DOCUMENT RESUME

ED 367 551 SE 054 327

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TITLE	Plant Growth and Development: An Outline for a Unit Structured Around the Life Cycle of Rapid-Cycling Brassica Rapa.
PUB DATE	91
NOTE	81p.
AVAILABLE FROM	Wisconsin Fast Plants, 1630 Linden Drive, Madison, WI 53706 ($10).
PUB TYPE	Guides - Classroom Use - Teaching Guides (For Teacher) (052)
EDRS PRICE	MF01/PC04 Plus Postage.
DESCRIPTORS	Biology; College Science; Higher Education; *Plant Growth; Plant Propagation; *Plants (Botany); Problem Sets; Science Activities; Science Education; *Science Instruction; Science Materials; Units of Study

ABSTRACT

This outline is intended for use in a unit of 10-12 lectures on plant growth and development at the introductory undergraduate level as part of a course on organismal biology. The series of lecture outlines is structured around the life cycle of rapid-cycling Brassica rapa (RCBr). The unit begins with three introductory lectures on general plant biology entitled: (1) "What It Means to Be a Plant"; (2) "The Plant Life Cycle"; and (3) "Seeds and Seed Dormancy." Students plant RCBr seeds at the beginning of lecture 4 and observe their plants at each successive class period, as the lecturer discusses aspects of plant development in the context of the RCBr life cycle. The remaining lecture titles are: (4) "Seed Germination"; (5) "Utilization of Food Sources"; (6) "Environmental Effects on Plant Growth and Development"; (7) "Hormonal Integration of Plant Growth and Development"; (8) "Hormonal Mediation of External Signals: A Case Study"; (9) "Flowering and Alternation of Generations"; and (10) "Photoperiodism and Flowering." Lectures 7 and 10 can be split to create 12 lectures. Figures referenced throughout the document are found in Appendix A. Appendix B includes a question set to assist students in their study and understanding of the unit. Appendices C and D are intended to provide students with some perspective in their approach to the unit. A bibliography includes 9 references. (MDH)

PLANT GROWTH AND DEVELOPMENT

An Outline for a Unit Structured Around the Life Cycle of Rapid-Cycling *Brassica rapa*

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This outline is intended for use in a unit of 10-12 lectures on plant growth and development at the introductory undergraduate level. It was developed by Professor Wayne M. Becker at the University of Wisconsin-Madison for a unit on this topic in a semester-long course on Organismal Biology. The course is part of a four-semester sequence that comprises the Biology Core Curriculum at this institution. Students come to this course as juniors, with a year each of calculus, organic chemistry, and physics, and a semester of cellular and molecular biology, but with no prior coursework in biology at the organismal level. The course begins with a consideration of plant growth and development, then moves on to topics in animal and human physiology.

The lecture series outlined here is structured around the life cycle of rapid-cycling *Brassica rapa* (RCBr) and has been developed in collaboration with Professor Paul H. Williams. The unit begins with three introductory lectures on general plant biology to lay the necessary foundations. Students then plant RCBr seeds at the beginning of lecture 4 and observe their plants at each successive class period, as the lecturer discusses aspects of plant development in the context of the RCBr life cycle. For a typical lecture course with a MWF format, the 12-lecture unit will conclude on the 18th day after planting, by which time the RCBr plants will have been flowering for at least a week and may have already begun to set seeds, if growth conditions are optimal.

The figures referenced throughout the outline can be found in Appendix A. Wherever possible, RCBr plants have been used to illustrate the various aspects of plant growth and development, though discussion of some topics (such as starch mobilization in germinating cereal grain and photoperiod-induced flowering) obviously draws upon other species, as appropriate. Most of the figures in Appendix A are suitable for use as slides or overhead transparencies. A question set is included as Appendix B to assist students in their study and understanding of the unit. Appendices C and D are intended to provide students with some perspective in their approach to the unit.

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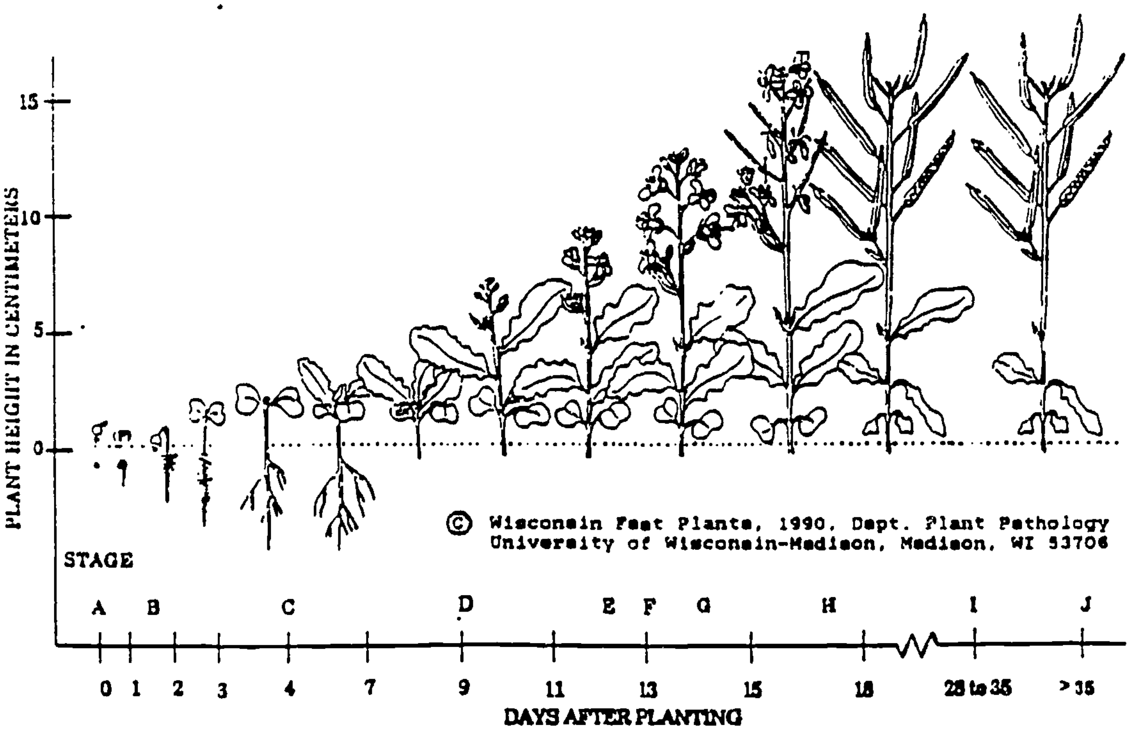

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PLANT GROWTH AND DEVELOPMENT

Lecture Schedule

Lecture	Week	Day	DAP*	Lecture Title	Outline Sections
1	1	M	--	What It Means to be a Plant	I
2		W	--	The Plant Life Cycle	II
3		F	--	Seeds and Seed Dormancy	III & IV
4	2	M	0	Seed Germination	V
5		W	2	Utilization of Food Reserves	VI
6		F	4	Environmental Effects on Plant Growth and Development	VII & VIII
7	3	M	7	Hormonal Integration of Plant Growth and Development (1)**	IX & X
8		W	9	Hormonal Integration of Plant Growth and Development (2)**	X (cont.)
9		F	11	Hormonal Mediation of External Signals: A Case Study	XI
10	4	M	14	Flowering and the Alternation of Generations	XII
11		W	16	Photoperiodism and Flowering (1)*	XIII
12		F	18	Photoperiodism and Flowering (2)*	XIII (cont.)

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* DAP = Days after planting; students plant RCBr seeds at the beginning of lecture 4 and observe plants regularly thereafter.

** This outline can be readily adapted to a unit of 10 or 11 lectures by condensing the material in lectures 7 and 8 and/or in lectures 11 and 12 into a single lecture each.

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PLANT GROWTH AND DEVELOPMENT

I. The Other Kingdom: What It Means to be a Plant

A. The Comparative Biology of Plants and Animals

1. Unity versus diversity in biology

    (a) Unity: Plants and animals face many common problems and needs.

    (b) Diversity: Plants and animals nonetheless display characteristically different solutions.

2. Higher plants (angiosperms, the flowering plants) have a body plan that is radically different from that of higher animals.

    (a) These differences probably arose as consequences of two quite different solutions to a common nutritional problem.

    (b) These differences have enormous repercussions for both organismal and developmental biology.

3. The most important distinction between plants and animals is that of nutritional mode.

    (a) Plants are autotrophs, whereas animals are heterotrophs.

    (b) Because of this fundamental distinction, plants and animals have radically different body plans and "life styles." (See Appendix C, "What It Means To Be A Plant")

4. Autotrophy profoundly affects the structure, function, and development of plants.

5. A consideration of the physiology and development of plants therefore involves topics and/or emphases different from the corresponding discussion for animals.

    (a) Example from physiology: The "circulatory" system of plants really involves two one-way streets (xylem and phloem) rather than a closed cyclic system.

    (b) Example from development: Because of the rigid walls that surround plant cells and render them stationary, morphogenesis in plants occurs mainly by differential cell division and expansion, without cell movement.

6. Hence, plants cannot be thought of as "green animals" nor can their physiology and development be approached or studied strictly in animal terms.

