PLANT GROWTH SUBSTANCES IN AGRICULTURE

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Robert J. Weaver
UNIVERSITY OF CALIFORNIA, DAVIS

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PREFACE

The minute amounts of naturally occurring growth substances that are present in plants control their growth and development. Such processes as root initiation, onset and termination of dormancy and rest, flowering, fruit set and development, abscission, senescence, and rate of growth are under hormonal control. In many agricultural plants, these processes can often be altered to man's benefit by proper application of plant growth substances, and it is quite possible that, in time, all physiological processes in plants will be controlled by application of growth substances.

Since the first plant hormones, the auxins, were identified approximately fifty years ago, rapid advances have been made, in both fundamental and applied research, in the field of plant growth substances. Three new general classes of hormones, the gibberellins, cytokinins, and inhibitors, including abscisic acid, have been recognized, and ethylene has also been recognized as a plant hormone.

This book is written largely from an agricultural point of view and stresses both present and possible future important commercial uses of growth substances in agriculture. However, coverage of the field of growth substances is made more complete by inclusion of chapters on their nomenclature and history, chemical and biological determination,

occurrence and chemical nature, and biological effects and mechanism of action. Some of the theory explaining the effects of exogenous regulators on plants is interwoven throughout the book. A chapter on growth substances in weed control is included since this is still the greatest commercial use for growth substances.

Spray recommendations are given for some crops, but I cannot assume responsibility for success or failure of a growth regulator treatment. Growers should always consult their farm advisor or extension agent before using growth regulators, since recommendations are constantly changing and vary according to local climate and soil.

Discussion of uses for plant regulators for agricultural crops does not necessarily imply that the United States Food and Drug Administration has approved all usages or that the compounds have been registered with the appropriate state or federal agencies. At the present time, with so much emphasis on improvement of the environment and prevention of pollution, registrations are in a state of flux—some of the old compounds are being eliminated and new ones are being added. Care should be taken that compounds are applied according to directions on the manufacturer's label as registered under the Federal Insecticide, Fungicide, and Rodenticide Act. The recommendations on the label should be carefully followed and the local county agent or farm advisor should be consulted if a question or problem arises.

Trade names are sometimes used in the text in combination with chemical names or abbreviations. This practice does not imply endorsement of any single product; trade names are given only as a convenience to the reader.

This textbook is designed principally for classroom instruction and should be appropriate for a one-semester college course in plant growth substances. From my teaching experience I would suggest that Chapter 2 ("Biological and Chemical Determination") can serve as the basis for a laboratory course in growth substances. The figures in this chapter that depict the procedures used in some of the bioassays should also prove helpful for such a course.

An extensive documentation of the literature has been included to provide the reader with sufficient references for an in-depth study of any subject of particular interest. With the present trend toward increased independent study, an extensive literature review is essential.

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ROBERT J. WEAVER

ABBREVIATIONS AND TRADE NAMES

The first-listed common name or abbreviation is the one most commonly used in the text. The synonyms in parentheses are also found in the literature. Trade names (initially capitalized) are sometimes also used as common names.

ABA 3-methyl-5-(1′-hydroxy-4′-oxo-2′,6,6-trimethyl-2′-cyclohexen-1′ yl)-*cis,trans*-2,4-pentadienoic acid (*syn.* abscisic acid; abscisin II; dormin)
abscisic acid *see* ABA
abscisin II *see* ABA
ACPC *see* Amo-1618
Actidione *see* cycloheximide
Alanap *see* NPA
Alar *see* SADH
Amchem 66–329 *see* ethephon
amiben 3-amino-2,5-dichlorobenzoic acid (*syn.* chloramben)
amitrole 3-amino-*s*-triazole (*syn.* 3-amino-1*H*-1,2,4-triazole; amino triazole; ATA)
amino triazole *see* amitrole
Amo-1618 Ammonium (5-hydroxycarvacryl)trimethyl chloride piperidine carboxylate (*syn.* 2-isopropyl-4-dimethylamino-5-methylphenyl 1-piperidine-carboxylate-methochloride, ACPC)
ATA *see* amitrole
BA 6-benzylamino purine (*syn.* benzyladenine; BAP; Verdan)
Banvel D *see* dicamba
BAP *see* BA
benzyladenine *see* BA
B-Nine, B-9, B-995 *see* SADH
BNOA β-naphthoxyacetic acid
BOA benzothiazole-2-oxyacetic acid (*syn.* BTOA)
BOH β-hydroxyethylhydrazine

