Plant Hormones

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Biosynthesis, Signal Transduction, Action!

Revised Third Edition

Edited by

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Springer

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The cover picture shows Mendel's dwarf (*le-1*, left) and tall (*LE*, right) peas. The tall, wild-type peas possess a gene encoding gibberellin 3â-hydroxylase (GA 3-oxidase) that converts GA_{20} to GA_1. GA_1 (inset) promotes stem elongation whereas GA_{20} is inactive. Tall plants possess a relatively high level of GA_1 but the level in dwarf plants is much lower. In the mutant dwarf plants the gene differs by one base and the protein by one amino acid from the wild-type tall and the enzyme activity is $1/20^{th}$ of the level in the tall plants (see Chapters A2, B2 and B7).

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Dedicated to
The late Arthur W. Galston, Richard P. Pharis
and to the memory of Kenneth. V. Thimann and A. Carl Leopold.
Gentlemen researchers in the field of plant hormones.

PLANT HORMONES:
Biosynthesis, Signal Transduction, Action!

Revised 3rd Edition 2010

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PREFACE TO THE REVISED VERSION

What an amazing period it has been since the third edition was published! The auxin receptor was discovered, followed shortly by the gibberellin receptor. Both turned out to be proteins involved in the targeting of negative repressors for destruction, so releasing the plus-hormone default developmental pathway or morphology. Not only that, but shortly thereafter the receptor for jasmonic acid was discovered to be closely related to the auxin receptor, though jasmonic acid needs to form a conjugate before it is active, adding a twist to the established story. Meanwhile many receptors have been proposed for abscisic acid, and while some of these have been subsequently disproved, creating quite a bit of confusion, there is even the suggestion there may indeed be multiple ABA receptors thus accounting for both the reports and the widely disparate actions of ABA.

The last 2–3 years have also seen the advent of two new hormones, or more precisely one new hormone and the final elucidation of one first proposed over 70 years ago. Thus florigen, the flowering hormone, has finally been shown to be a phloem-transported protein, rather than a small molecule on the model of previously known plant hormones. Add to that a branching hormone (as explaining branching solely on auxin always had some difficulties). This branching hormone proved to be in a class of chemicals known as strigolactones for their ability to cause germination of parasitic *Striga* or witch-weed seeds; clearly a compound of multiple roles in nature.

This revision includes information on all the above developments, in addition to all the material originally in the 3rd edition. The additions to the chapters already present can be found immediately following the references to the chapters in question; each includes further references at the end of the addition. The two new chapters, on florigen and strigolactones, are in section E numbered E2A (following chapter E2) and E3A (following chapter E3), placing them in a logical order as a plant is followed from vegetative plant through to reproduction.

The book thus provides researchers and students with an even more comprehensive coverage of the Plant Hormones, how they are made, what they do, and how they do it!

Peter J. Davies
Ithaca, New York
August 2009

PREFACE

Plant hormones play a crucial role in controlling the way in which plants grow and develop. While metabolism provides the power and building blocks for plant life, it is the hormones that regulate the speed of growth of the individual parts and integrate these parts to produce the form that we recognize as a plant. In addition, they play a controlling role in the processes of reproduction. This book is a description of these natural chemicals: how they are synthesized and metabolized; how they work; what we know of the molecular aspects of the transduction of the hormonal signal; a description of some of the roles they play in regulating plant growth and development; their role in stimulating defensive responses; and how we measure them. Emphasis has also been placed on the new findings on plant hormones deriving from the expanding use of molecular biology as a tool to understand these fascinating regulatory molecules. Even at the present time, when the role of genes in regulating all aspects of growth and development is considered of prime importance, it is still clear that the path of development is nonetheless very much under hormonal control, either via changes in hormone levels in response to changes in gene transcription, or with the hormones themselves as regulators of gene transcription.

This is not a conference proceedings, but a selected collection of newly written, integrated, illustrated reviews describing our knowledge of plant hormones, and the experimental work which is the foundation of this knowledge. The aim of this book is to *tell a story* of what is known at the present time about plant hormones. This volume forms the third edition of a book originally published in 1987 under the title *Plant Hormones and Their Role in Plant Growth and Development,* with the second edition, published in 1995, being titled *Plant Hormones: Physiology, Biochemistry and Molecular Biology*. The title has been changed again from the previous editions in order to reflect the changing nature of the field of plant hormones. The changes that have taken place in the nine years since the last edition are particularly striking: genetics and mutations have moved from one chapter to almost all, Arabidopsis has gone from a mention to central stage in almost every chapter, signal transduction has changed from one example to a major section, the concept of negative regulators has emerged and the role of signal destruction has become an underlying theme. The new edition bears only a superficial resemblance to its first forebear!

The information in these pages is directed at advanced students and professionals in the plant sciences: molecular biologists, botanists, biochemists, or those in the horticultural, agricultural and forestry sciences. It should also form an invaluable reference to molecular biologists from other disciplines who have become aware of the fact that plants form an exiting class of organisms for the study of development, and who need information on the regulators of development that are exclusive to plants. It is intended that the book should serve as a text and guide to the literature for graduate level courses in the plant hormones, or as a part of courses in plant, comparative, or molecular aspects of development. Scientists in other disciplines who wish to know more about the plant hormones and their role in plants should also find this volume a valuable resource. It is hoped that anyone with a reasonable scientific background can find valuable information in this book expounded in an understandable fashion.

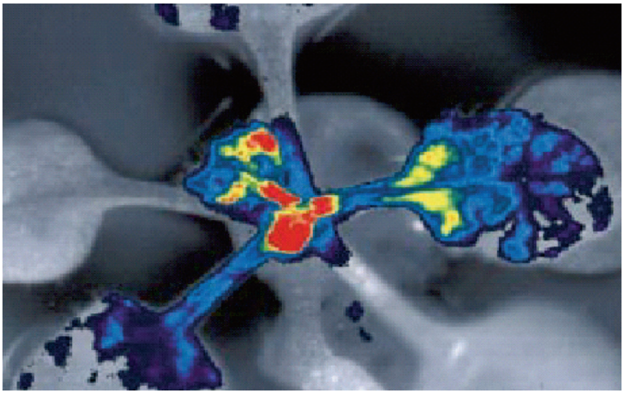
Gone are the days when one person could write a comprehensive book in an area such as plant hormones. I have thus drawn together a team of fifty one experts who have individually or jointly written about their own area. At my direction they have attempted to tell a story in a way that will be both informative and interesting. Their styles and approaches vary, because they each have a tale to tell from their own perspective. The choice of topics has been my own. Within each topic the coverage and approach has been decided by the authors. While the opinions expressed by the authors are their own, they are, in general, also mine, because I knew their perspective before I invited them to join the project.

Where appropriate the reader will find cross references between chapters. In addition the extensive, sub-divided index at the end of the volume should allow this book to be used as a reference to find individual pieces of information. Sometimes the same information can be found in more than one location, though usually from a different perspective. Rather than edit out such duplication, I have chosen to let it remain so that the complete story on any topic can be obtained without having to excessively transfer between chapters.

A volume such as this cannot be encyclopedic. Nevertheless, we have covered the majority of topics in which active research is taking place. The author of each chapter has provided a set of references that will guide the reader to further information in the area. So as not to disrupt the narrative excessively, and to maintain the book at a reasonable length, the chapter authors were asked to severely limit the number of citations to those papers of greatest or most recent significance, and to also bring to the attention of readers other reviews in which other papers are cited and discussed, so that you, the reader, can find the original information. As such a reference citation at any point within the chapters may be to a later paper in a series, or to a review covering the material, from which the original citation(s) can be obtained if desired; it does not imply that this is the original reference to the work discussed. The authors wish to apologize to their colleagues whose significant work is not directly cited for their lack of inclusion due to the strictures placed on them by the editor.

I would like to thank all the authors who made this volume possible, and produced their chapters not only in timely fashion, but in line with the many restrictions placed on them by this editor. Finally I would like to thank my wife, Linda, who put up with my many hours of absences during which I edited, produced and formatted this book, and to the continuing support and cooperation of Jacco Flipsen and Noeline Gibson from Kluwer Academic Publishers.