B. Brassica as a Model Plant

1. The genus Brassica contains many economically important species, some of which are also important research tools.

2. Brassica rapa, the wild mustard plant, is a typical species in this genus (Figure 1; all Figures in Appendix A).

3. "Rapid-cycling" variants of B. rapa and several related species have generation times that are significantly shorter than those of most other plants--in some cases, as short as five weeks (Figure 2).

4. Because they complete their life cycle so quickly and therefore produce multiple generations per year, such rapid-cycling Brassica (RCBr) variants are very useful, both in research and for teaching purposes.

5. We will use RCBr plants as our "mascot" in this unit.

   (a) RCBr plants will be used to illustrate lecture topics from lecture 2 onward.

   (b) They will also serve as the basis for a research proposal that you will write as a part of this unit.

   (c) In addition, they will be used as model organisms for the first four weeks of laboratory (with Dr. Paul Williams).

C. Plant Structure: The Angiosperm Body Plan

1. The concept of meristems: All plant parts develop from permanently immature growing points called meristems.

2. The angiosperm body plan involves an aboveground shoot system and a belowground root system. (Figure 3)

   (a) The shoot system arises from the shoot meristem of the embryo.

   (b) The root system arises from the root meristem of the embryo.

3. The shoot system consists of stem and leaves and has two different types of meristems.

   (a) Features of the stem: nodes and internodes

   (b) Features of the leaf: petiole and blade

   (c) The shoot apex (or apical bud) consists of the shoot apical meristem and leaf primordia. (Figure 4)

   (d) The axillary (or lateral) bud gives rise to lateral branches.

4. The root system can involve several different types of roots, but has a single kind of meristem.

    (a) A root can either be a <u>taproot</u> or a <u>lateral root</u>.

    (b) The <u>root apex</u> (or <u>root tip</u>) consists of the <u>root apical meristem</u> and the overlying <u>root cap</u>. (Figure 5)

    (c) Most absorption of water and mineral salts occurs through the <u>root hairs</u>, which are extensions of root epidermal cells.

5. The vascular system of a plant is not a "circulatory system" in the animal sense; it is more like two one-way streets, one usually going up and the other usually going down.

    (a) <u>Xylem</u>: tissue responsible for movement of water and dissolved mineral salts from the roots to the rest of the plant.

    (b) <u>Phloem</u>: tissue responsible for movement of sugars, amino acids, and other nutrients from the leaves to the rest of the plant.

6. The flower is the reproductive structure of the angiosperm. (Figure 6)

    (a) The flower as a modified shoot, floral parts as modified leaves

    (b) Nonreproductive floral parts: <u>pedicel</u>, <u>receptacle</u>, <u>sepals</u>, <u>petals</u>

    (c) Male reproductive parts: <u>stamens</u>, each consisting of a slender <u>filament</u> which supports an enlarged <u>anther</u> containing <u>pollen sacs</u> with haploid <u>pollen grains</u> inside

    (d) Female reproductive parts: <u>carpels</u>, each consisting of a flat, sticky <u>stigma</u>, a slender <u>style</u>, and, at the base, an expanded, hollow <u>ovary</u> containing one or more <u>ovules</u>, each with a haploid <u>embryo sac</u> inside

    (e) Most flowers contain both stamens and carpels, but some (those of a corn plant, for example) are either male (tassel; stamens only) or female (ear; carpels only)

II. The Plant Life Cycle: How the Other Half Lives

A. Introduction to Plant Development

1. Plant development must be considered in the context of the entire life cycle.

2. We will therefore begin our discussion of plant development with

an overview of the angiosperm life cycle.

3. Role of RCBr Plants

    (a) Our discussion here in lecture will be illustrated by observations made on rapid-cycling Brassica (RCBr) plants that you will grow from seed and observe during the next several weeks. (See Appendix E: "The Cycle of Life")

    (b) You will be provided with a Brassica kit this morning; by planting your seeds today and observing the plants as they grow, you should find that they illustrate most of the remaining topics in this unit, at about the time we get to each. (Recall Figure 2)

B. The Angiosperm Life Cycle (Figure 7; see also Appendix D)

1. Male and female gametes are produced by the respective reproductive parts.

    (a) The male gamete, or sperm, develops from one of the haploid nuclei of the pollen grain within the pollen sacs of the anthers.

    (b) The female gamete, or egg cell, develops from one of the haploid nuclei of the embryo sac within the ovules of the ovary. (In addition to the egg cell, the embryo sac also contains a central cell with two haploid polar nuclei, which eventually combine to form a diploid fusion nucleus.)

2. Pollination is the process whereby shed pollen is transferred from the anther to the stigma of the same or another flower. (Figure 8)

    (a) Pollination in plants is analogous to mating in animals.

    (b) Common pollinating agents include wind, insects, birds, and bats.

    (c) Pollination is accomplished when a pollen grain lands or is deposited on a receptive stigma, where the pollen grain germinates and the pollen tube begins its growth down the style to the ovule.

    (d) The germination of "foreign" pollen is apparently prevented by chemical substances in the stigma; a similar mechanism may prevent self-pollination in some species.

    (e) Growth of the pollen tube occurs only at the tip (with the vegetative nucleus leading the way), is exceedingly rapid, and may be chemotactic.

    (f) Division of the generative nucleus to form the two sperm nuclei usually occurs as it moves down the growing pollen tube (although in some species this occurs before the pollen is shed).

(g) The pollen tube grows down the style, enters the ovary, and grows up the funiculus (stalk) of the ovule into the micropyle to reach the embryo sac.

3. Fertilization occurs when the tip of the pollen tube reaches the embryo sac and discharges the two sperm nuclei. (Figure 9)

(a) One sperm nucleus fertilizes the egg to form the diploid zygote.

(b) The second sperm nucleus enters the central cell and unites with the fusion nucleus to form the triploid endosperm nucleus.

(c) This process is called double fertilization and is unique to angiosperms.

(d) The ploidy level and eventual fate of several structures in the embryo sac are indicated in Table 1:

TABLE 1

Structure in embryo sac	Ploidy level	Fate during Subsequent Seed Maturation
Zygote	2n	Divides mitotically and differentiates into the embryo
Endosperm nucleus	3n	Divides mitotically to form the endosperm tissues which nourishes the developing embryo before (and in many cases also after) germination
Ovule	2n*	Matures into the seed
Integuments	2n*	Harden into the seed coats as the seed matures
Ovary	2n*	Develops into the fruit (which sometimes also incorporates other accessory structures such as the receptacle)**

*Tissues of maternal origin only

**In the mustard family (Brassicaceae), the fruit is formed from two fused carpels and is called a silique. At maturity, the two sides (or valves) of the fruit split off, leaving the seeds attached to a persistent central portion of the silique from which they arose.

4. Embryogenesis is the process whereby the diploid zygote gives rise to a multicellular embryo, all within the ovule. (Figure 10)

    (a) The first cell division of the zygote is unequal, generating a small cell from which the embryo will develop and a large basal cell which gives rise to the suspensor, a short filamentous support structure. (Figure 10A)

    (b) Subsequent divisions (stages B-H of Figure 10) lead to the mature embryo, a polar structure with differentiated tissue and two meristems. (Figure 11A)

    (c) The shoot meristem is a group of small, relatively undifferentiated cells at the end of the embryo opposite the suspensor.

    (d) The root meristem forms at the opposite end, near the suspensor.

    (e) Localized growth on either side of the shoot meristem leads to formation of the cotyledons.

    (f) The axis connecting the shoot and root meristems is called the hypocotyl (hypocotyl = "below the cotyledons").

    (g) The shoot meristem is inactive during early embryogenesis (cotyledons arise adjacent to, but not within, the meristem), but may become activated during late embryogenesis, giving rise to the first leaf primordia which make up the plumule.

    (h) The root meristem usually becomes active in late embryogenesis to produce an elongated radicle, or embryonic root.

5. The mature dicot embryo usually consists of the following structures (Figure 11)

    (a) A shoot meristem, with or without plumule

    (b) A root meristem, with or without evidence of radicle elongation

    (c) Two cotyledons, usually containing food reserves

    (d) A hypocotyl region between the root meristem and the point of attachment of the cotyledons

6. As the embryo develops, the ovule matures into a seed and the ovary develops into a fruit.

7. Germination occurs when a seed containing a viable embryo is exposed to favorable environmental conditions.

8. Vegetative growth and development then gives rise to the mature vegetative plant.

9. Eventually, the vegetative plant is induced to flower, which initiates a phase of reproductive growth and development that allows the plant to complete its life cycle.

D. "Control Points" Around the Life Cycle

1. There are several crucial points at which the course of development can be controlled, thereby allowing the life cycle to accommodate seasonal changes in environment.
   (a) Seed germination

   (b) Induction and breaking of dormancy

   (c) Flowering

2. These are the points in the life cycle at which the organism is most sensitive to external stimuli, thereby allowing the organism to respond to, and even to anticipate, changes in its environment.

III. Development Around the Life Cycle

A. Lecture Discussion Topics

1. Having convinced ourselves that development in plants occurs throughout the life cycle, we want now to examine selected aspects of plant development in some detail.

2. Because of time constraints, we will focus on four specific developmental phenomena:

   (a) Seeds and seed dormancy

   (b) Seed germination

   (c) Seedling growth and development

   (d) Reproductive growth and development (flowering)

IV. Seeds and Seed Dormancy

A. Utility and Function of the Seed

1. The seed represents a dehydrated, resistant structure in which the embryonic plant is protected from a temporarily hostile environment.