BTOA *see* BOA
BTP *see* PBA
Captan *N*-trichloromethylmercapto-4-cyclohexene-1,2-dicarboximide
carbaryl *see* Sevin
Cardavan 3-isopropyl-4-dimethylamino-6-methyl-phenyl 1-piperidine carboxylate methyl chloride
CBBP *see* Phosfon-D
CCC (2-chloroethyl)trimethylammonium chloride (*syn.* chlorocholine chloride; chlormequat; Cycocel)
CEPA *see* ethephon
chloramben *see* amiben
chlormequat *see* CCC
chlorocholine chloride *see* CCC
chloroflurenol (a morphactin) 2-chloro-9-hydroxyfluorene-9-carboxylic acid
chloropropham *see* CIPC
CIPC isopropyl *m*-chlorocarbanilate (*syn.* isopropyl *N*-(3-chlorophenyl)carbamate; chloropropham)
CO11 *N*-dimethylamino maleamic acid
3-CP 3-chlorophenoxy-α-propionic acid
3-CPA 3-chlorophenoxy-α-propionamide
4-CPA 4-chlorophenoxyacetic acid (*syn.* *p*-chlorophenoxyacetic acid; PCPA)
cycloheximide 3-[2-(3,5-dimethyl-2-oxocyclohexyl)-2-hydroxyethyl]-glutarimide (*syn.* isocyloheximide; Actidione)
Cycocel *see* CCC
2,4-D 2,4-dichlorophenoxyacetic acid
dalapon 2,2-dichloropropionic acid
2,4-DB 4-(2,4-dichlorophenoxy)-butyric acid
2,4-DEB 2-(2,4-dichlorophenoxy)ethyl benzoate
DEF tributylphosphorotrithioate
2,4-DEP tris[2-(2,4-dichlorophenoxy)ethyl] phosphite (*syn.* Falone; Falodin)
2,4-DES *see* sesone
2,6-D 2,6-dichlorophenoxyacetic acid
dicamba 3,6-dichloro-*o*-anisic acid (*syn.* Banvel D; mediben; 2-methoxy-3,6-dichloro benzoic acid)
dichlorprop *see* 2,4-DP
diuron 3-(3,4-dichlorophenyl)-1,1-dimethylurea
DMSO dimethylsulfoxide
DNA desoxyribonucleic acid
DNOC 4,6-dinitro-*o*-cresol or sodium 4,6-dinitro-*o*-cresylate
dormin *see* ABA
2,4-DP 2-(2,4-dichlorophenoxy)-propionic acid (*syn.* dichloroprop)
Duraset *N-meta*-tolyl phthalamic acid (*syn.* 7R5)
EDNA *N,N'*-dinitroethylenediamine
EDTA ethylenediaminetetraacetic acid (*syn.* (ethylenedinitrilo)tetraacetic acid)
EHPP ethylhydrogen 1-propylphosphonate
Elgetol sodium 4,6-dinitro-*o*-cresylate; *see* DNOC
endothall 7-oxabicyclo(2.2.1)-heptane-2,3-dicarboxylic acid (*syn.* 3,6-endoxohexahydrophthalic acid)
ethephon (2-chloroethyl)phosphonic acid (*syn.* Ethrel; CEPA; Amchem 66-329)
Ethrel *see* ethephon
Falodin *see* 2,4-DEP
Falone *see* 2,4-DEP

FAP *see* kinetin

FeEDDA Fe-ethylenediamine-di-(*o*-hydroxyphenol) acetic acid

fenoprop *see* 2,4,5-TP

Ferbam ferric dimethyl dithiocarbamate

FW-450 sodium salt of α,β-dichloroisobutyric acid (*syn.* Mendok)

GA_3 gibberellic acid (2β,4a,7-trihydroxy-1-methyl-8-methylene-4aα,4bβ,-gibb-3-ene-1α,10β-dicarboxylic acid, 1,4a-lactone) (Subscripts indicate specific analogues, such as GA_1, GA_2.)

Gibberellin(s) One or more of the known gibberellins (see GA_3). General references to exogenous gibberellins may be assumed to refer to GA_3 or KGA_3, commercially available compounds that have equal activity when used on an acid equivalent basis.