Peter J. Davies
Ithaca, New York
June 2004



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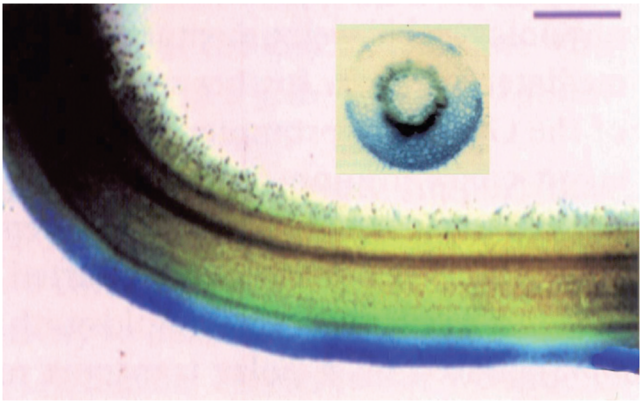

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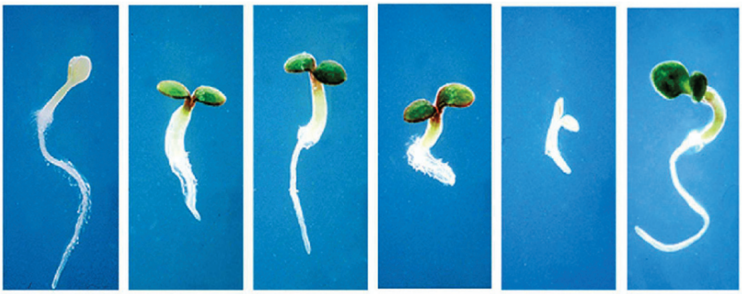

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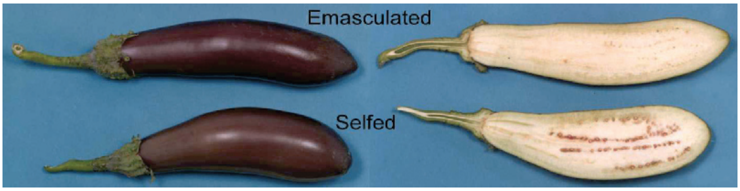

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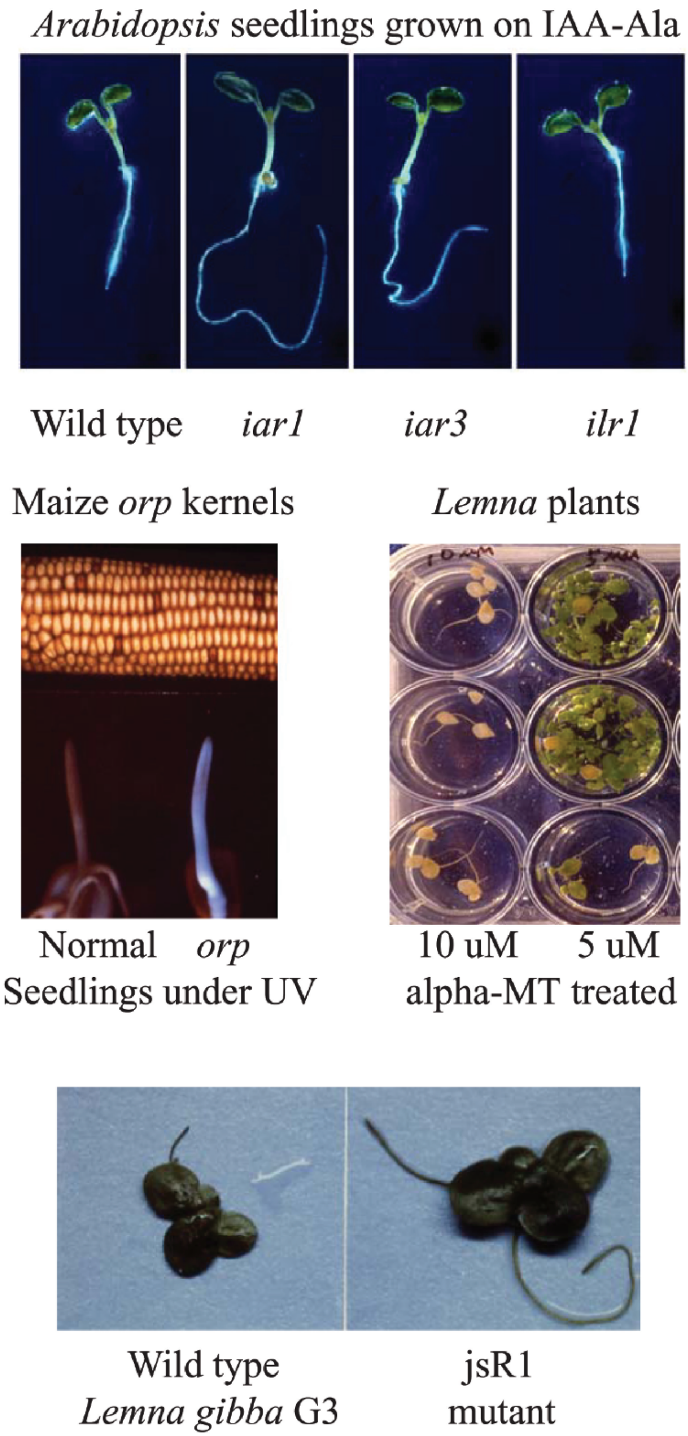

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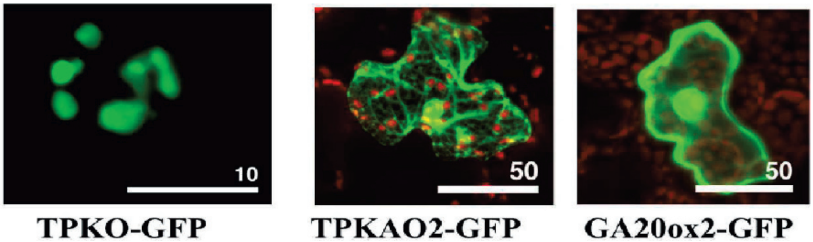

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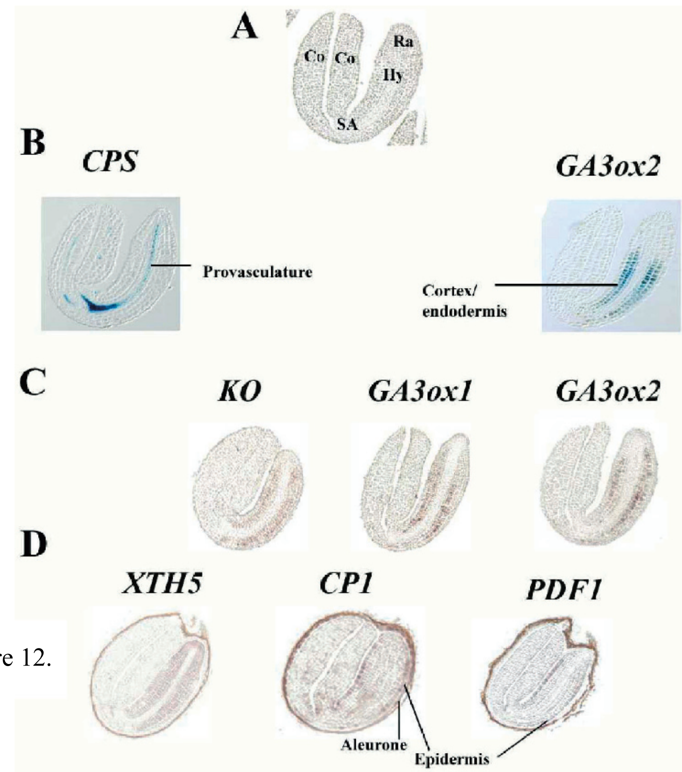

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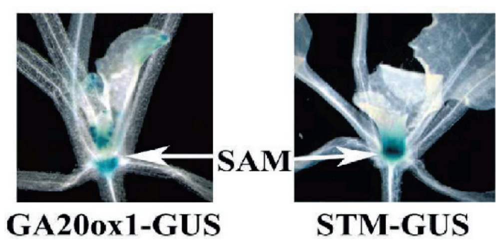

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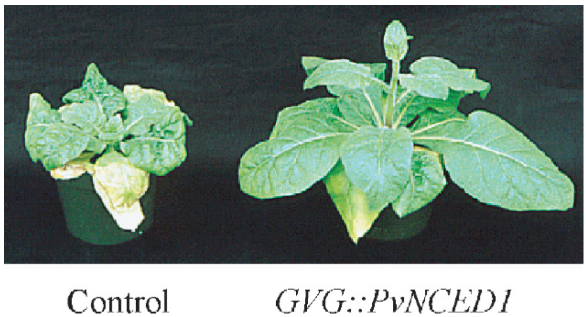