2. The mature seed is very resistant to environmental adversity and can survive surprisingly rigorous conditions for long times.

3. The seed is also the form in which the species is most readily propagated and disseminated.

4. Many of the features of seeds can be explained in terms of their function in propagation and their survival during adversity.

B. Essential Features of a Seed (Figure 11)

1. The most important feature of the seed is the desiccated embryo inside.

    (a) The embryo is a multicellular, differentiated structure derived from the diploid zygote by repeated cell division and specialization.

    (b) Embryogenesis terminates upon desiccation of the seed, leaving a dry, metabolically inactive embryo, arrested at a stage in which it is poised for later development.

    (c) Unlike the embryo of higher animals, the "mature" plant embryo does not possess all of the major organs of the adult body; instead, the major adult organs (shoots and roots) are represented only by their respective meristems, with unlimited growth potential.

    (d) The arrested embryo still carries on metabolic activity, but at a greatly reduced level.

2. The food supply for the embryo is also packaged in the seed.

    (a) The primary source of nourishment during embryogenesis is the endosperm, derived from the triploid endosperm nucleus.

    (b) By the time of seed desiccation, the food reserves that are on hand to meet the needs of subsequent germination may be either still in the endosperm (typical monocot pattern; seen in corn and cereal grains) or already absorbed into the cotyledons (typical dicot pattern; seen in bean or pea).

    (c) Common food reserves are starch, lipid and/or protein.

3. The third essential feature of the seed is the protective covering around the embryo and endosperm.

    (a) These seed coats (or testae) are derived from the integuments of the ovule.

    (b) They are dry, hard, and relatively impervious to water and gases.

C. The Physiological Status of Seeds (Dormancy vs. Quiescence)

1. Seeds are quiescent if the embryo resumes growth promptly upon exposure to favorable conditions (supplies of water, oxygen and warmth).

2. Seeds are <u>dormant</u> if they require some special conditions or "trigger" before they can resume growth; this is usually an evolutionary safeguard against germination at the "wrong" time.

3. Seed dormancy is an important selective advantage, but has been bred out of most cultivated plants.

D. Factors Responsible for Seed Dormancy

1. Impermeable seed coat

   (a) Explanation: the testae are impermeable to water until softened or broken by abrasion, fire, microbial action or passage of the seed through the alimentary tract of a bird or animal

   (b) Examples: legumes, black locust, lotus

2. Chemical inhibitors

   (a) Explanation: some plants contain water-soluble germination inhibitors which prevent germination until washed out

   (b) Examples: desert plants which must not germinate until enough water is on hand to allow completion of the life cycle

3. Embryo dormancy

   (a) In some seeds, the embryo itself is dormant.

   (b) Embryo dormancy can usually be broken either by exposure to low temperature or by exposure to red light (example: lettuce seed).

   (c) These environmental requirements for germination can frequently be overcome by the application of <u>gibberellin</u>, one of the plant hormones we will discuss later.

4. Immature embryo

   (a) Explanation: the embryo itself is immature when the seed is shed and germination cannot occur until the embryo has undergone further postimbibitional development

   (b) Example: orchid embryo requires symbiotic relationship with fungus

V. Seed Germination and Seedling Emergence

A. Definition of Germination

1. <u>Germination</u> involves the resumption of active growth and development by the embryonic plant and marks the end of the dormant or quiescent state.

2. Germination is usually taken to include all events from the initial uptake of water until protrusion of the radicle.

B. Requirements for Germination

1. For dormant seeds, dormancy must be overcome by one or more of the following mechanisms:

   (a) Abrasion of seed coat

   (b) Leaching out of inhibitors

   (c) Exposure to red light

   (d) Exposure to low temperature

   } or treatment with gibberellin

2. The seed must be exposed to conditions favorable for growth.

   (a) Adequate water supply

   (b) Adequate oxygen supply

   (c) Some minimal amount of warmth

C. Events in Germination (Figure 12)

1. State I: water uptake (<u>imbibition</u>), a physical process leading to a marked swelling which usually results in rupture of the seed coat

2. State II: hydration of cells and reactivation of cellular metabolism (particularly energy metabolism and protein synthesis)

3. Stage III: division and/or enlargement of cells in the <u>radicle</u> (embryonic root), leading to protrusion of the radicle through the seed coat

D. Seedling Emergence (Figure 13)

1. Once the radicle emerges from the seed, germination is over.

2. Further postgerminative growth and development involves continued growth of the radicle and emergence and rapid elongation of the shoot.

3. As the radicle grows downward in the soil, lateral roots and root hairs develop.

4. Emergence of the plumule above ground is accomplished in one of several different ways:

   (a) In many dicots, the hypocotyl elongates, pulling the cotyledons upward out of the soil into the air, where they separate to expose the plumule, which then begins active growth and gives rise to the stem and foliage leaves of the seedling. (example: bean, Figure 13A)

(b) In other dicots, elongation of the hypocotyl does not occur; instead, the cotyledons remain in the soil, and the plumule is elevated to the surface by rapid elongation of the epicotyl (the stem region between cotyledons and the first true leaves; epicotyl = "above the cotyledons"). (example: peas, Figure 13B)

(c) In most monocots, the single cotyledon (scutellum) remains within the seed, while the plumule and its surrounding coleoptile sheath grow upward; about the time the coleoptile breaks through the surface of the soil, the first foliage leaf grows through the tip of the coleoptile and emerges into the light and air. (example: corn, Figure 13C; wheat, Figure 14A)

VI. Utilization of Food Reserves During Seed Germination

A. Food Reserves in the Seed

1. The food reserves required to sustain the seedling until it reaches the surface and can begin photosynthesis are stored either in the cotyledons (most dicots) or in the endosperm (most monocots).

2. Food reserves are most commonly stored as starch (cereal grains), lipid (oil-bearing seeds) and/or protein (beans).

3. Activation or synthesis of the enzymes involved in the utilization of the food reserves is an important metabolic aspect of seed germination.

4. Once stored food reserves are depleted, maternal provision for the heterotrophic embryo and seedling is over, and the young plant is "on its own."

B. Regulation of Enzyme Activities During Germination

1. A major metabolic feature of germination is a sudden, marked increase in enzyme activities.

2. Particularly important are the enzymes involved in utilization of food reserves and in energy metabolism.

3. Regulation of enzyme activities may be effected at several different levels.

   (a) Some enzymes are apparently already present in the desiccated embryo and are simple activated upon hydration (posttranslational control).

(b) Other enzymes are synthesized de novo, using pre-existing mRNA's and ribosomes which are activated upon germination (translational control).

(c) Still other enzymes appear only after the mRNA itself has been synthesized (transcriptional control).

C. Regulation of Starch Utilization During Cereal Grain Germination: A Case Study (Figure 14)

1. Hydrolysis of starch by the enzyme amylase is an important aspect of germination in many species.

    (a) Many species of plants, notably the cereal grains, depend upon starch as the primary food reserve in the seed.

    (b) The starch is stored in the endosperm (Figure 14A) and is rapidly hydrolyzed during germination to nourish the developing seedling.

    (c) Starch hydrolysis is due to the appearance of the enzyme α-amylase, which adds water across the glycosidic (glucose-glucose) bonds of starch, thereby degrading the starch to the disaccharide maltose.

2. Amylase function during cereal grain germination has been most extensively studied with malting barley ("malt" = brewer's term for germinated barley seed).

3. Amylase appearance during germination is regulated by the hormone gibberellin. (Figure 14B)

    (a) The appearance of amylase (and other hydrolytic enzymes) is triggered by gibberellin which is produced by the embryo.

    (b) The target cells which respond to the gibberellin are those of the aleurone layer that surrounds the starchy endosperm.

    (c) The progressive appearance of enzyme activity is due to de novo enzyme synthesis.

4. Amylase mRNA is also synthesized de novo (Figure 15)

    (a) Early inhibitor studies indicated that RNA synthesis was also required for the appearance of amylase activity.

    (b) Subsequently, in vitro protein synthesis was used to show the progressive appearance during germination of a translatable mRNA for amylase, suggesting de novo synthesis of the messenger during early germination.

    (c) More recently, the case for transcriptional regulation has been further strengthened by evidence from Northern blotting, in which a sequence-specific DNA probe is used to assay for mRNA molecules directly, rather than testing for their ability to direct the synthesis of specific polypeptides *in vitro*. (Figure 16)

VII. Environmental and Hormonal Regulation of Plant Growth and Development

A. External and Internal Signals

1. As our *Brassica* seedlings are growing, we will pause to consider the impact of both external (environmental) and internal (hormonal) factors involved in the regulation of plant growth and development.

2. External factors are important because the growth and development of a plant is profoundly influenced by environmental signals, which are used to synchronize the life cycle of the plant with its physical environment.

3. Internal factors are important because almost all aspects of the growth and development of a plant and most of its responses to external factors are under the control of an intricate balance of chemical growth substances called *hormones*.

B. Approach

1. We will look first at the main external factors affecting plant development (this lecture).

2. Then we will consider the major groups of plant hormones (next lecture).

3. Thereafter, we will return to our *Brassica* plants to see how several of these factors and hormones interact to control vegetative development and flowering.