HAN a petroleum fraction of high aromatic content (approximately 87 percent by weight)

heteroauxin *see* IAA

IAA indoleacetic acid (*syn.* indole-3-acetic acid; 3-indoleacetic acid; indolylacetic acid; heteroauxin)

IAAld indoleacetaldehyde (*syn.* indole-3-acetaldehyde)

IAEt ethylindoleacetate (*syn.* ethyl-3-indoleacetate; indole-3-ethylacetate)

IAMe methylindoleacetate (*syn.* methyl-3-indoleacetate; indole-3-methylacetate)

IAN indoleacetonitrile (*syn.* indole-3-acetonitrile)

IBA indolebutyric acid (*syn.* indole-3-butyric acid)

indoleacetic acid *see* IAA

2iP 6-(γ,γ-dimethylallylamino)-purine

IPA indolepropionic acid

IPC isopropyl carbanilate (*syn.* isopropyl *N*-phenylcarbamate, propham)

IPyA indolepyruvic acid (*syn.* indole-3-pyruvic acid)

isocycloheximide *see* cylcohexamide

IT 3233 (a morphactin) *N*-butyl-9-hydroxyfluorene-9-carboxylate

IT 3456 (a morphactin) methyl-2-chloro-9-hydroxyfluorene-9-carboxylate

KGA_3 potassium gibberellate (potassium salt of GA_3)

kinetin 6-furfurylamino purine (*syn.* *N*-furfuryladenine, FAP)

maleic hydrazide *see* MH

MCPA [(4-chloro-*o*-tolyl)oxy]-acetic acid (*syn.* 4-chloro-2-methylphenoxyacetic acid, Methoxone)

MCPB 4-[(4-chloro-*o*-tolyl)oxy]-butyric acid (*syn.* 4-chloro-2-methylphenoxybutyric acid)

MCPES 2-[(4-chloro-*o*-tolyl)-oxy]ethyl sodium sulfate

MCPP 2-[(4-chloro-*o*-tolyl)oxy]-propionic acid (*syn.* 2-(2-methyl-4-chlorophenoxy)propionic acid, mecoprop)

mecoprop *see* MCPP

mediben *see* dicamba

MENA methyl ester of naphthaleneacetic acid

Mendok *see* FW-450

Methoxone *see* MCPA

MH 1,2-dihydro-3,6-pyridazinedione (*syn.* 6-hydroxy-3-(2*H*)-pyridazinone, maleic hydrazide)

NAA naphthaleneacetic acid (*syn.* α-naphthaleneacetic acid)

NAAm naphthaleneacetamide (*syn.* NAD, NAAmide)

NAAmide *see* NAAm

Nacconol NR an alkylarylsulfonate

NAD *see* NAAm
naptalam *see* NPA
NPA *N*-1-naphthylphthalamic acid (*syn.* naptalam, Alanap)
paraquat 1,1′-dimethyl-4,4′-bipyridinium ion
PBA 6-(benzylamino)-9-(2-tetrahydropyranyl)-9*H*-purine (*syn.* SD8339, BTP)
PCPA *see* 4-CPA
Phosfon *see* Phosfon-D
Phosfon-D 2,4-dichlorobenzyltributylphosphonium chloride (*syn.* Phosfon, CBBP)
Phosfon-S ammonium analogue of Phosfon-D
Phygon XL 2,3-dichloro-1,4-naphthoquinone
picloram 4-amino-3,5,6-trichloropicolinic acid (*syn.* Tordon)
POA phenoxyacetic acid
propham *see* IPC
QC 8-hydroxyquinoline citrate
7R5 *see* Duraset
RNA ribonucleic acid
SADH succinic acid-2,2-dimethylhydrazide (*syn. N,N*-dimethylaminosuccinamic acid, Alar, B-Nine, B-9, B-995)
SAPL *N*-pyrrolidino-succinamic acid
SD8339 *see* PBA
sesone 2-(2,4-dichlorophenoxy)-ethyl sodium sulfate (*syn.* 2,4-DES)
Sevin 1-naphthyl *N*-methyl carbamate (*syn.* carbaryl)
silvex *see* 2,4,5-TP
simazine 2-chloro-4,6-bis(ethylamino)-*s*-triazine
2,4,5-T 2,4,5-trichlorophenoxyacetic acid
2,4,5-TB 2,4,5-trichlorophenoxybutyric acid
2,3,5,6-TBA 2,3,5,6-tetrachlorobenzoic acid
2,3,6-TBA 2,3,6-trichlorobenzoic acid
2,4,5-TES sodium 2-(2,4,5-trichlorophenoxy)ethyl sulfate
TIBA 2,3,5-triiodobenzoic acid
Tordon *see* picloram
2,4,5-TP 2-(2,4,5-trichlorophenoxy)propionic acid (*syn.* fenoprop, silvex)
UDMH unsymmetrical dimethylhydrazine
Verdan *see* BA
zeatin 6-(4-hydroxy-3-methyl-2-butenylamino)purine

CONTENTS

Chapter 1

NOMENCLATURE AND HISTORICAL ASPECTS

Plant growth substances play a major role in plant growth and development. This fact was stated by Went many years ago in his now-famous pronouncement, *Ohne Wuchstoff, kein Wachstum* ("Without growth substance, no growth"). Went found that to grow in length, tissues must receive growth substances. Although the naturally occurring (endogenous) growth substances normally control plant growth, modifications of growth can be produced by applications of exogenous growth substances, some of which may produce effects beneficial to man.