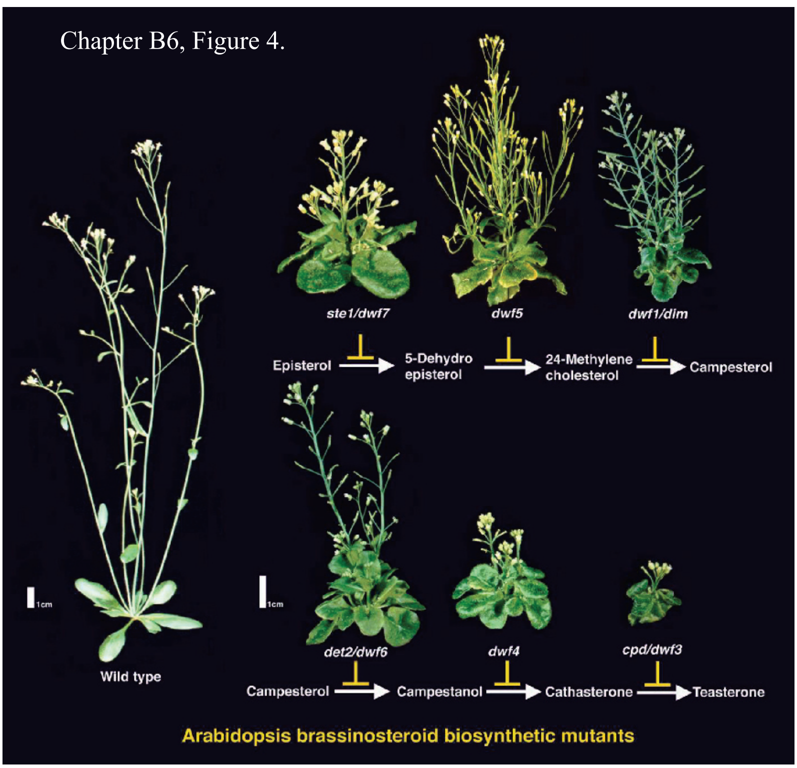

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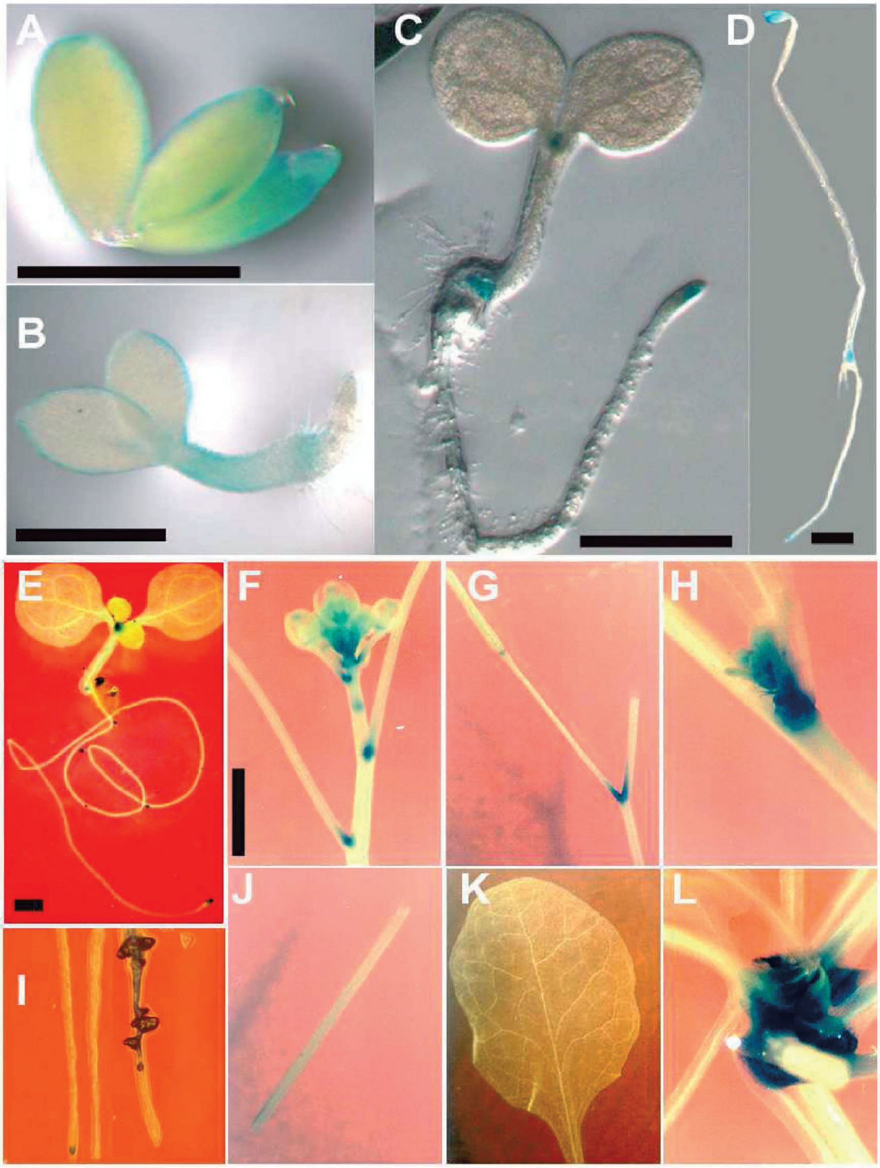

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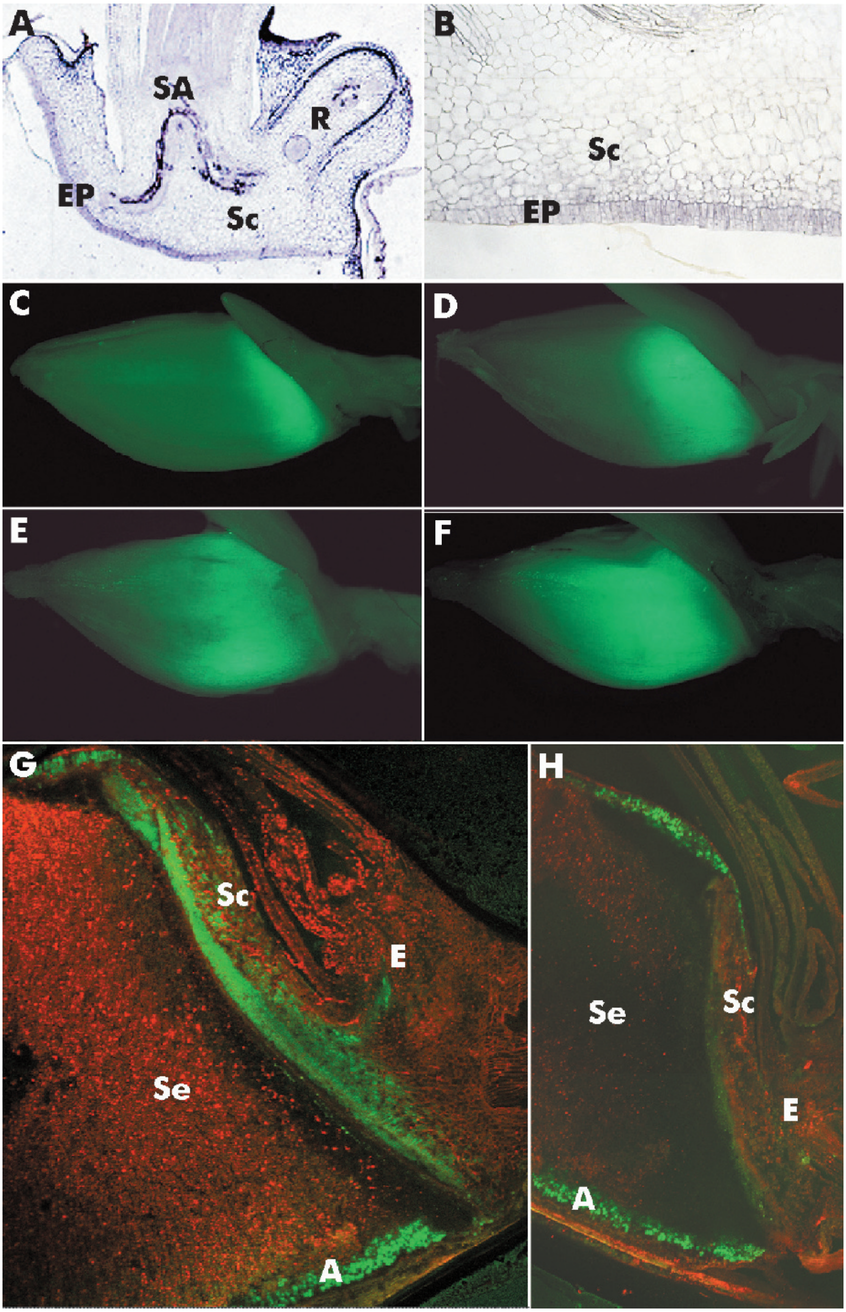