VIII. The Impinging Environment: Environmental Effects on Plant Development

A. The Intimate Interaction of Plants with Their Environment

1. Because of their immobility, plants need external signals to synchronize their growth and development with a physical environment from which they cannot escape.

2. Plants make extensive use of environmental cues to initiate and direct almost all aspects of their development.

3. A vital part of the study of plant development therefore concerns the ways in which plants sense and respond to environmental factors which in animals often elicit only behavioral responses.

B. Keying the Angiosperm Life Cycle to the Environment

1. Figure 17 indicates some of the major external signals which influence the growth and development of flowering plants at

various stages of the life cycle and serve to key the life cycle to the environment.

2. Not surprisingly, major clusterings of such signals appear at three points in the life cycle: flowering, germination, and the induction and breaking of dormancy.

3. The main external stimuli involved in keying the plant life cycle to its environment are gravity, water, temperature, and light.

4. Each of these factors is mentioned briefly here, with several discussed later in more detail in the appropriate developmental contexts.

C. The Effects of <u>Gravity</u> on Plant Growth (<u>Gravitropism</u>; Figure 18)

1. Roots almost always grow downward (<u>positive gravitropism</u>).

2. Shoots almost always grow upward (<u>negative gravitropism</u>).

D. The Effects of <u>Water</u> (Moisture) on Plant Growth and Development

1. Like all organisms, plants need water as a component of protoplasm, as a solvent, for maintenance of cell turgidity, and as a reagent in many cellular reactions (including, in plants, photosynthesis).

2. In general, the water requirement of a plant is more critical than that of an animal because of its immobility and its great losses of water by <u>transpiration</u>.

3. Water is also important developmentally

   (a) It is a necessary prerequisite for seed germination, to hydrate cells and activate metabolic processes.

   (b) It is also required in some seeds to wash away inhibitors of germination.

E. The Effects of <u>Temperature</u> on Plant Growth and Development

1. Since plants have no way of maintaining a constant internal temperature, all plant processes, both physiological and developmental, are vitally dependent upon the external temperature.

2. Physiological effects include enzyme activation, chlorophyll synthesis, respiration, photosynthesis, transpiration, cytoplasmic streaming, and salt uptake.

3. Temperature also affects plant development; in fact, much of the life cycle of the typical temperate-zone angiosperm is best understood as an adaptation to recurring seasons of unfavorable temperature.

4. <u>Dormancy</u> is the result of seasonal changes in temperature.

    (a) All temperate-zone plant species must make provision for overwintering.

    (b) In woody perennials, the shoot apices cease active growth and become encased in bud scales (<u>bud dormancy</u>).

    (c) Perennial herbaceous plants overwinter belowground as <u>bulbs</u>, <u>corms</u> or <u>rhizomes</u>.

    (d) Annual plants overwinter in the form of dormant or quiescent seeds.

5. Breakage of dormancy requires a favorable temperature.

    (a) Resumption of growth of shoot apices is temperature-dependent.

    (b) Initiation of growth from dormant underground organs requires warm weather.

    (c) All seeds require a certain minimal temperature for germination.

    (d) In addition, many seeds, buds, or underground organs require a certain period of cold exposure before they will emerge from dormancy.

    (e) In agricultural practice, dormancy in such seeds is broken by deliberate exposure of the seed to low-temperature storage conditions (<u>stratification</u>).

6. Some plants require a period of chilling (<u>vernalization</u>) before they will flower.

<u>Note</u> the distinction in terms: <u>vernalization</u> is the deliberate exposure of plants or seedlings to cold to induce flowering, whereas <u>stratification</u> involves the deliberate exposure of seeds to cold to break dormancy and permit germination.

F. The Effects of <u>Light</u> on Plant Growth and Development

1. Light is the single most important external factor which influences plant growth and development.

    (a) Light is essential to all green plants as the source of energy for photosynthetic carbon fixation.
    (b) Light affects a number of other physiological processes as well.

    (c) Light also affects both vegetative and reproductive growth and development.

2. Effects of light on vegetative growth (photomorphogenesis)

   (a) Light is required to initiate germination in some seeds.

   (b) Light inhibits cell elongation and cell division when seedlings arrive above ground. (Figure 19)

   (c) Light stimulates structural differentiation of plant cells.

   (d) These (and other) effects are responses to red light and often require only a transient exposure to light to initiate the response.

3. Effects of light on direction of growth (phototropism)

   (a) Light also influences the direction of plant growth.

   (b) Shoot tips usually bend toward the light (positive phototropism).

   (c) Root tips usually bend away from the light (negative phototropism).

   (d) These effects are responses to blue light and require the constant presence of the light source.

4. Effects of photoperiod on reproductive and vegetative growth (Figure 20)

   (a) Sensitivity to changing day length (photoperiodism) allows plants to anticipate seasonal changes in the environment.

   (b) The transition from vegetative to reproductive growth (flowering) is under photoperiodic control in many species. (Figure 20A)

   (c) The induction and/or breaking of dormancy is often a photoperiodic response. (Figure 20B)

5. Photobiology deals with the study of biological detection of and response to light.

   (a) The effectiveness of light depends upon its intensity, its quality (wavelength composition), its duration, and the extent to which it is absorbed by the organism.

   (b) The detection of light by a biological system requires a photosensitive pigment.

   (c) The pigment involved in photosynthesis is chlorophyll.

   (d) The pigment involved in photoperiodism and in many photomorphogenetic effects is phytochrome.

(e) The pigment involved in phototropism is not known for sure, but is probably a <u>carotenoid</u> or a <u>flavoprotein</u>.

(f) Other photoreceptors are almost certainly involved in other responses of plants to light.

IX. The Hormones Within: Internal Integration of Plant Growth and Development

A. The Need for Internal Integration and Communication

1. All multicellular organisms require interaction and communication between tissues and cells to synchronize both physiological and development processes.

2. Response to external signals requires intercellular communication in both plants and animals, since the site of detection of the signal is almost always different from the site of response.

   (a) In animals, the response to external stimuli is usually behavioral, often rapid, and is mediated by either the central nervous system or by one or more hormones.

   (b) In plants, the response is almost always a modification of the pattern of growth and development, is usually much slower than in animals, and is mediated by growth substances which may also be called hormones.

B. The Concept of a Plant Hormone

1. In animals, a <u>hormone</u> is a substance that is synthesized in particular secretory cells (usually in a gland) and transported via the circulatory system to another part of the body where extremely small amounts of it influence a specific physiological process.

2. <u>Plant hormones</u> (also called <u>phytohormones</u>) differ from this definition in several respects:

   (a) It is often not possible to differentiate clearly between the site of hormone synthesis and its site of action in plants, and specific glandular tissue or secretory cells are not involved.

   (b) A plant hormone can elicit a remarkably wide range of responses, depending upon the tissue or organ in which it is acting, the developmental stage of the tissue, and the concentration of the hormone in that tissue at that stage.

3. Plant hormones are all small organic molecules with molecular weights less than 500; larger molecules would almost certainly have difficulty penetrating the cell wall.

4. Plant hormones differ greatly in their effects.

    (a) Some plant hormones promote growth and development; other have inhibitory (but still physiological) effects.

    (b) Some plant hormones have different effects on different tissues.

    (c) In some cases, a hormone may have different effects at different concentrations.

5. Normal development is almost always the result of a delicate and changing balance of hormones.

X. Introduction to the Plant Hormones

A. The Auxins

1. Discovery (Figures 21 and 22)

    (a) Charles and Francis Darwin: The phototropic response of seedlings involves the transmission of some "influence" from the apical tip to the lower part (1880).

    (b) F.W. Went: The "influence" is a chemical stimulus called <u>auxin</u> (1928)

2. Chemistry (Figure 23)

    (a) The most common natural auxin is indoleacetic acid (IAA), which is probably synthesized from tryptophan.

    (b) Napthaleneacetic acid (NAA) is a synthetic auxin commonly used to induce adventitious roots on plant cuttings.

    (c) Other important synthetic auxins include the chlorinated derivatives of phenoxyacetic acid (2,4-D and 2,4,5-T).

    (d) The herbicidal effects of 2,4-D and 2,4,5-T are due to the metabolic derangements caused by auxins at high concentration and to the inability of the plant cell to degrade and detoxify these synthetic compounds.

B. The Gibberellins

1. Discovery

    (a) E. Kurosawa: The "foolish seedling disease" of rice in the Orient was caused by a substance produced by the fungus <u>Gibberella fijikuroi</u>; the causative substance was called <u>gibberellin</u> (1926).

    (b) Gibberellin was first isolated from <u>Gibberella</u> cultures in 1954.

(c) The first gibberellin from a higher plant was isolated, purified, and structurally identified in 1956.

(d) Since then, more than 70 different gibberellins have been isolated from a wide variety of species of both fungi and higher plants.

(e) The effect of gibberellin on stem elongation is seen especially well in dwarf mutants. (Figure 24)

2. Chemistry (Figure 23B)

(a) All of the gibberellins are derivatives of an isoprenoid-type compound with four rings, little or no unsaturation, and a lactone bridge.

(b) Gibberellic acid (GA_3) is the most abundant gibberellin in fungi and is the most active in most bioassays for the hormone.

(c) Differences between the gibberellins lie in the number and placement of double bonds and hydroxyl groups.

