PHYSIOLOGY OF GROWTH AND DEVELOPMENT

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17

Biosynthesis of Hormones

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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.*

REGULATORY FACTORS IN HORMONE ACTION:

LEVEL, LOCATION AND SIGNAL TRANSDUCTION

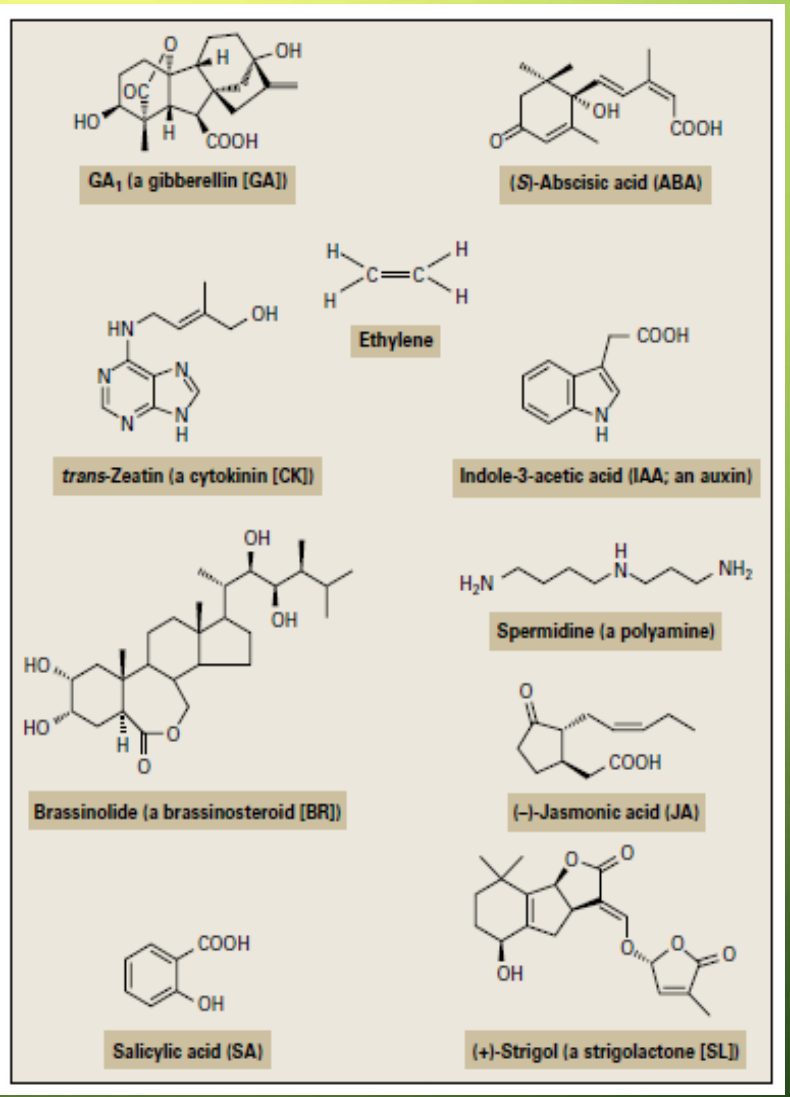
The way in which a plant hormone influences growth and development depends on:

1) The amount present: this is regulated by biosynthesis, degradation and conjugation.

2) The location of the hormone: this is affected by movement or transport.

3) The sensitivity (or responsiveness) of the tissue: this involves the presence of receptors and signal-transduction chain components.

FIGURE 17.1 *Structures of representatives from the 10 types of plant hormones discussed in this chapter.*



17.1 Gibberellins

Gibberellins (GAs) were first isolated from the fungus *Gibberella fujikuroi* in 1926 by the Japanese scientist Eiichi Kurosawa, who was investigating the causative agent of *bakanae*, the "foolish seedling" disease of *Oryza sativa*, which was frequently responsible for major reductions in grain yield.

FIGURE 17.2 O. sativa *seedling infected with* Bakanae *(foolish seedling) disease caused by the fungal pathogen,* Gibberella fujikuroi.

The compounds proved to be identical, and the structure of gibberellic acid, now known as GA3, was elucidated in 1956. Shortly thereafter, GAs were shown to be endogenous components of plants, and it became apparent that they were not merely an interesting group of fungal metabolites but endogenous regulators of many aspects of higher plant growth and development.

1.1 Among more than 100 GAs identified from plants, only a few act as bioactive hormones

- Among more than 100 GAs identified from plants, only a few function as bioactive hormones.
- Many nonbioactive GAs present in plants are biosynthetic precursors of bioactive forms or are inactivated metabolites.
- The most commonly found bioactive GAs in plants are GA1 and GA4.

GA1 and GA4, both have a hydroxyl group on c-3β, a carboxyl group on c-6, and a γ-lactone between c-4 and c-10.

The recent identification of a soluble GA receptor, GIBBERELLIN INSENSITIVE DWARF 1 (GID1), from *O. sativa* and its homologs in *Arabidopsis* and *Hordeum vulgare* has demonstrated that these structural requirements for bioactive GAs are reflected in their affinity for the GID1 receptor.