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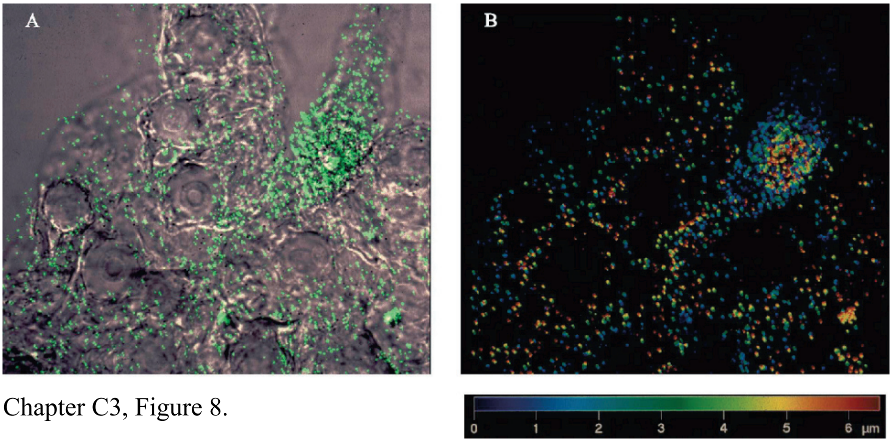

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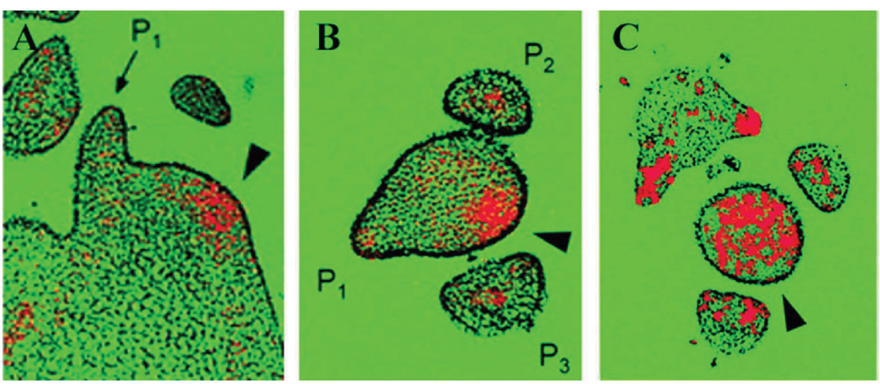

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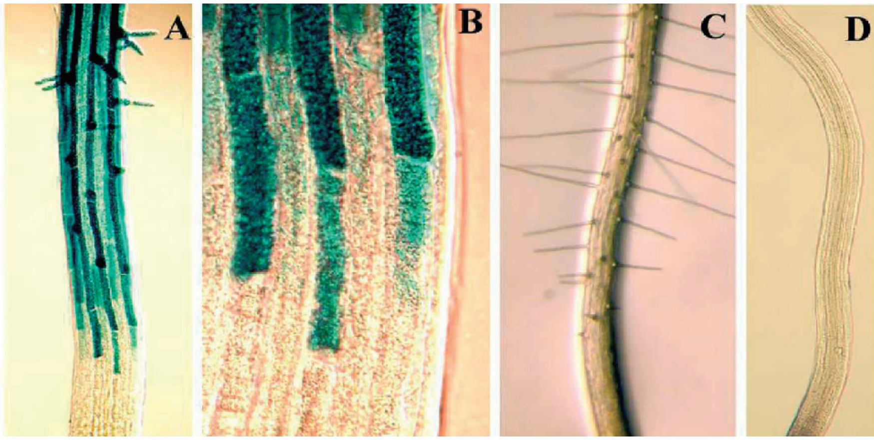

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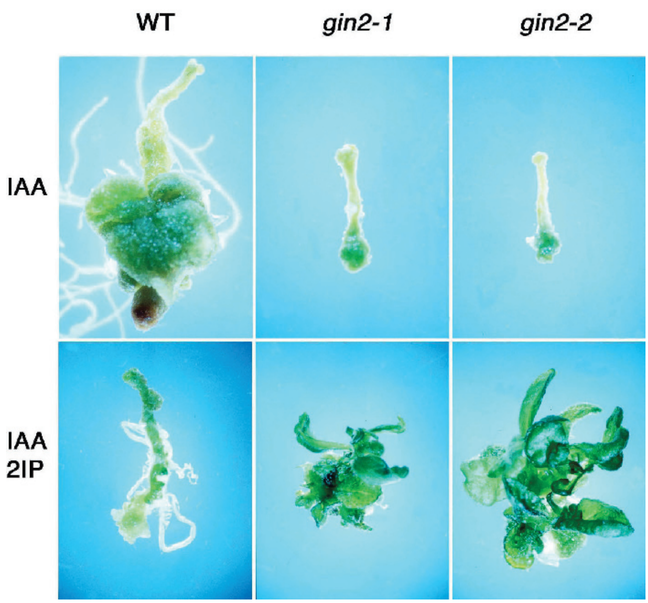

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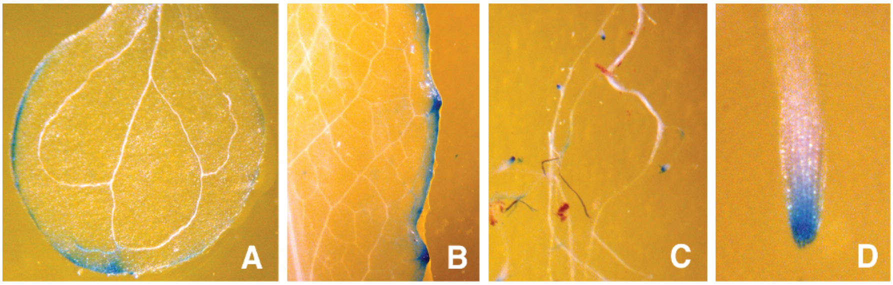

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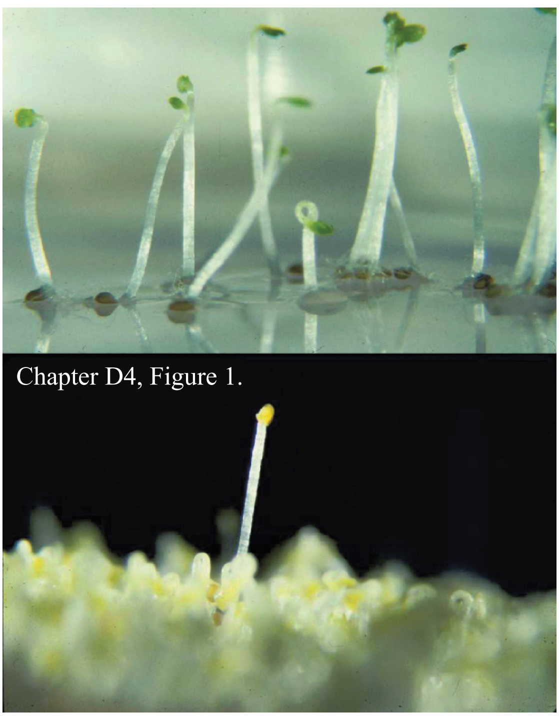

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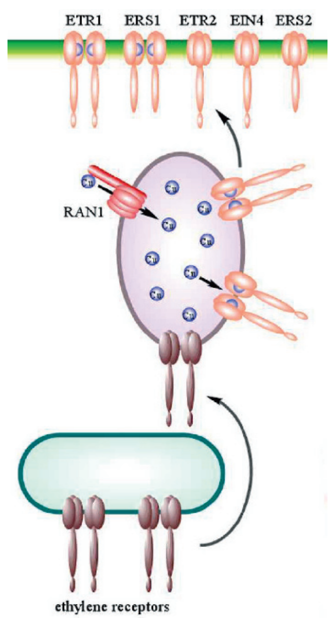