C. The Cytokinins

1. Discovery

(a) J. Van Overbeek: Coconut milk (liquid endosperm) contains a factor which promotes growth of isolated embryos in vitro.

(b) F.C. Steward and co-workers: This factor caused cell division in differentiated adult cells of carrot.

(c) F. Skoog and colleagues: The factor caused cell division and resumption of growth in cultured tobacco tissue.

(d) C.O. Miller and F. Skoog: The factor in coconut milk was a purine derivative; aged or heated DNA had a similar effect, due to the presence of kinetin, a substituted adenine.

(e) The first naturally-occurring promoters of cell division were isolated in 1964 (zeatin) and 1967 (isopentenyl adenine).

(f) This group of growth factors came to be known as cytokinins, because of their stimulatory effect upon cell division (cytokinesis).

2. Chemistry (Figure 23C)

(a) The naturally-occurring and synthetic cytokinins are usually N-substituted adenines and their ribosides or ribotides.

(b) Zeatin and isopentenyl adenine (i^6Ade) are two naturally-occurring cytokinins.

(c) Kinetin and 6-benzylamino purine (BAP) are the most common synthetic cytokins.

D. Abscisic Acid

1. Discovery

(a) Wareing: Studies on the onset of dormancy led to the isolation in 1956 of a growth inhibitor which was termed <u>dormin</u> to indicate its dormancy-inducing activity.

(b) Addicott and colleagues: Studies on abscission of various plant organs led to the isolation from cotton bolls of a factor which was called <u>abscisin</u> because of its role as an accelerator of abscission.

(c) The two factors were eventually shown to be the same chemical compound which by mutual agreement is now called <u>abscisic acid</u>.

2. Chemistry (Figure 23D)

(a) Abscisic acid, like the gibberellins, is composed of isoprenoid units and can be derived metabolically from mevalonic acid.

(b) Their synthesis from a common starting compound may provide a regulatory mechanism in the plant by a switch from the production of abscisic acid (growth inhibitor) to gibberellins (growth promoters) or <u>vice versa</u>.

E. Ethylene

1. Discovery

(a) One rotten apple in a barrel has long been known to cause the whole lot to spoil.

(b) This effect is due to the production by the rotten apple of the volatile agent <u>ethylene</u>, which causes necrosis of healthy fruit nearby, leading to their spoilage and further ethylene production.

(c) In recent years, it has become clear that ethylene is a normal plant metabolite produced in minute quantities by healthy cells and involved in a variety of regulatory phenomena, especially fruit ripening. (Figure 25A)

(d) IAA promotes ethylene production (Figure 25B), suggesting an interaction between auxins and ethylene in growth regulation.

2. Chemistry

   (a) Structure: $CH_2=CH_2$

   (b) Origin: Ethylene is thought to be derived from carbon atoms 3 and 4 of the amino acid methionine.

F. Florigen

1. Discovery -- to be discussed later in conjunction with flowering

2. Chemistry -- completely unknown (the only evidence for its existence is physiological, not chemical)

XI. Seedling Growth and Development: Auxins and the Tropisms

A. Hormonal Mediation of External Signals: A Case Study

1. Having examined the main environmental factors that influence plant growth and development and the major groups of hormones that mediate the plants responses, we now return to our <u>Brassica</u> seedlings to consider a specific example.

2. The specific phenomena selected for this case study involve the plants responses to gravity (gravitropism) and light (phototropism) during vegetative growth and development as mediated by the hormone auxin.

B. Gravitropism and Phototropism During Early Postgerminative Growth and Development. (Figure 26)

1. <u>Gravitropism</u>: Which way is down? (Figure 26A)

   (a) Critical to the success of the plant is downward growth of the root and upward growth of the shoot (gravitropism).

   (b) The root cap and shoot tip play critical roles in mediating these gravitropic responses.

   (c) Graviperception may depend on amyloplast settling for the initial detection of gravity, although the evidence is as yet inconclusive (and somewhat contradictory).

   (d) The gravitropic response involves a gravitationally-induced difference in auxin concentration across the shoot or root tip, resulting in differential growth of cells on the two sides of the plant axis.

   (e) The link between amyloplast settling and differential auxin distribution may be calcium ions, which are released from the ER, activating both a calcium pump and an auxin pump in the plasma membrane.

2. Phototropism: Where is the sun? (Figure 26B)

    (a) Growth of the shoot toward the sun (phototropism) is of obvious advantage to a photosynthetic organism.

    (b) Again, the response is mediated by the shoot tip, although it has actually been studied most intensively in the coleoptiles of cereal grains.

    (c) Photoperception apparently involves a light-induced unequal distribution of auxin at the tip which results in an unequal growth rate on the two sides of the shoot below. (Figure 26C)

    (d) Phototropism is a response to blue light; the photoreceptor is not well-established. (probably a carotenoid or a flavoprotein; almost certainly not phytochrome)

3. Phototropism and gravitropism share several properties

    (a) The stimulus (gravity or light) results in an unequal distribution of auxin.

    (b) The change in auxin distribution almost certainly results from the lateral migration of auxin rather than from differential auxin synthesis or degradation.

    (c) The subsequent bending of the root or shoot in the region back from the tip is due to differential cell enlargement in response to different auxin concentrations.

C. Auxin and Cell Wall Expansion

1. The role of auxin in mediating the phototropic and gravitropic responses is just one manifestation of the characteristic effect of this hormone on cell wall extension and cell elongation.

    (a) Elongation or enlargement of plant cells requires basic changes in the primary cell wall.

    (b) The cell wall is a rigid structure consisting of cellulose microfibrils embedded in non-cellulosic constituents of the wall.

    (c) The non-cellulosic constituents are linked together by covalent bonds but are bound to the cellulose microfibrils only by hydrogen bonds.

2. Auxin causes irreversible stretching of the cell wall, probably by effecting transient acidification of the cell wall, which leads to weakening of hydrogen bonds and "loosening" of the cell wall (the acid growth hypothesis).

    (a) Auxin is thought to activate a proton pump in the plasma membrane.

(b) Protons are extruded into the cell wall, reducing the pH to around 4.

(c) Under these conditions, hydrogen bonds between cellulose microfibrils and the non-cellulosic matrix are transiently disrupted, allowing microfibrils to move within the matrix.

(d) With the cell wall "loosened" in this way, the cell expands in response to turgor pressure from within. (Figure 27)

(e) After enlargement, the cell wall is stabilized by deposition of additional cell wall material.

3. The direction of cell elongation is determined by the orientation of the cellulose microfibrils in the wall. (Figure 28)

XII. Flowering and the Alternation of Generations.

A. Flowering: The Transition to Reproductive Development

1. To complete its life cycle, a vegetatively-growing plant must at some point undergo a transition to flowering, which initiates the reproductive phase of angiosperm development.

2. This transition involves a sequence of physiological and structural changes in the vegetative shoot apex that terminate its meristematic activity and transform it into a reproductive (or floral) apex, which gives rise to the floral structures.

3. Note that unlike higher animals, higher plants do not have permanent reproductive organs; instead, they are formed when needed by the induction of flowering.

4. The induction of flowering involves a variety of environmental factors, including daylength and temperature, as we will see shortly.

B. The Morphology of Flowering

1. The transition from a vegetative to a floral apex involves a marked increased in mitotic activity of the apex, accompanied by changes in dimensions and organization.

2. The initial and early stages of development of the sepals, petals, stamens, and carpels are quite similar to those of leaves.

3. The floral parts usually appear in a fixed order (sepals/petals/stamens/carpels) and always have the same relative spatial relation to one another.

4. The haploid gametes required for sexual reproduction (sperm and egg cells) are generated within the reproductive parts of the flower (the stamens and the carpels, respectively).

5. When we examine the stamens and carpels carefully, we encounter a structural and genetic complexity that reflects the alternation of generations characteristic of all plants, and needs to be understood in that context.

C. Plants and the Alternation of Generations

1. All sexually-reproducing organisms have a life cycle that involves an alternation between the haploid and diploid forms. (Figure 29)

2. There is a great diversity in the relative prominence of the haploid and diploid states, particularly in the plant kingdom.

    (a) The most primitive eukaryotes tend to be haploid for most of their life cycle, with meiosis occurring immediately after fertilization (eg, fungi).

    (b) On the other extreme, animals tend to be diploid for almost all of their life cycle, since meiosis leads directly to gamete formation and gametes fuse to restore the diploid state (gametic meiosis; Figure 29A).

    (c) Among plants, a variety of intermediates can be found between these two extremes, and distinct haploid and diploid organisms can always be distinguished in regular alternation (sporic meiosis; Figure 29B).

3. Plants always display an alternation of generations between haploid and diploid organisms. (Figure 30)

    (a) In plants, meiosis results not in the direct production of gametes, but of haploid spores which divide mitotically to produce a multicellular haploid organism, the gametophyte ("gamete-producing plant").

    (b) The haploid gametophyte gives rise in turn to gametes which upon fertilization produce the diploid sporophyte ("spore-producing plant").

    (c) All plants are therefore characterized by a recurring alternation of generations between a haploid gametophyte and a diploid sporophyte generation.

4. In angiosperms, the male and female gametophytes are produced and retained within the male and female floral structures.