GA3 and GA7, 1,2-double bond analogs of GA1 and GA4, respectively, are also active per se in plants.

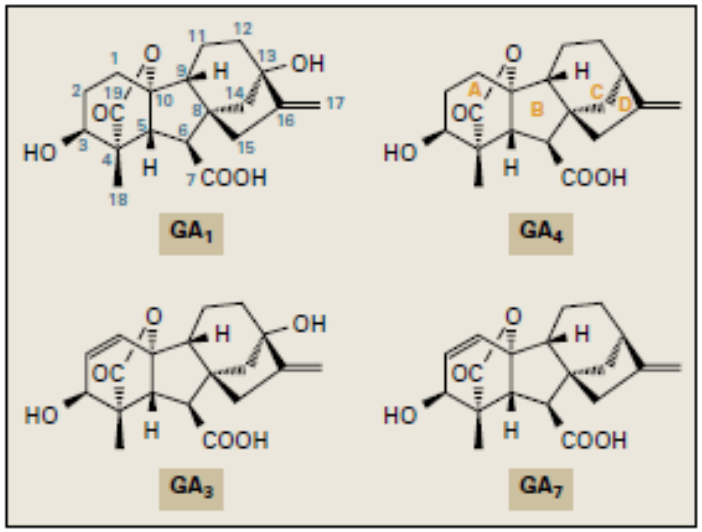


FIGURE 17.3 *Structures of bioactive GAs in plants.*

1.2 Bioactive GAs affect many aspects of plant growth and development

- GAs are best known for their influence on:

stem elongation and leaf growth

FIGURE 17.4 *Effect of GA_3 on stem elongation of dwarf* P. sativum *seedlings: (left) control plants, (right) plants seven days after treatment with 5 μg of GA_3.*
Source: A. Crozier, University of Glasgow, UK; previously unpublished.

FIGURE 17.5 *Promotion of Tanginbozu dwarf* O. sativa (d35) *leaf sheath elongation 3 days after treatment with GA_3: (left) control; (center) 100 pg of GA_3 per seedling; (right) 1 ng of GA_3 per seedling.*
Source: A. Crozier, University of Glasgow, UK; previously unpublished.

- *Effects*

  - Stem growth
  - Bolting in long day plants
  - Induction of seed germination
  - Enzyme production during germination
  - Fruit setting and growth
  - Induction of maleness in dioecious flowers

1.3 GA biosynthesis starts in the plastid

- The initial steps in biosynthesis of GAs involve formation of isopentenyl diphosphate and its conversion to geranylgeranyl diphosphate (GGDP), a common precursor for various terpenoids, such as carotenoids and phytol.