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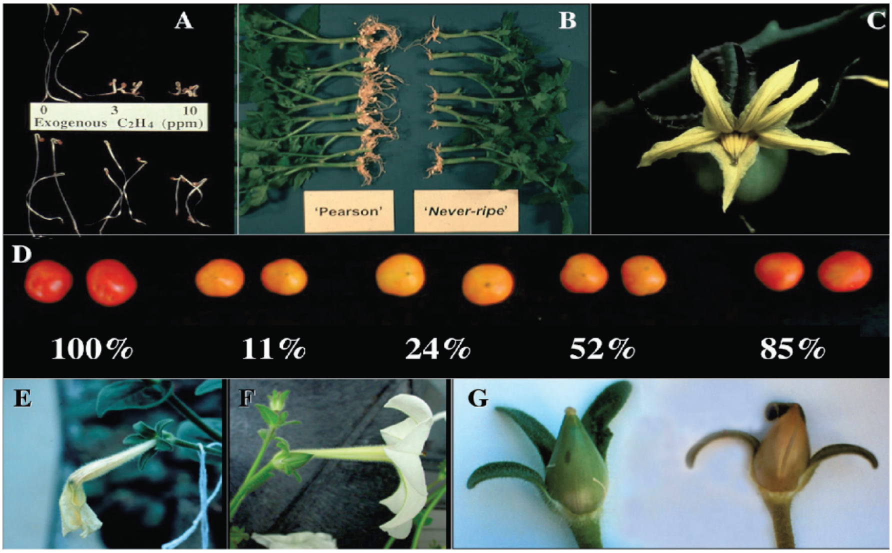

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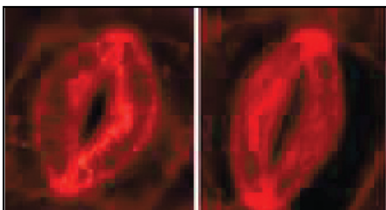

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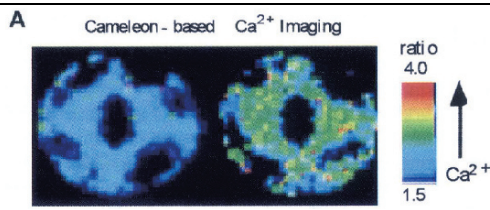

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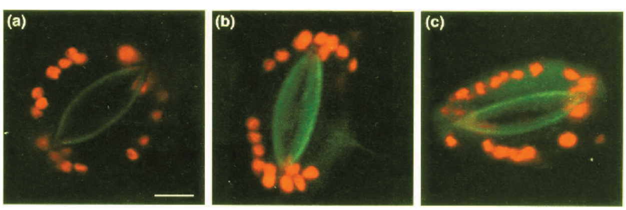

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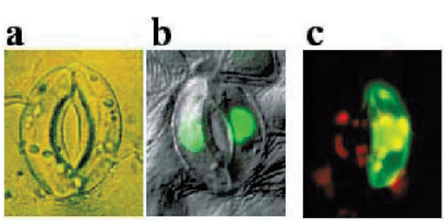

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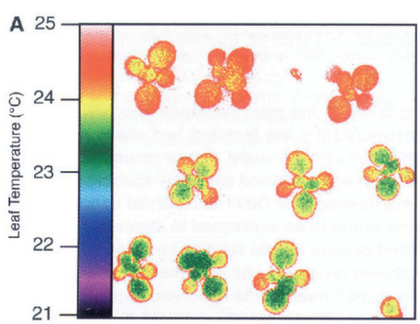

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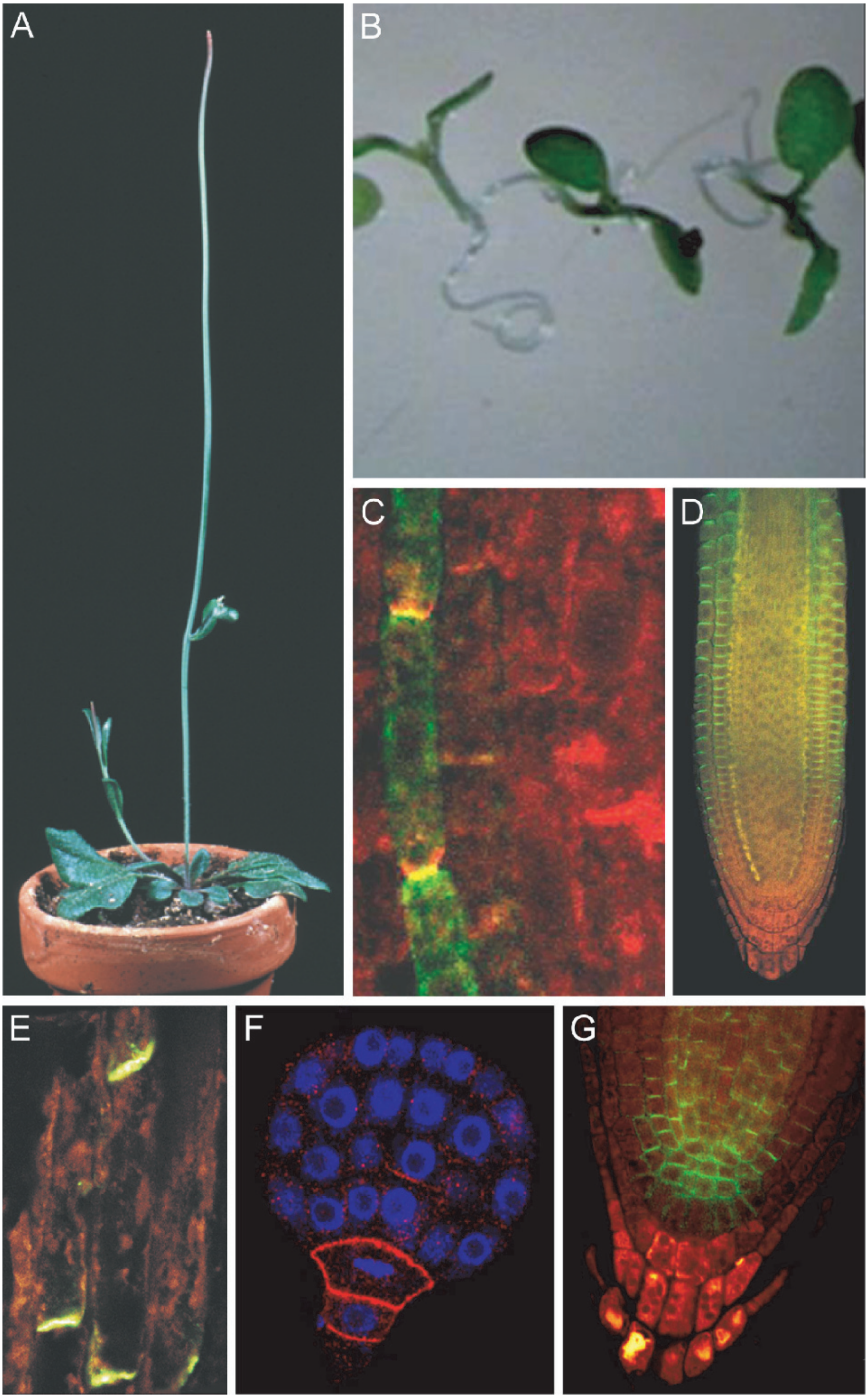

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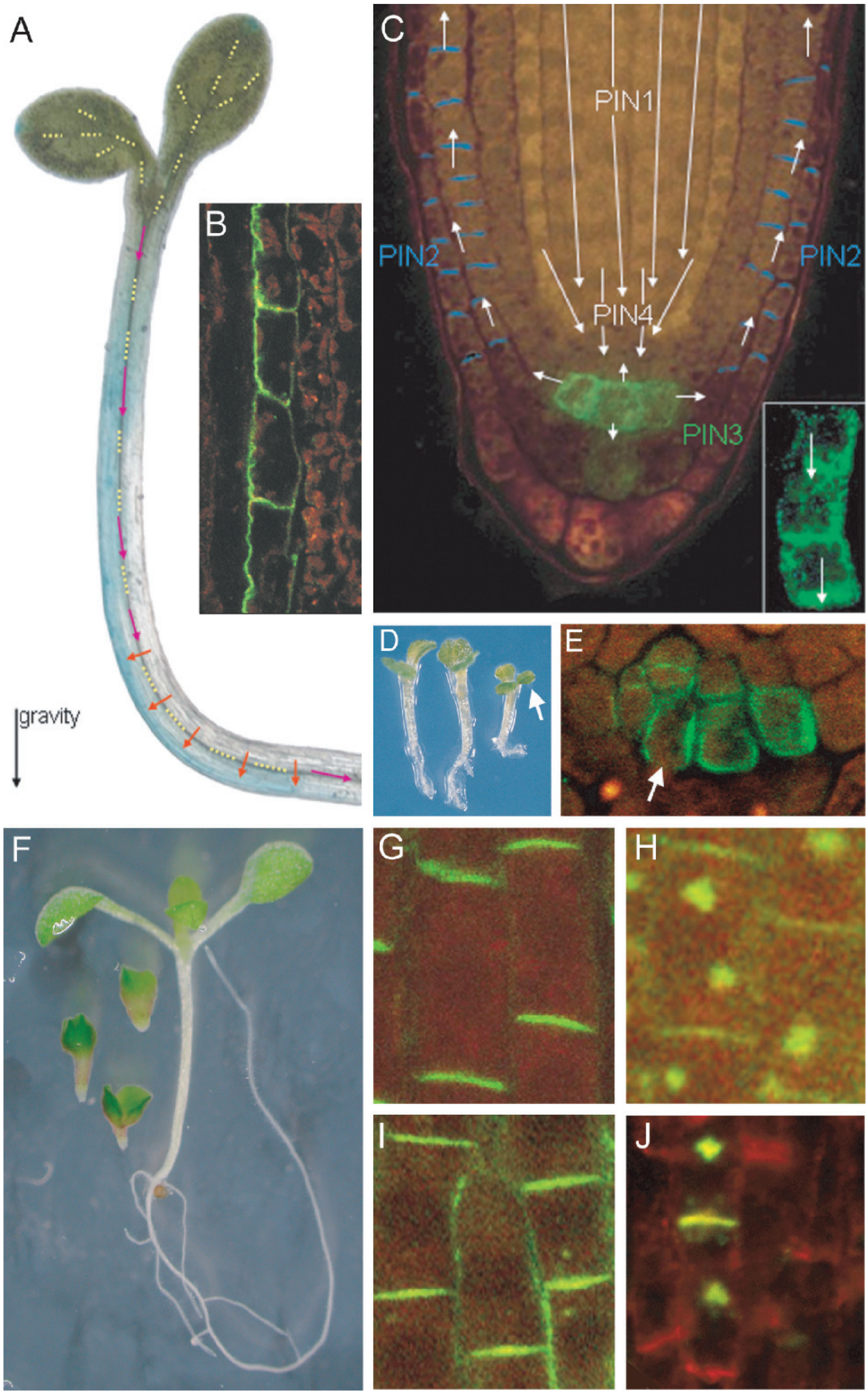