    (a) The male gametophyte is the pollen grain (also called the microgametophyte) which arises from the haploid microspore produced when the microspore mother cell in the pollen sac of the stamen undergoes meiosis. (Figure 30, right)

    (b) The female gametophyte is the embryo sac (also called the megagametophyte) which arises from the haploid megaspore produced when the megaspore mother cell in the ovule of the carpel undergoes meiosis. (Figure 30, left)

XIII. Photoperiodism and Flowering

A. The Role of Photoperiodism in Floral Induction

1. Induction of flowering, like many other aspects of plant development, must be carefully synchronized with the growing season.
    - (a) The plant should develop to a reasonable size before converts to a determinate pattern of growth and invests its energy in flowering and seed production.
    - (b) Yet it must allow sufficient time for seed development and fruit ripening before a season of environmental adversity arrives (winter or the dry season, most commonly).
2. Successful synchronization of flowering with the growing season means that the plant needs some reliable seasonal cue.
3. Most environmental parameters which might be used as seasonal cues are in fact not very reliable indicators (consider temperature in Wisconsin for example).
4. Instead, plants depend most commonly upon the relative length of night and day (photoperiod) to synchronize flowering (and other seasonal activities) to changing environmental conditions.

B. The Relationship Between Photoperiod and Flowering

1. Flowering is correlated closely with the season. (Figure 31)
    - (a) A given species of plant flowers at roughly the same date each year at a given latitude.
    - (b) But different species flower at characteristically different times (e.g., tulips in spring, cereal grains in summer, chrysanthemum in fall).
2. Recognition of the importance of day length for flowering came around 1920 (work of Garner and Allard).
    - (a) Mutant tobacco ("Maryland Mammoth") wouldn't flower until December.
    - (b) Soybeans flower at the same time at a given latitude regardless of when planted, but flower sooner and sooner when planted farther and farther south.
3. The ability to respond to photoperiods (actually, to dark periods, as we shall see) of different length is called photoperiodism.
4. The day length that is crucial to the control of flowering is called the critical photoperiod.

5. Plants can be classified according to their day length requirements for flowering. (Figure 32 and Table 2)

   (a) Short-day plants (SDP) flower only when the day length is less than some characteristic critical photoperiod (example: *Xanthium*, cocklebur).

   (b) long-day plants (LDP) flower only when day length is greater than some characteristic critical photoperiod (example: spinach, radish, wheat).

   (c) Day-neutral plants are unaffected by length of day, but appear to depend instead on internal or structural features.

   Note: Most variants of *Brassica rapa* are day-neutral, and therefore are not dependent on photoperiod to trigger flowering.

6. The daylength requirements of SDP and LDP may be either absolute or quantitative. (Table 2)

   (a) Flowering of an absolute SDP or LDP will never occur in the absence of the appropriate photoperiod.

   (b) Flowering of a qualitative SDP or LDP is simply delayed by the absence of the appropriate photoperiod.

7. More complicated requirements involving long-day conditions followed by short day (LDSD) or *vice versa* (SDLD) are now also recognized, but we will ignore these.

C. Mechanism of Photoperiodism

1. Plants actually measure the length of night rather than the length of day.

   (a) Experiments with artificially long days and nights: short-day plants flower whenever the dark period exceeds some threshold value irrespective of the length of the light period

   (b) Night-break experiments: interruption of the period of darkness with a short period of light inhibits flowering in short-day ("long-night") plants and promotes flowering in long-day ("short-night") plants (Figure 32).

2. Photoperiodism is an inductive phenomenon, in that a few favorable day-night cycles will evoke the response even if the plant is subsequently returned to conditions which would otherwise favor continued vegetative development.

   (a) The number of cycles of inductive photoperiod required varies from species to species.

TABLE 2

Classification of Plants According To Photoperiod Required for Flowering	Critical Photoperiod (hrs. of light)
SHORT-DAY PLANTS	
Bryophyllum pinnatum	12
Chrysanthemum	15
Xanthium (cocklebur)	15.6
Kalanchoe blossfeldiana	12
Euphorbia (poinsettia)	12.5
Oryza sativa (winter rice)	12
Fragaria (strawberry)	10
Nicotiana tabacum (Maryland Mammoth tobacco)	14
QUANTITATIVE SHORT-DAY PLANTS	
Cannabis sativa	
Gossypium hirsutum (cotton, one variety)	
Saccharum officinarum (sugarcane)	
Solanum tuberosum (potato, one variety)	
LONG-DAY PLANTS	
Anethum graveolens (dill)	10
Hibiscus syriacus	12
Avena sativa (oats)	9
Dactylis glomeratus (orchid grass)	12
Lolium perenne (rye grass)	9
Sedum spectabile	13
Triticum aestivum (wheat)	12
QUANTITATIVE LONG-DAY PLANTS	
Brassica rapa (turnip)	
Hordeum vulgare (spring barley)	
Nicotiana tabacum (Havana tobacco)	
Secale cereale (spring rye)	
Sorghum vulgare	
Triticum aestivum (spring wheat)	
DAY-NEUTRAL PLANTS	
Cucumis sativus (cucumber)	
Gomphrena globosa (globe amaranth)	
Ilex aquifolium (English holly)	
Poa annua	
Zea mays (maize)	

(b) The timing of the inductive photoperiod can be remarkably precise.

3. The most effective wavelengths of light for triggering photoperiodic responses are in the red region of the spectrum.

    (a) An <u>action spectrum</u> is a plot of effect of light vs. wavelength used.

    (b) The action spectrum for the night-break effect has a peak at about 660 nm (red light).

4. The effect of red light can be completely canceled by subsequent exposure to far-red light (730 nm).

5. Exposure to alternating red and far-red flashes results in the response characteristic of the last flash seen, provided that the interval between flashes isn't long enough for the previous signal to become "fixed."

6. These findings suggested the involvement of a photoreversible pigment system with 2 interconvertible forms, one sensitive to red light, the other to far-red light.

    (a) This pigment is called <u>phytochrome</u> (<u>phyto</u> = plant, <u>chrome</u> = color or pigment).

    (b) Phytochrome exists in a red-sensitive form (Pr) and a far-red-sensitive form (Pfr) with absorption maxima at 660 nm and 730 nm, respectively. (Figure 33)

    (c) Pr and Pfr are interconvertible. (Figure 34)

    (d) Pfr turns over at a more rapid rate than does Pr.

D. Discovery and Characterization of Phytochrome

1. The existence of phytochrome was postulated in 1959 on the basis of studies like those described above, and was proven in 1965 by isolation of the pigment.

    (a) Dark-grown (non-green) seedlings were used as the source of the pigment to avoid interfering absorption due to chlorophyll.

    (b) The isolated pigment is blue and changes color slightly upon exposure to red or far-red light.

2. Phytochrome consists of a protein plus the light-absorbing pigment.

    (a) The protein has a molecular weight of about 124,000.

    (b) The pigment is a linear tetrapyrrole capable of undergoing a cis-trans isomerization in response to light.

Plant Structure, Growth, and Development: Figures for the Unit

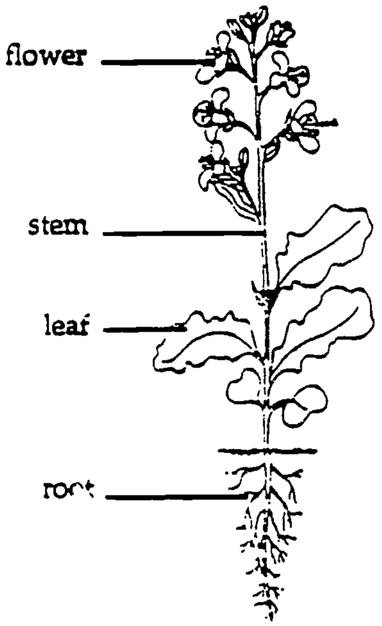

Figure 1. Structural features of *Brassica rapa,* the wild mustard plant. "Rapid-cycling" variants of this and several related species have generation times significantly shorter than those of conventional plants. Such variants are capable of producing up to 10 generations per year, thereby revolutionizing both traditional breeding and genetic engineering experiments.