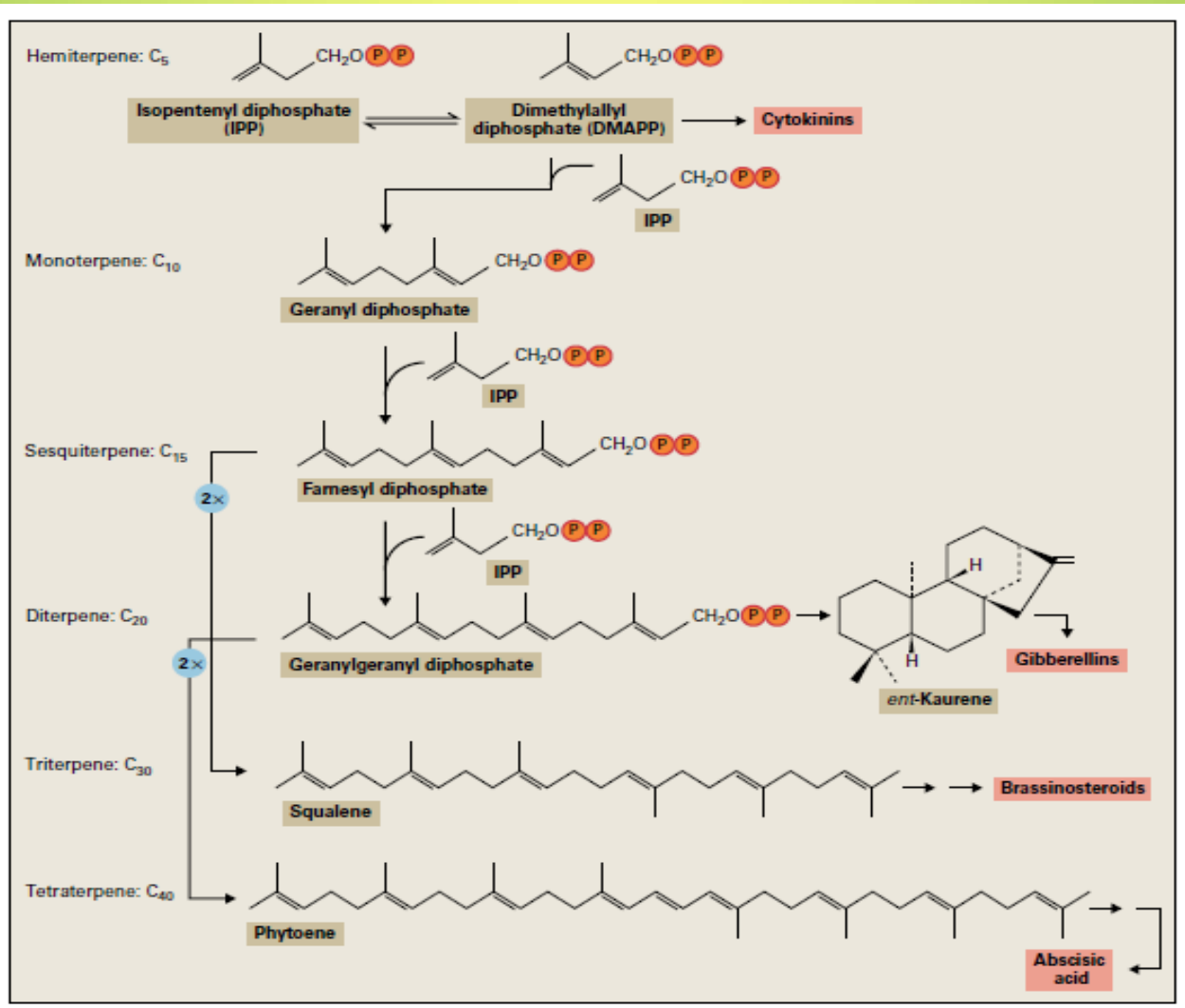
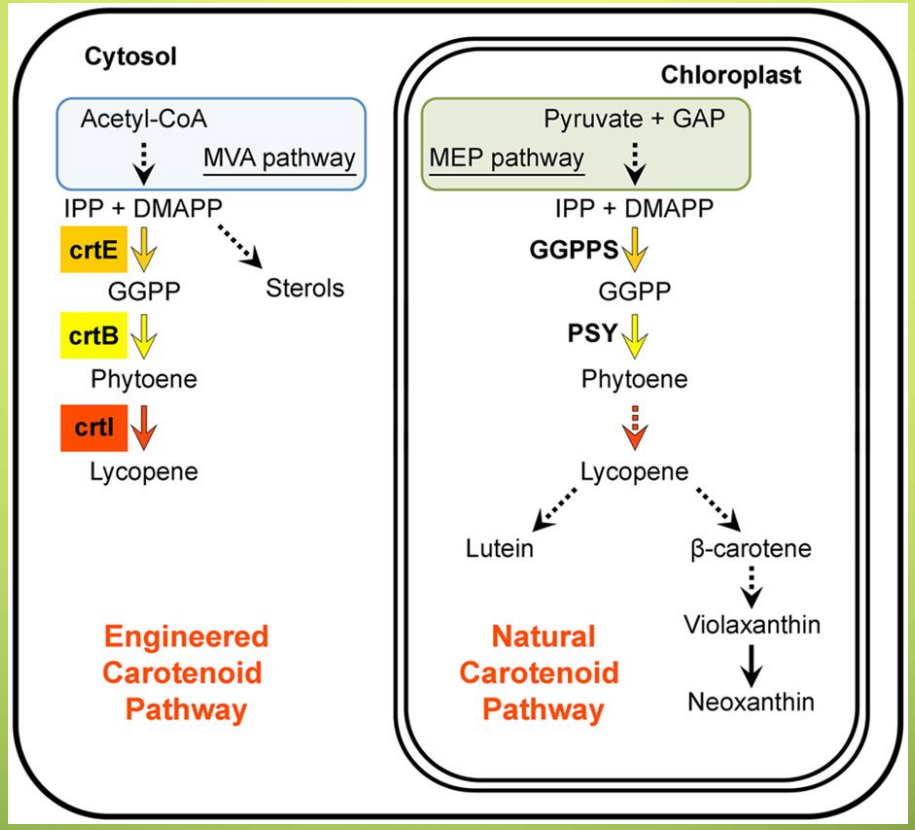
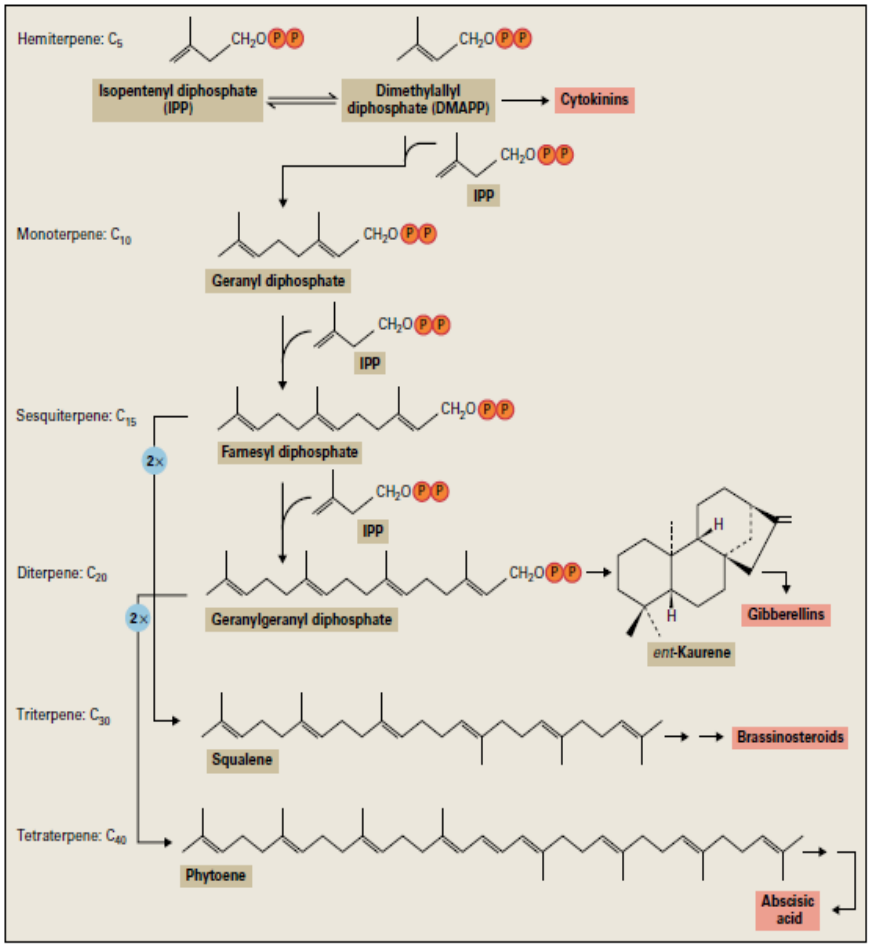