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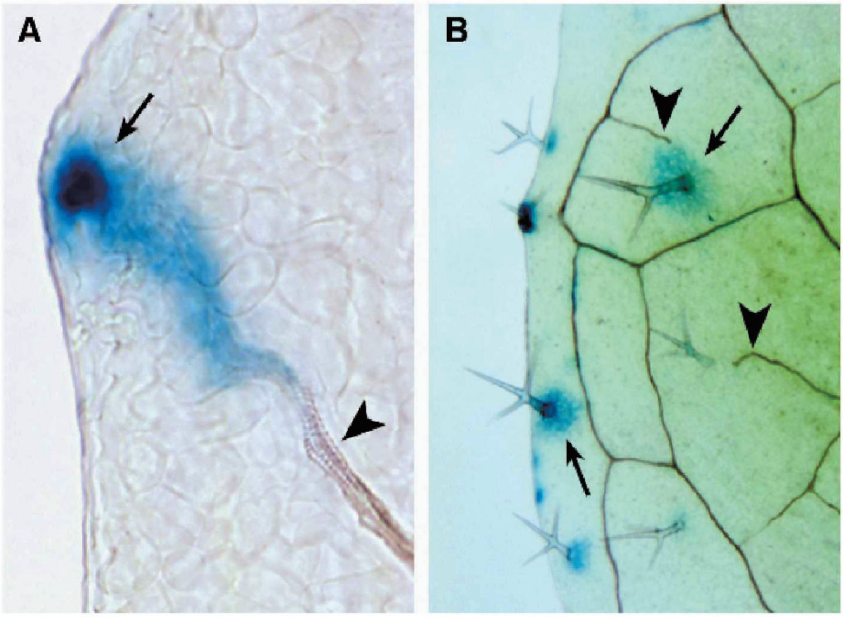

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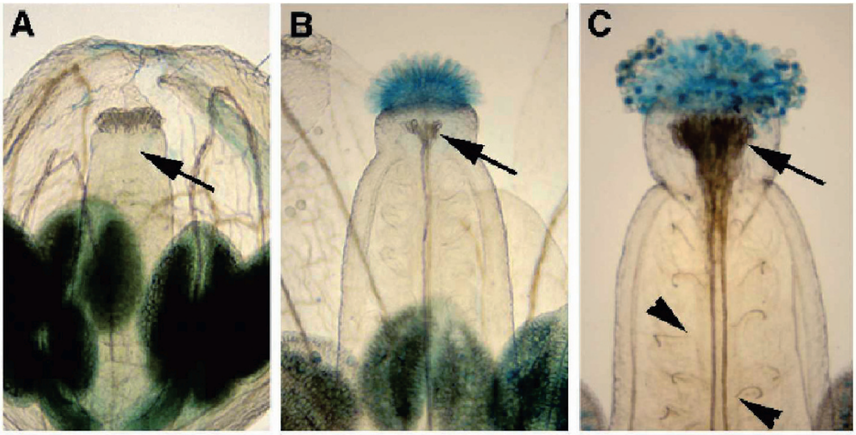

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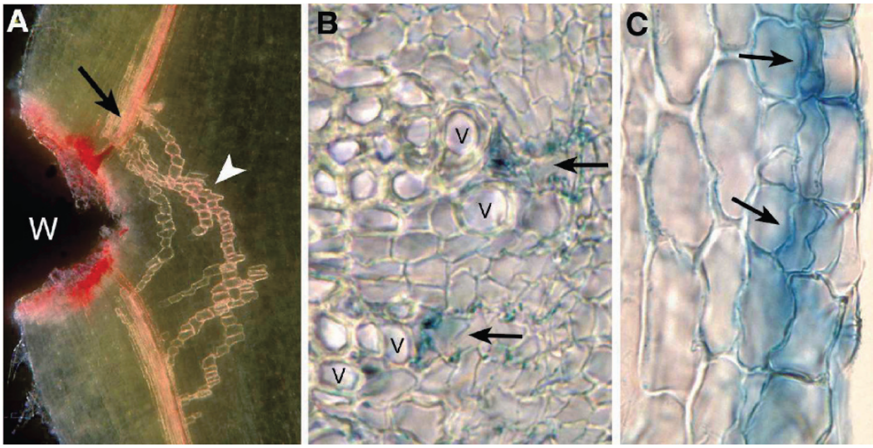

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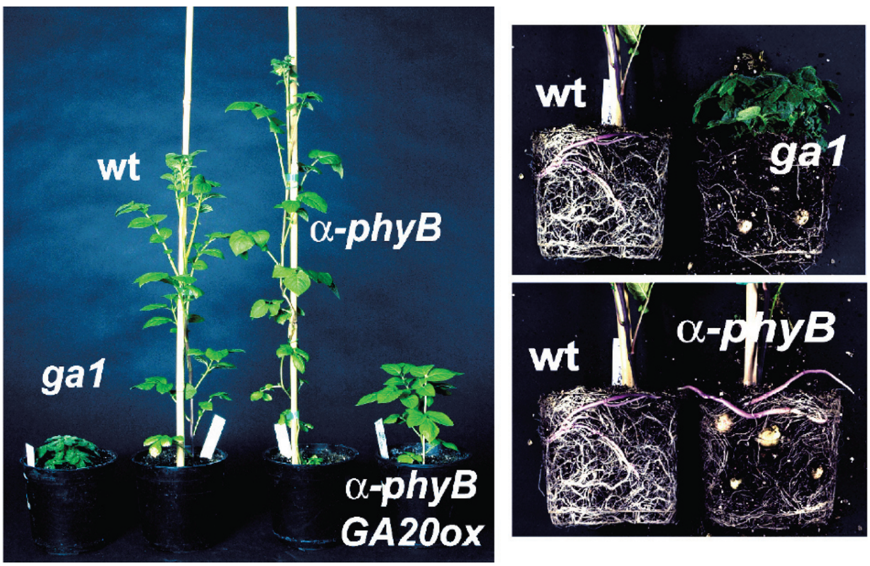

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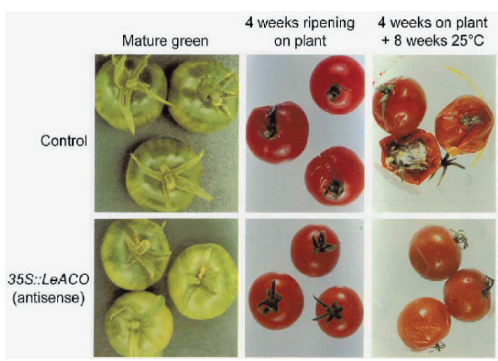