Research on naturally occurring growth substances is gradually revealing the hormonal control mechanisms of plant growth and development. Both these experimental studies and basic research have led to the use of synthetic growth substances in agriculture, where they have assumed an importance equal to that of pesticides and fungicides. Plant regulators are now widely used in weed control, control of fruit development, defoliation, propagation, and size control.

NOMENCLATURE OF PLANT GROWTH SUBSTANCES

General Terms

A definition of plant growth substances is indeed a prerequisite to any study of their historical development and is of utmost importance for those desiring to communicate intelligently on the subject. At present, four general classes of plant hormones are recognized: auxins, gibberellins, cytokinins, and inhibitors. Inhibitors will be considered to be a fourth class of plant regulators here, although they do not comprise such a clearly delineated group as the other three. The hormonal properties of ethylene have also been recognized.

The word "hormone" was first coined by animal physiologists (Bayliss and Starling, 1904). Historically there has been considerable confusion about growth substance terminology. In 1951 K. V. Thimann, President of the American Society of Plant Physiologists, resolved to clarify this terminology and suggested the appointment of a committee to propose a uniform nomenclature for growth substances (van Overbeek *et al.*, 1954). The definitions recommended by that committee will be used in this text. For nomenclature introduced subsequent to the work of this committee, the most commonly accepted definitions will be used.

Plant regulators are defined as organic compounds—other than nutrients—which, in small amounts, promote, inhibit, or otherwise modify any plant physiological process *Nutrients* are defined as materials that supply the plants with energy or essential mineral elements. *Plant hormones* (synonym: *phytohormones*) are regulators produced by plants, which, in low concentrations, regulate plant physiological processes. Hormones usually move within the plant from a site of production to a site of action.

The term "hormone," correctly used, is restricted to naturally occurring plant products. The term "regulator," however, is not necessarily restricted to synthetic compounds but can also include hormones. The term "regulator" has very wide boundaries. It can apply to any material that modifies a plant physiological process. The term should be used instead of "hormone" when referring to agricultural chemicals used for crop control. The word "regulator" may be further defined by adding to it the name of the process that it influences. For example, *growth regulators* (synonym: *growth substances*), regulators that affect growth, include the auxins. *Growth hormones,* hormones that

regulate growth, include, among others, the B-complex vitamins, which are required for root growth and are produced primarily in the shoot. *Flowering regulators*, if they exist, are regulators that induce flowering; *flowering hormones*, if they exist, are hormones that initiate the formation of floral primordia or promote their development.

Auxins

Auxin is a generic term for a group of compounds characterized by their capacity to induce elongation in shoot cells. Some auxins are naturally occurring, others are produced synthetically. Auxins resemble IAA in the physiological action they induce within plant cells, the most critical of which is elongation. These compounds are generally either acids with an unsaturated cyclic nucleus or derivatives of such acids. *Auxin precursors* are compounds that can be converted to auxins in the plant. *Antiauxins* are compounds that inhibit the action of auxins, presumably by competing with them for the same points of attachment on a receptor substance or substances. By increasing the concentration of auxin, the inhibitory effect of some antiauxins can be completely overcome. It should be emphasized that none of these terms are mutually exclusive; for example, under certain circumstances some compounds can be auxins as well as antiauxins.

There are other inhibitors of auxin action that cannot be classified as antiauxins and are not believed to retard auxin action by direct competition with auxin for the same points of attachment. Increasing the concentration of auxin cannot completely overcome their inhibitory effect.

Gibberellins

In the years since the committee on terminology met in the early 1950's, there has been rapid development of three other main types of plant regulators: gibberellins, cytokinins, and inhibitors. Ethylene has also been recognized as a plant hormone. A *gibberellin* may be defined as a compound that has a gibbane skeleton (Fig. 3–3) and that stimulates cell division or cell elongation or both (Paleg, 1965). Gibberellin can cause a striking increase in shoot elongation in many species that is especially marked when certain dwarf mutants are treated. For example, when some dwarf mutants of maize and peas are treated with gibberellin, they grow very rapidly and become as tall as untreated normal plants. Apparently, the failure of these dwarf mutants to produce enough gibberellin for normal growth can be remedied by appli-