FIGURE 17.6 *Terpenoid biosynthesis pathway, showing biosynthetic origins of GAs as well as CKs, BRs, and ABA.*



The methylerythritol 4-phosphate (MEP- The non-mevalonate pathway) pathway is the recently discovered source of isoprenoid precursors isopentenyl diphosphate (IDP) and dimethylallyl diphosphate (DMADP) in most bacteria, some eukaryotic parasites, and the plastids of plant cells. The precursors lead to the formation of various isoprenoids having diverse roles in different biological processes. Some isoprenoids have important commercial uses. the glyceraldehyde 3-phosphate (GAP)-pyruvate pathway are alternative routes for the biosynthesis of the central isoprenoid precursor, isopentenyl diphosphate.



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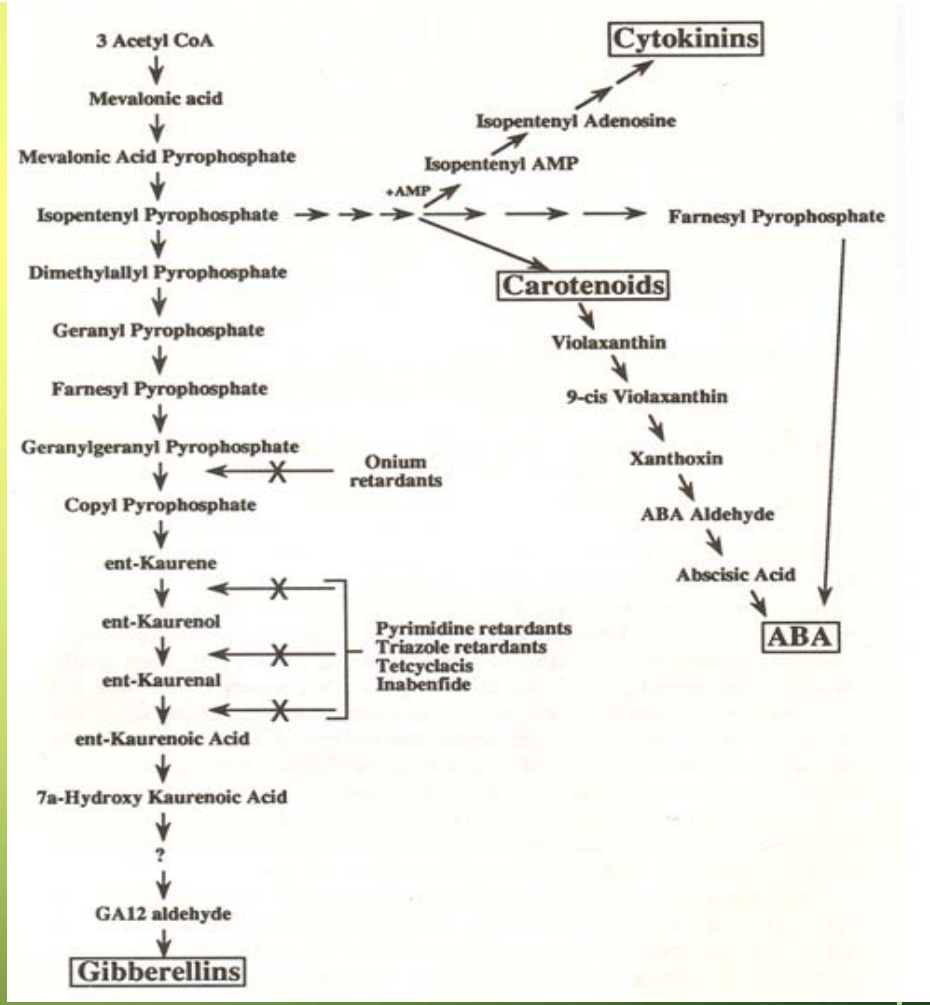

methylerythritol phosphate (MEP) pathway in plastids provides the majority of isopentenyl diphosphate to GAs, whereas only a minor contribution is from the cytosolic mevalonate pathway.