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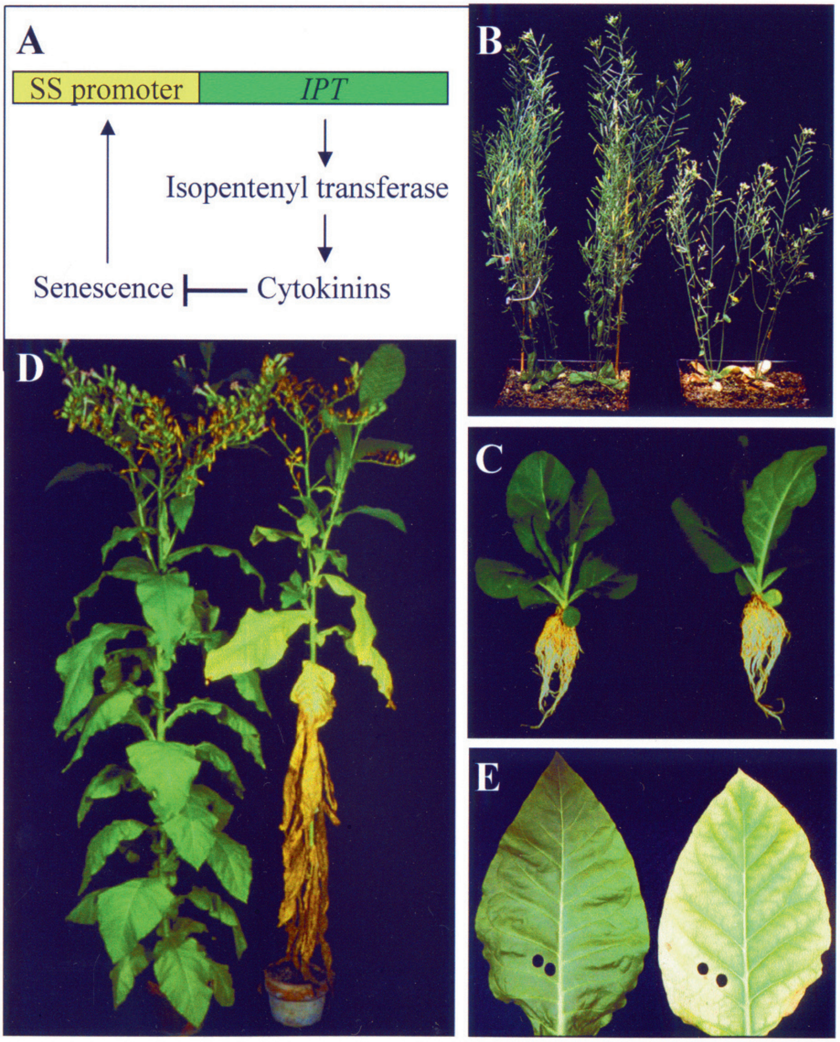

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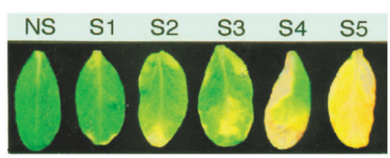

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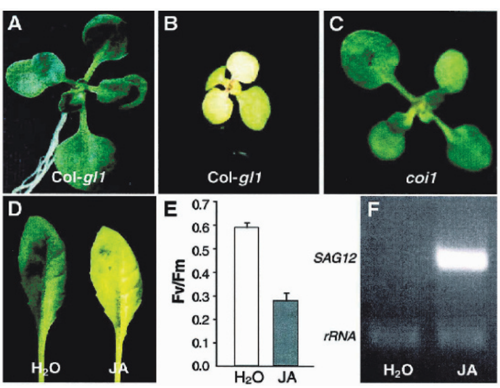

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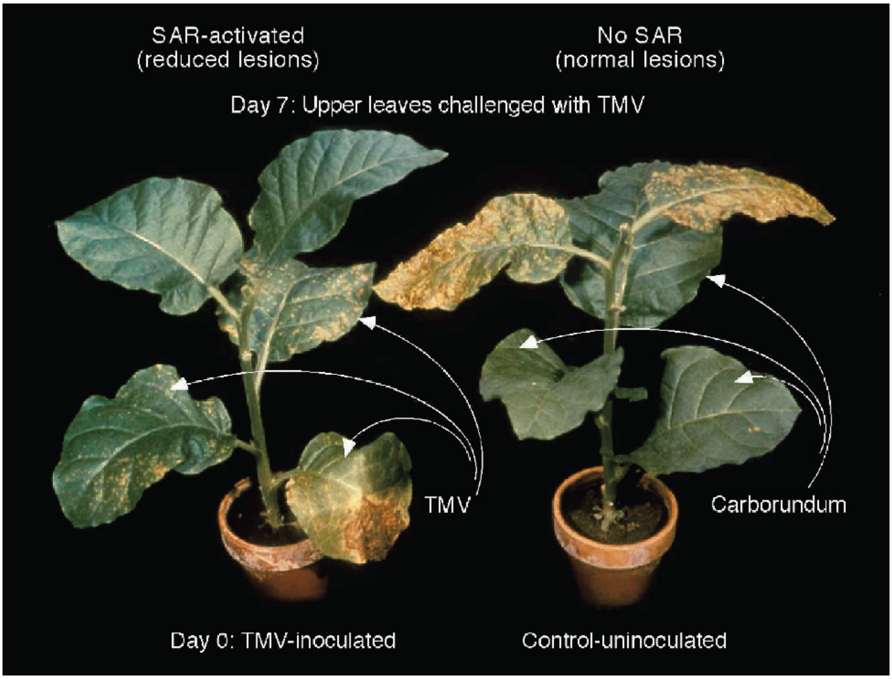

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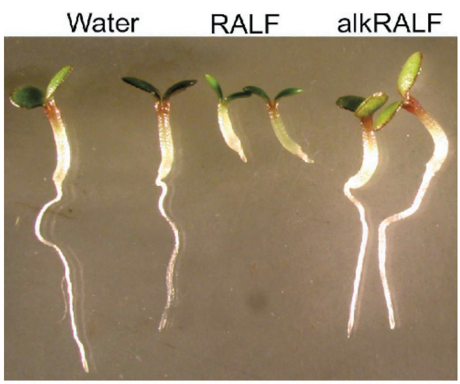

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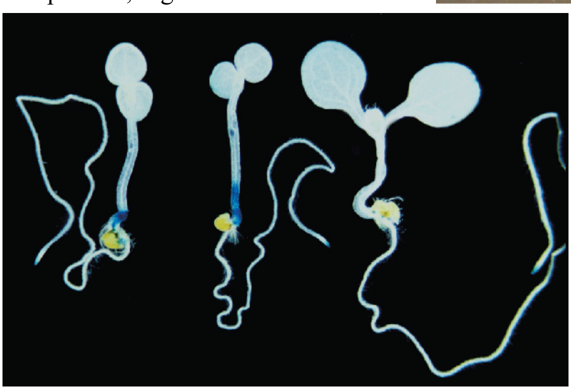