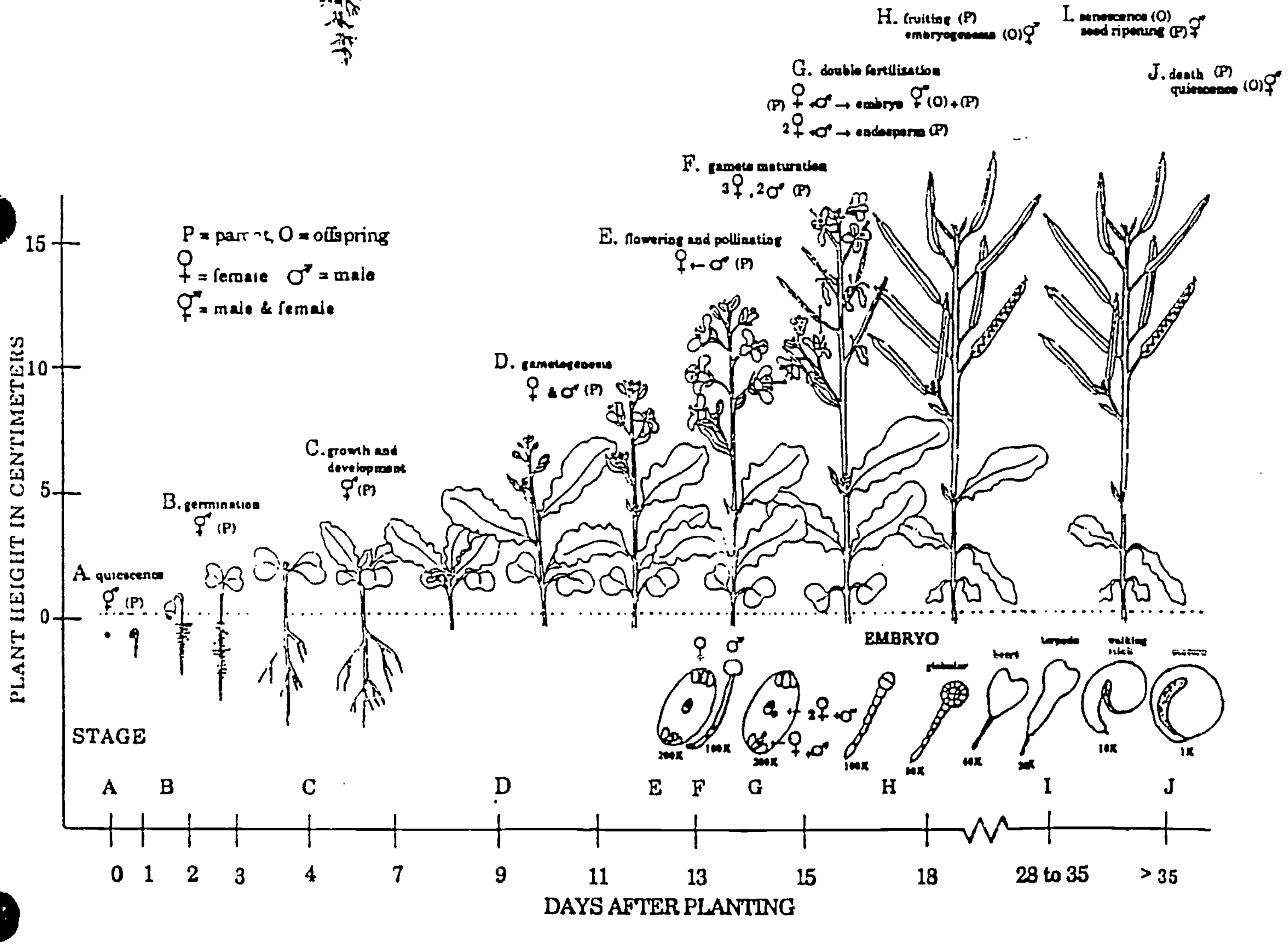

Figure 2. Time scale for the growth and development of *Brassica rapa,* the rapid-cycling plant shown in Figure 1.

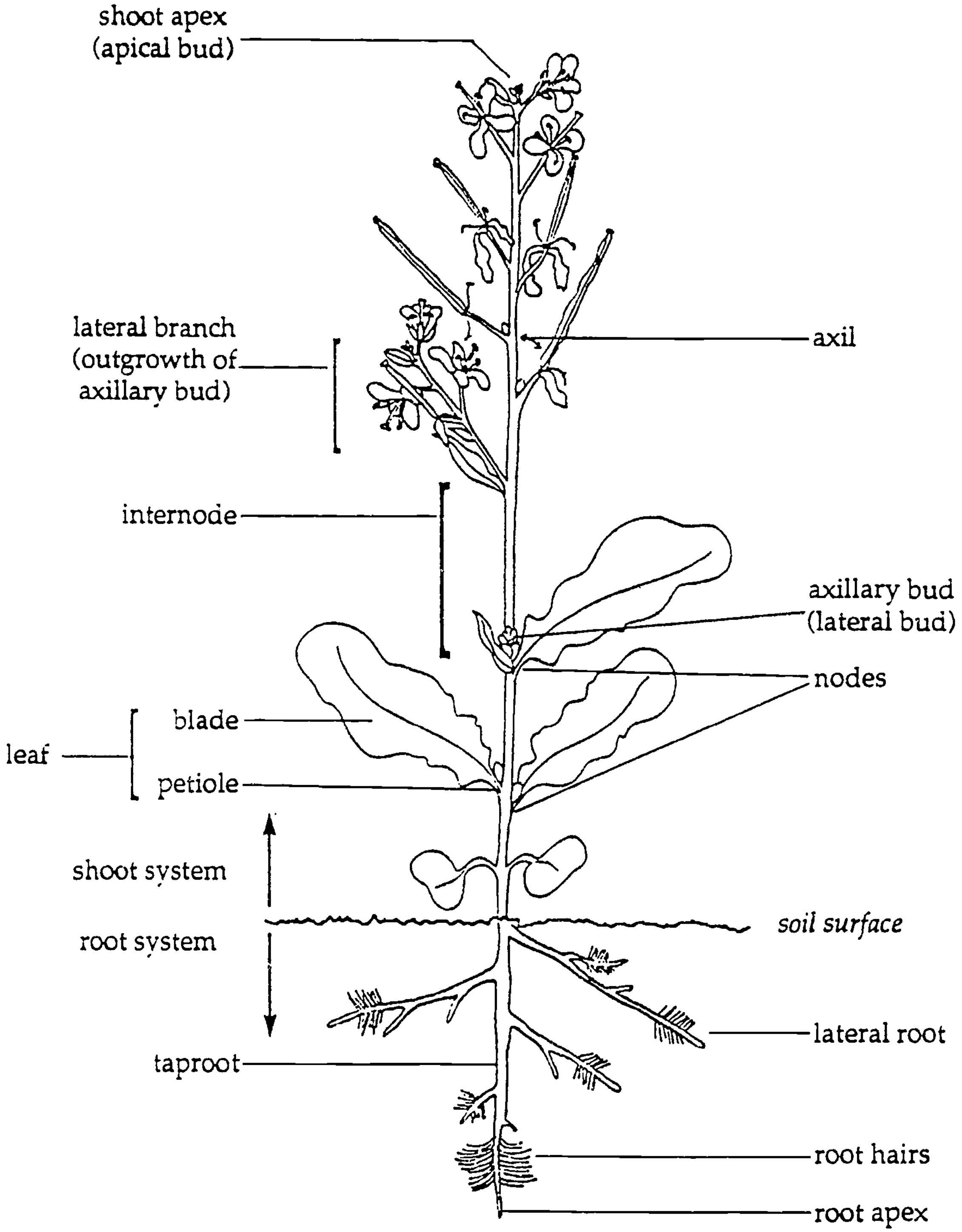

Figure 3. The body plan of a typical angiosperm, illustrating major structural features of the shoot and root systems.

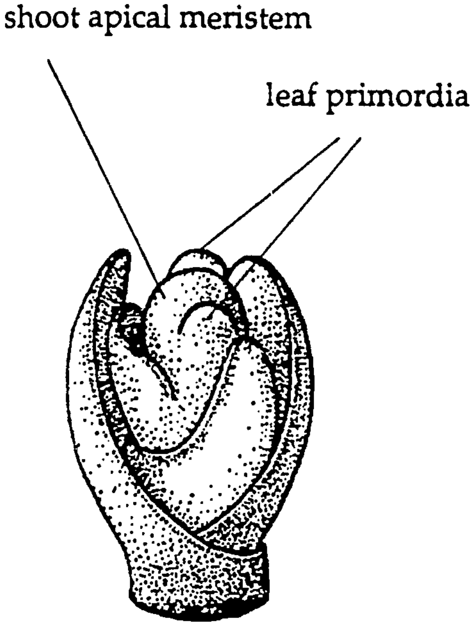

Figure 4. A typical shoot apex, or apical bud, showing the shoot apical meristem and numerous leaf primordia.

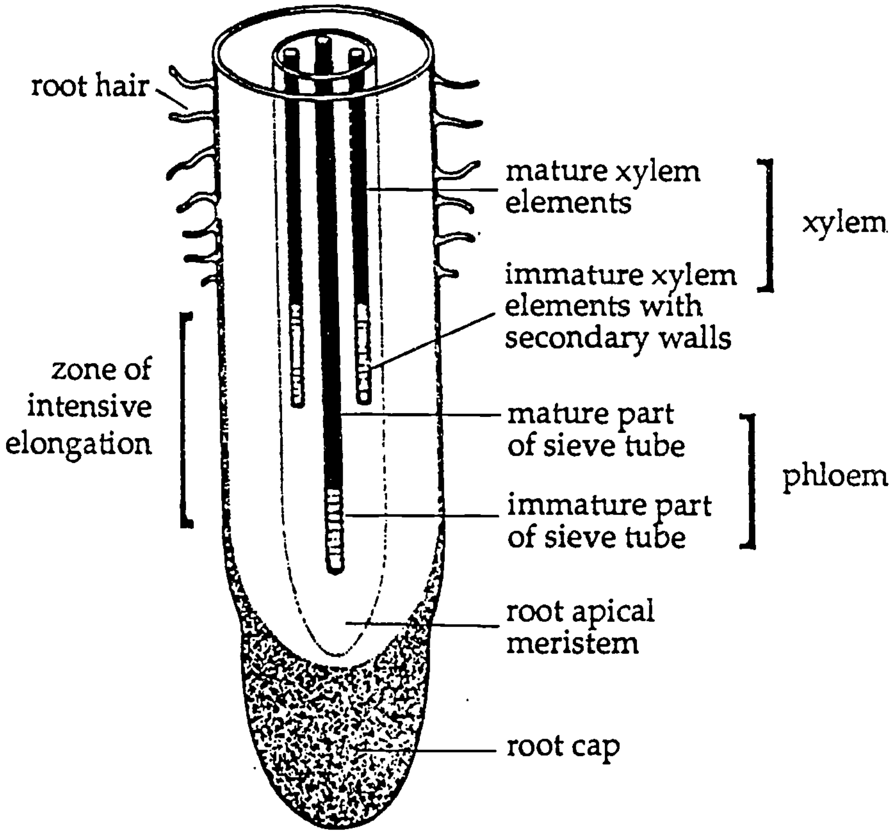

Figure 5. A typical root apex, or root tip, showing the root apical meristem just behind the root cap. There is a zone of especially intensive cell elongation not far behind the meristem. Both phloem and xylem are well differentiated in the region of the root hairs, back of the zone of intensive elongation.