1.4 In plants, the synthesis of *ent*-kaurene from geranylgeranyl diphosphate is catalyzed by two distinct enzymes

1.5 Cytochrome P450 monooxygenases convert *ent*-kaurene to GA12

ent-Kaurene is oxidized to GA12 by NADPH-dependent, membrane-bound CYP450 monooxygenases: *ent*-kaurene oxidase (KO, CYP701A) and *ent*-kaurenoic acid oxidase (KAO, CYP88A).

- KO catalyzes the three-step oxidation on C-19 to synthesize ent-kaurenoic acid.

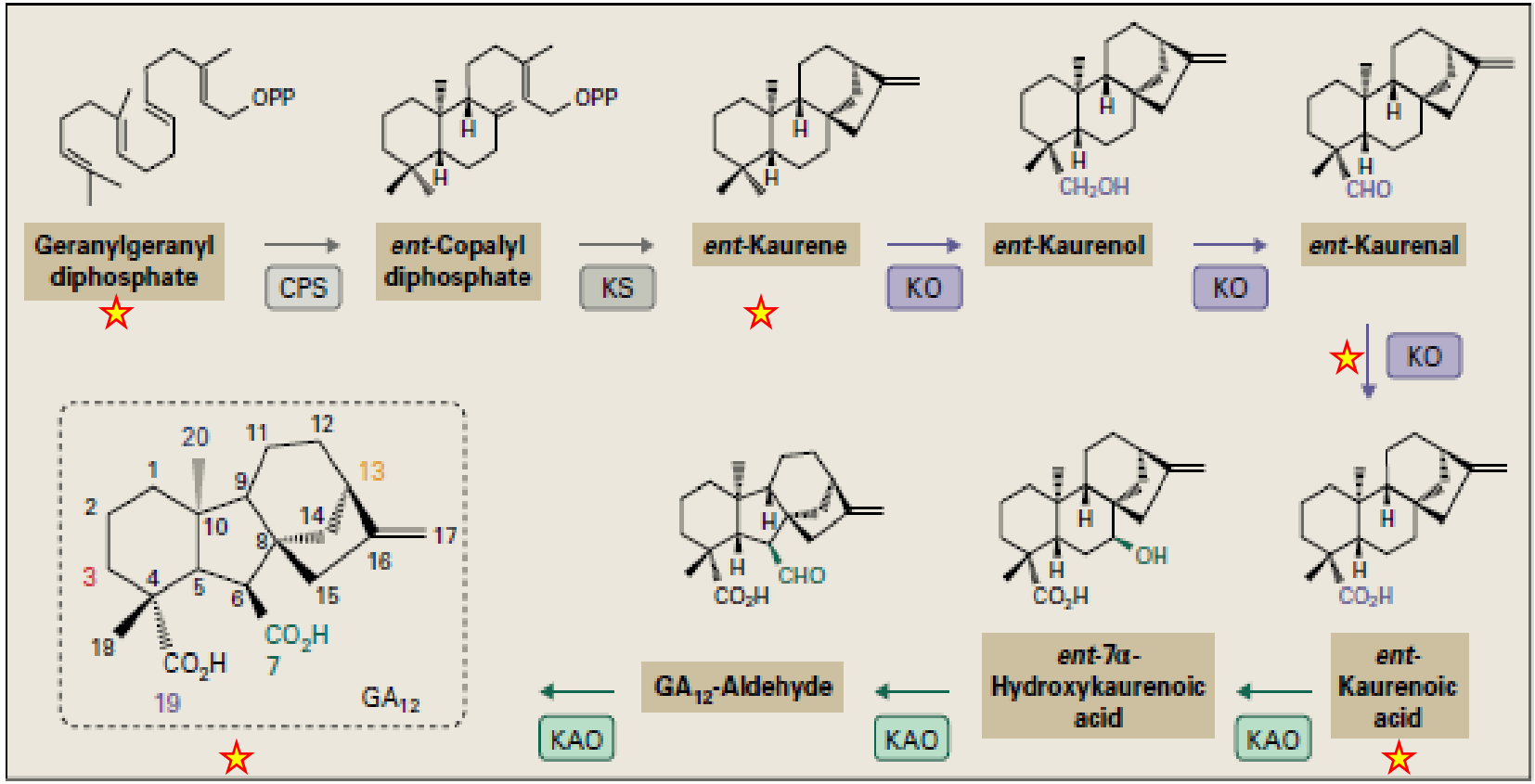

FIGURE 17.7 *Early stages of plant GA biosynthesis. CPS, ent-copalyl diphosphate synthase; KS, ent-kaurene synthase; KO, ent-kaurene oxidase; KAO, ent-kaurenoic acid oxidase. Colored carbon atoms on GA_{12} are oxidized for the synthesis of GA_1 (see also Fig. 17.9).*

The nitrogen-containing heterocyclic compounds

paclobutrazol, uniconazole, tetcyclasis, and ancymidol

retard plant growth by inhibiting KO.