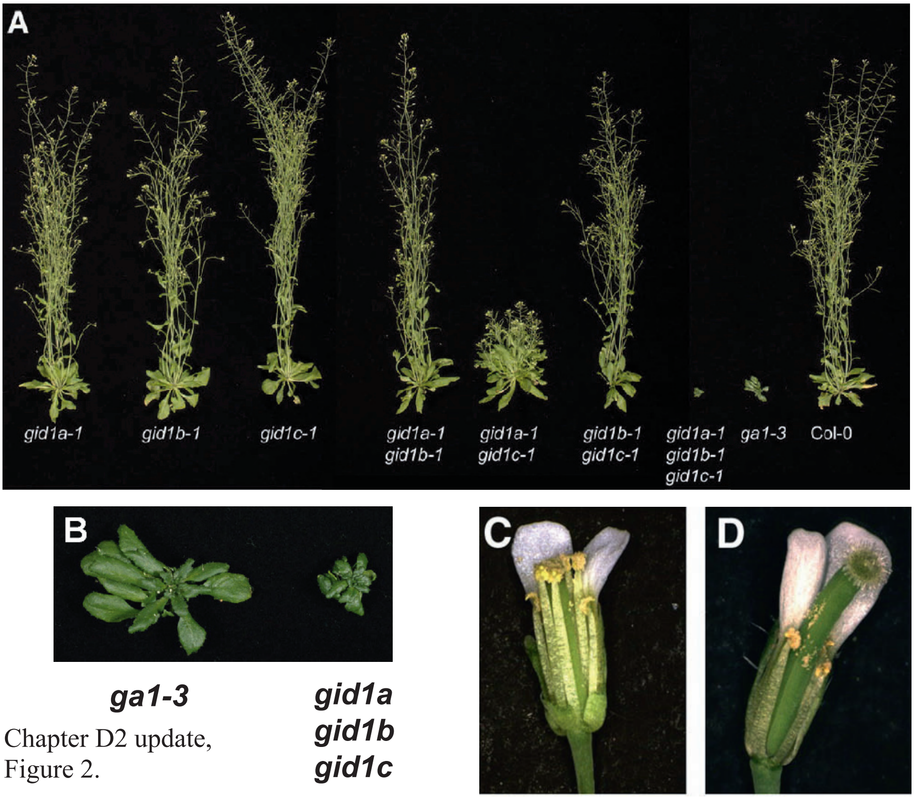

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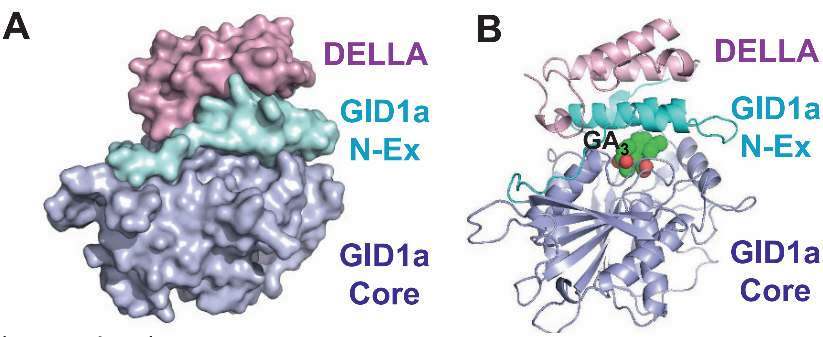

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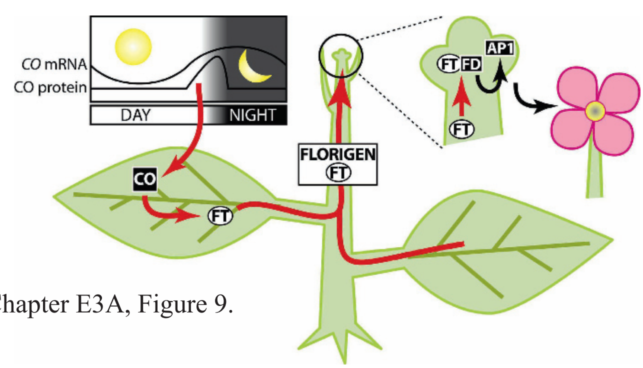

Chapter E3A, Figure 9.

A. INTRODUCTION

A1. The Plant Hormones: Their Nature, Occurrence, and Functions

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INTRODUCTION

The Meaning of a Plant Hormone

Plant hormones are *a group of naturally occurring, organic substances which influence physiological processes at low concentrations*. The processes influenced consist mainly of growth, differentiation and development, though other processes, such as stomatal movement, may also be affected. Plant hormones[1] have also been referred to as 'phytohormones' though this term is infrequently used.

In their book *Phytohormones* Went and Thimann (10) in 1937 define a hormone as a substance which is transferred from one part of an organism to another. Its original use in plant physiology was derived from the mammalian concept of a hormone. This involves a localized site of synthesis, transport in the bloodstream to a target tissue, and the control of a physiological response in the target tissue via the concentration of the hormone. Auxin, the first-identified plant hormone, produces a growth response at a distance from its site of synthesis, and thus fits the definition of a *transported* chemical messenger. However this was before the full range of what we now consider plant hormones was known. It is now clear that plant hormones do not fulfill the requirements of a hormone in the mammalian sense. The synthesis of plant hormones may be localized (as occurs for animal hormones), but it may also occur in a wide range of tissues, or cells within tissues. While they may be transported and have their action at a distance this is not always the case. At one extreme we find the transport of

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1 The following abbreviations are used throughout this book with no further definition: ABA, abscisic acid; BR, brassinosteroid; CK, cytokinin; GA gibberellin; IAA, indole-3-acetic acid

cytokinins from roots to leaves where they prevent senescence and maintain metabolic activity, while at the other extreme the production of the gas ethylene may bring about changes within the same tissue, or within the same cell, where it is synthesized. Thus, transport is not an essential property of a plant hormone.

The term 'hormone' was first used in medicine about 100 years ago for a stimulatory factor, though it has come to mean a transported chemical message. The word in fact comes from the Greek, where its meaning is 'to stimulate' or 'to set in motion'. Thus the origin of word itself does not require the notion of transport *per se*, and the above definition of a plant hormone is much closer to the meaning of the Greek origin of the word than is the current meaning of hormone used in the context of animal physiology.

Plant hormones[2] are a unique set of compounds, with unique metabolism and properties, that form the subject of this book. Their only universal characteristics are that they are natural compounds in plants with an ability to affect physiological processes at concentrations far below those where either nutrients or vitamins would affect these processes.

THE DISCOVERY, IDENTIFICATION AND QUANTITATION OF PLANT HORMONES.

The Development of the Plant Hormone Concept and Early Work.

The plant hormone concept probably derives from observations of morphogenic and developmental correlations by Sachs between 1880 and 1893. He suggested that "Morphological differences between plant organs are due to differences in their material composition" and postulated the existence of root-forming, flower forming and other substances that move in different directions through the plant (10).

At about the same time Darwin (3) was making his original observations on the phototropism of grass coleoptiles that led him to postulate the existence of a signal that was transported from the tip of the coleoptile to the bending regions lower down. After further characterizations by several workers of the way in which the signal was moved, Went in the Netherlands was finally able to isolate the chemical by diffusion from coleoptile tips into agar blocks, which, when replaced on the tips of decapitated coleoptiles, resulted in the stimulation of the growth of the decapitated coleoptiles, and their bending when placed asymmetrically on these tips. This thus demonstrated the existence of a growth promoting chemical that was

[2] The term "plant growth substance" is also used for plant hormones but this is a rather vague term and does not describe fully what these natural regulators do - growth is only one of the many processes influenced. The international society for the study of plant hormones is named the "International Plant Growth Substance Association" (IPGSA). While the term plant growth regulator is a little more precise this term has been mainly used by the agrichemical industry to denote synthetic plant growth regulators as distinct from endogenous growth regulators.

synthesized in the coleoptile tips, moved basipetally, and when distributed asymmetrically resulted in a bending of the coleoptile away from the side with the higher concentration. This substance was originally named *Wuchsstoff* by Went, and later this was changed to *auxin*. After some false identifications the material was finally identified as the simple compound indoleacetic acid, universally known as IAA (11).

Discovery of Other Hormones

Other lines of investigation led to the discovery of the other hormones: research in plant pathogenesis led to gibberellins (GA); efforts to culture tissues led to cytokinins (CK); the control of abscission and dormancy led to abscisic acid (ABA); and the effects of illuminating gas and smoke led to ethylene. These accounts are told in virtually every elementary plant physiology textbook, and further elaborated in either personal accounts (9, 11) or advanced treatises devoted to individual hormones (see book list at the end of the chapter) so that they need not be repeated here. More recently other compounds, namely brassinosteroids (Chapters B7 and D7), jasmonates (Chapter F1) (including tuberonic acid, Chapter E5), salicylic acid (Chapter F2), and the peptides (Chapter F3) have been added to the list of plant hormones, and these are fully covered in this book for the first time. Polyamines, which are essential compounds for all life forms and important in DNA structure, have also been categorized as plant hormones as they can modulate growth and development, though typically their levels are higher than the other plant hormones. However, as little further understanding of their exact function in plants at the cellular and molecular levels has been added in the last few years, no individual chapter has been devoted to polyamines in this edition (a chapter on polyamines can be found in the previous edition (4): 2E Chapter C1).

It is interesting to note that, of all the original established group of plant hormones, only the chemical identification of abscisic acid was made from higher plant tissue. The original identification of the others came from extracts that produced hormone-like effects in plants: auxin from urine and the fungal cultures of *Rhizopus*, gibberellins from culture filtrates of the fungus *Gibberella*, cytokinins from autoclaved herring sperm DNA, and ethylene from illuminating gas. Today we have at our disposal methods of purification (such as high performance liquid chromatography: HPLC, following solid phase extraction: SPE cartridges) and characterization (gas chromatography-mass spectrometry: GC-MS, and high performance liquid chromatography-mass spectrometry: HPLC-MS) that can operate at levels undreamed of by early investigators (Chapter G1). Thus while early purifications from plant material utilized tens or even hundreds of kilograms of tissues, modern analyses can be performed on a few milligrams of tissue, making the characterization of hormone levels in individual leaves, buds, or even from tissues within the organs much more feasible. Thus it is not surprising to see the more-recently discovered hormones being originally