynthesis. From about 10<sup>1</sup> to 10<sup>9</sup> sec photosynthesis is studied as agriculture and ecology. At these times we recognize higher plants, photosynthetic bacteria, and algae as primary products of photosynthesis; and indeed even other organisms as secondary products of photosynthesis. For the complete process of photosynthesis to occur, from the primary light absorption of (10<sup>-15</sup> sec) to the production of the oldest plants (10<sup>11</sup> sec), a time lapse of 26 orders of magnitude is necessary.<sup>3</sup>

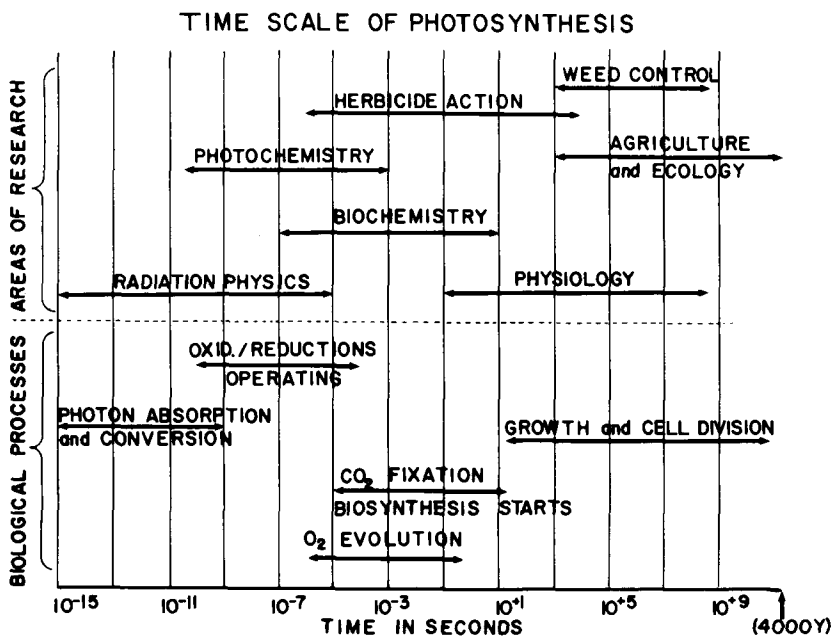


FIGURE 1. Time scale of photosynthesis in seconds. Adapted from Kamen.<sup>2,3</sup> Light absorption in  $10^{-15}$  sec initiates photosynthesis and it ends in the growth of plants with an old plant being the bristle cone pine in about  $10^{11}$  sec.

The time relationships during photosynthesis of herbicide action and weed control research also are shown on Figure 1. The initial events of herbicide action such as binding to an enzyme or membrane can begin to occur near  $10^{-6}$  or  $10^{-7}$  sec if present within a plant at its site of action; but from the time of field application herbicide action will not be this fast. Herbicide action continues over several time orders of magnitude and is studied in weed control research from about  $10^2$  to  $10^8$  sec. Clearly a number of early events, e.g., photon stabilization and photochemistry, have occurred in the overall process of photosynthesis before any known herbicide action occurs. Most herbicide action that we will consider occurs during biochemical reaction times and often is reflected in assimilatory activities of plants.

### III. ASSIMILATORY ACTIVITIES OF PHOTOSYNTHESIS

Photosynthetic assimilation not only involves light,  $\text{CO}_2$ , and  $\text{H}_2\text{O}$  (Equation 1), but the process also provides plants with a mechanism for assimilating other essential elements. Our understanding of photosynthesis as an assimilatory process for essential elements, other than carbon, has been developing over the last half century.<sup>3,4</sup> Assimilation is used in this chapter to refer to the net incorporation of an element into plant organic matter. Some assimilatory processes only occur during photosynthesis, while others utilize the products of photosynthesis. For example, the net fixation and reduction of  $\text{CO}_2$  only occurs during photosynthesis, and photosynthesis is needed for plants to reduce quantities of nitrogen and sulfur. An element such as phosphorus may be assimilated whether nonphotosynthetically, as during oxidative phosphorylation, or photosynthetically, as during photophosphorylation. However, other essential elements, such as metals in metalloenzymes, can be assimilated quite independently of photosynthesis.

If we consider C, N, S, and P assimilation in greater detail, we find that these elements generally are not directly assimilated, but rather are transformed prior to, or during, assimilation.