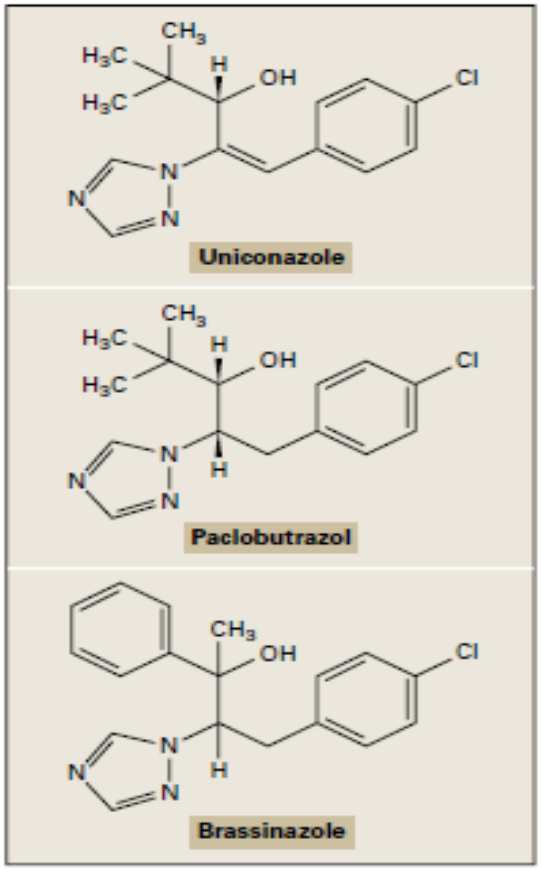

FIGURE 17.8 *Structures of uniconazole, paclobutrazol, and brassinazole. Uniconazole and paclobutrazol are triazoles that inhibit KO (see Fig. 17.7). However, uniconazole is not specific and also suppresses BR biosynthesis. The structurally related compound, brassinazole, is a strong BR inhibitor, blocking at least one CYP450 mediated step in the BR biosynthesis pathway (see Fig. 17.58). Its effect on GA biosynthesis is undetermined.*

1.6 Conversion of GA12 to bioactive GAs involves two pathways: one in which c-13 is hydroxylated early, and one in which c-13 is not hydroxylated

1.7 Bioactive GAs are rendered inactive via multiple metabolic routes in plants

- The best-characterized inactivation reaction is oxidation on C-2, catalyzed by GA 2-oxidase.
- The *Eui* gene encodes a CYP450 monooxygenase, CYP714D1, which inactivates GAs by epoxidation of the 16,17-double bond of various GAs, including GA4, GA9, and GA12.
- methylation of GAs is a common inactivation reaction in other plants.
- GAs can be converted into conjugates in plants. Conjugation of GAs to glucose

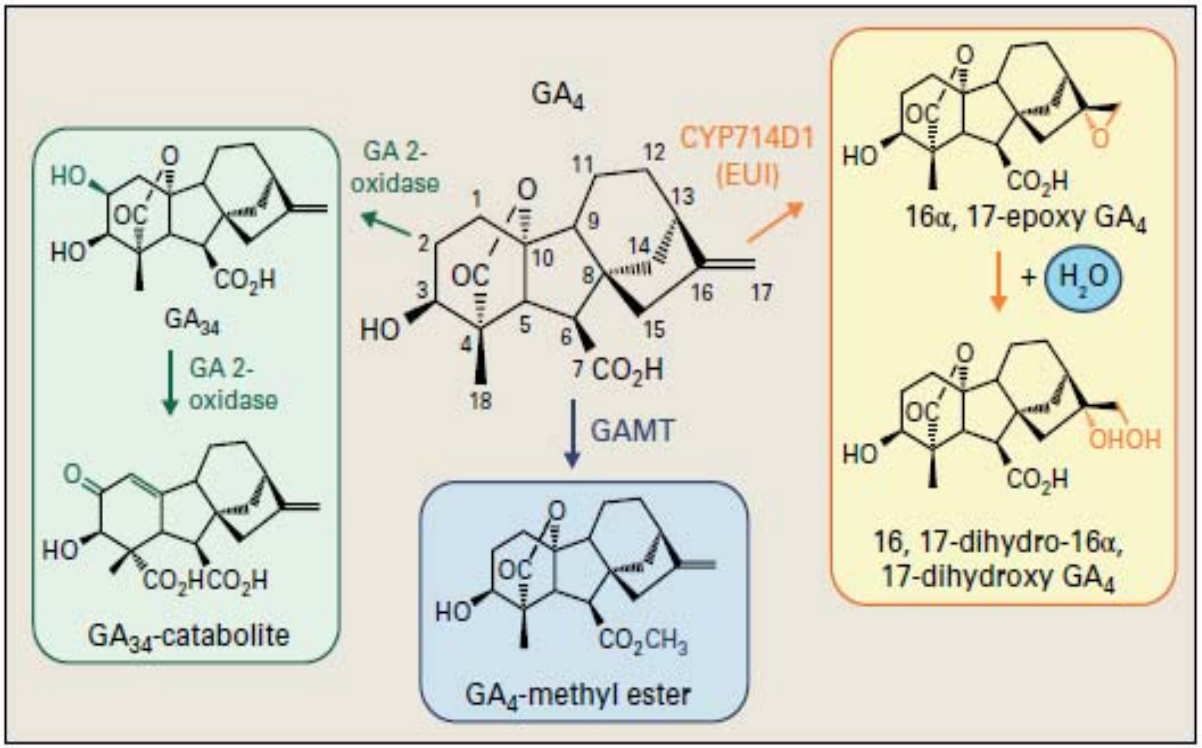

FIGURE 17.10 *GA_4 inactivation pathways. Inactivation by GA 2-oxidase introduces a 2β-hydroxyl group. In some cases, further metabolism occurs to form GA-catabolites, in which C-2 is oxidized to a ketone and the lactone is opened with the formation of a double bond. 16α,17-epoxy GAs produced by CYP714D1 (EUI) are hydrolyzed to give 16,17-dihydrodiols either in plants or during purification. GAMT catalyzes methylation of the C-6 carboxyl group. GAs are also converted into various glucose conjugates in plants (not shown).*

1.8 There are remarkable differences in GA biosynthesis pathways and enzymes between plants and fungi

1.9 Some enzymes that participate in GA biosynthesis are feedback-regulated

- The concentration of bioactive GAs in plants is under homeostatic control via feedback regulation.
- The effect of GA concentration is targeted to late biosynthesis enzymes, GA 20-oxidase and GA 3-oxidase, and the GA inactivating enzyme, GA 2-oxidase.

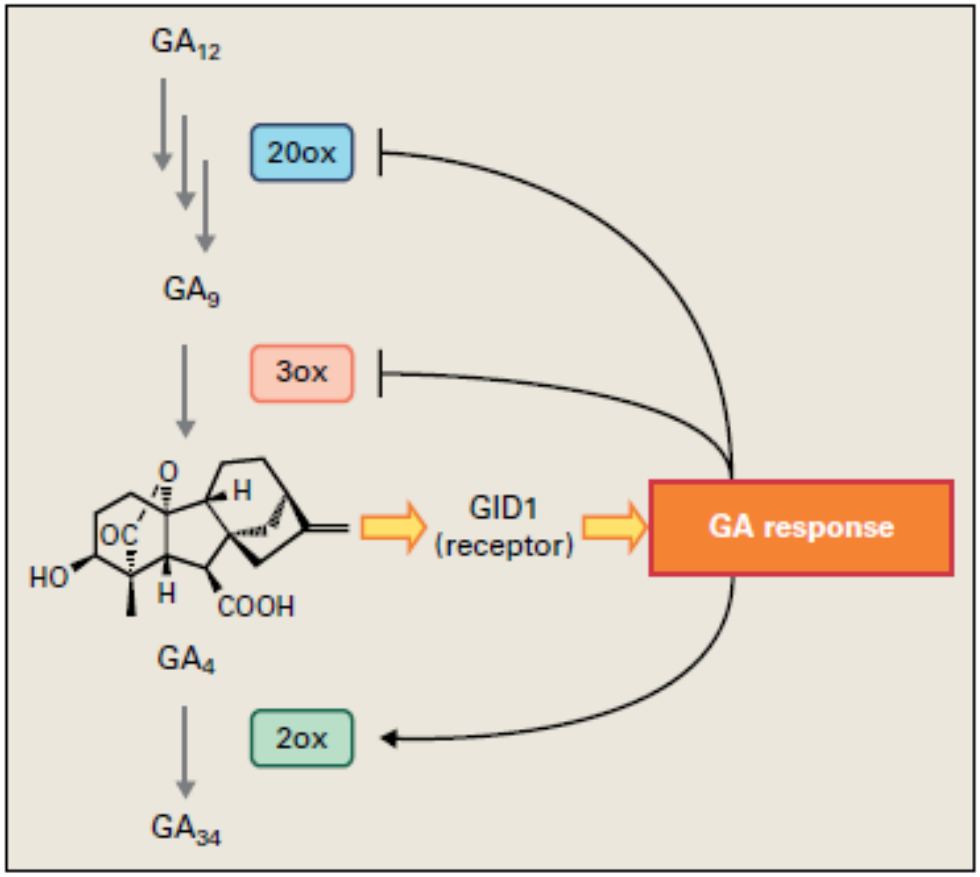

FIGURE 17.11 *Feedback regulation of GA biosynthesis and inactivation pathways. T-bars and black arrow depict negative and positive regulation, respectively. Gray arrows indicate metabolic conversions. 20ox, GA 20-oxidase; 3ox, GA 3-oxidase; 2ox, GA 2-oxidase.*

1.10 GA Mediates light-induced germination of lettuce seeds

- Evidence suggests that in some cases, bioactive GAs function as key mediators between perception of environmental signals And the resulting growth responses.
- A clear link between GA metabolism and phytochrome has been established in the case of red light (RL)-induced germination.
- Following a pulse of RL, germination is preceded by elevated GA 3-oxidase expression and an increase in the GA1 content.

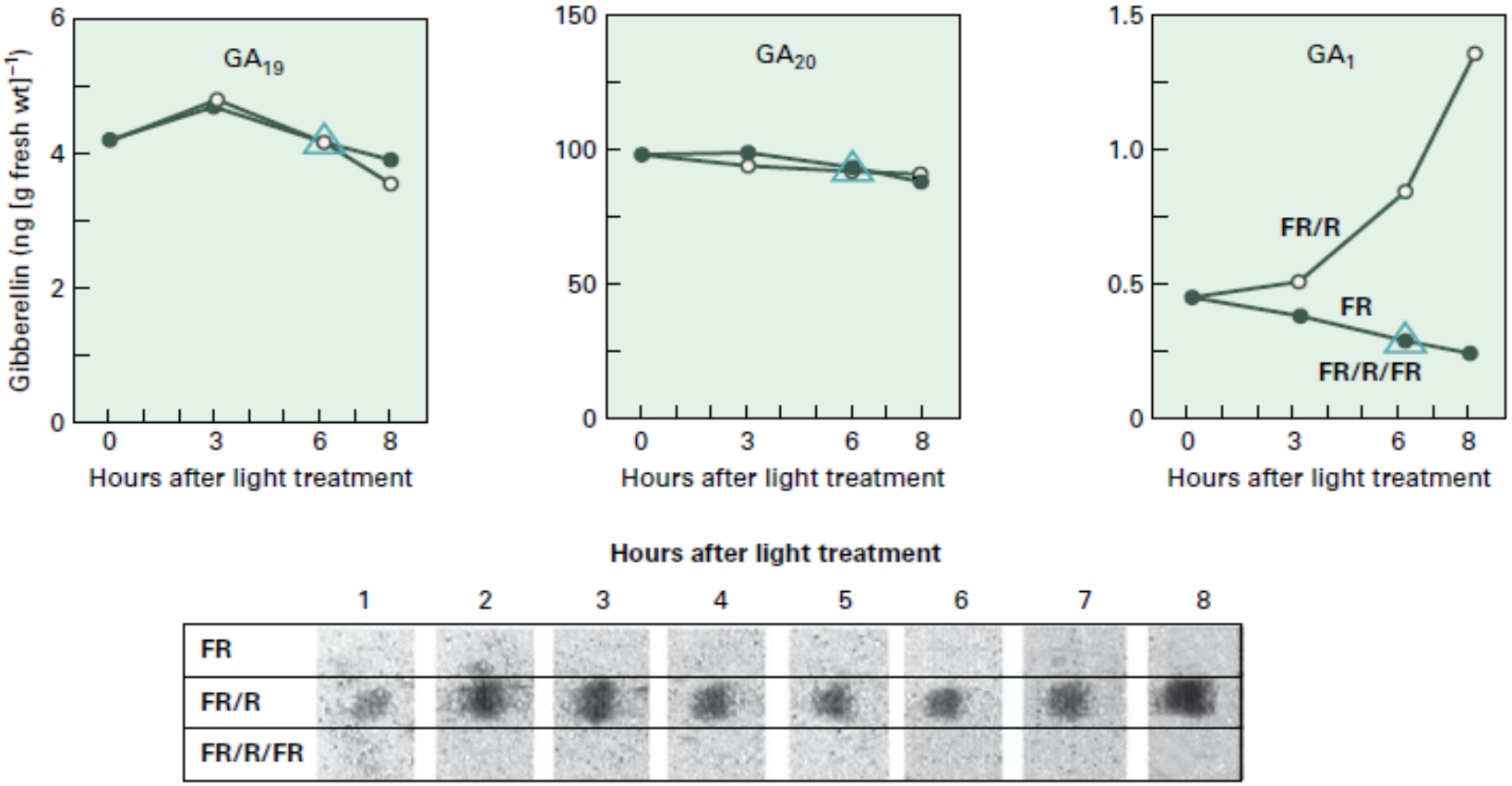

FIGURE 17.12 *Regulation of GA in Grand Rapids* L. sativa *by red (R) and far-red (FR) light. (Upper panels) Effects of R and FR light on GA levels. Note that phytochrome-mediated, R light induced seed germination is associated with increased GA_1 content. (Lower panels) Hybridization of a GA 3-oxidase cDNA clone to northern blots containing 50 µg of total RNA extracted from* L. sativa *seed after treatment with R and FR light. Source*: Electrophoretograms: Toyomasu et al. (1998). Plant Physiol. 118: 1517–1523.

1.11 Mutations in the GA pathway led to major advances in agriculture

- In the 1960s, the introduction of semi-dwarf cultivars of cereal crops, including *O. sativa* and *Triticum* spp., in combination with increased fertilizer use, led to a dramatic increase in food production worldwide. The impact of these advances in agriculture was termed the "green revolution".

FIGURE 17.13 *A semi-dwarf* O. sativa *cultivar carrying the* sd-1 *gene (dee-geo-woo-gen, left) and its tall isogenic line (woo-gen, right).*