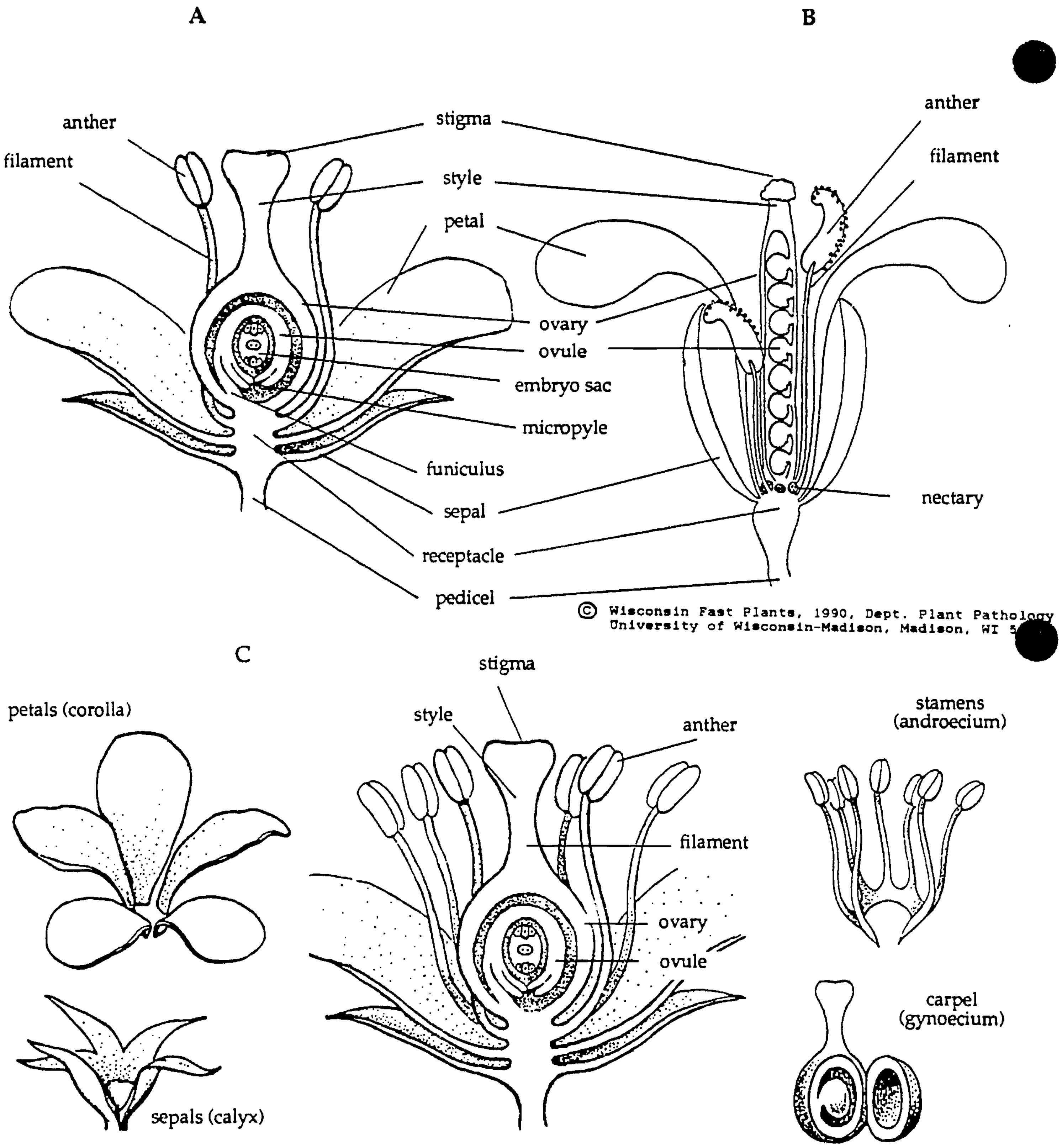

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Figure 6. Floral structure. A, half of a generalized flower, shown in median longitudinal section to illustrate its main parts. B, the *Brassica* flower, to illustrate terminology applied to a specific species (detailed anatomy of the ovule not shown here.) C, the individual floral parts shown in isolation. Terms in parentheses are the collective names for the several floral parts.

A5

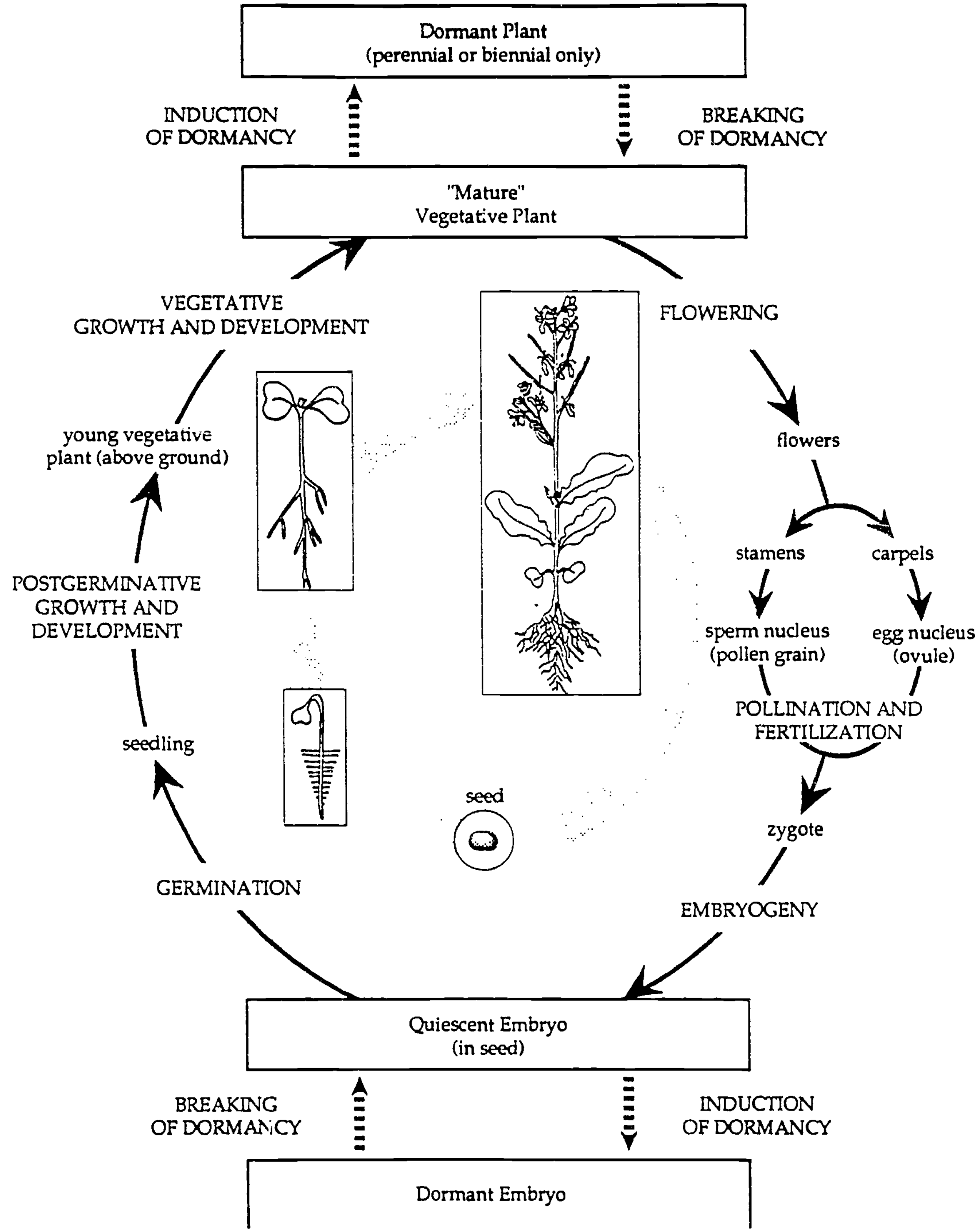


Figure 7. The general life cycle of an angiosperm. The solid lines indicate the major processes of the angiosperm life cycle, and the broken lines indicate the option of dormancy, either for the embryo (bottom) or the mature vegetative plant (top). The drawings illustrate several phases in the life cycle of *Brassica rapa* (wild mustard).

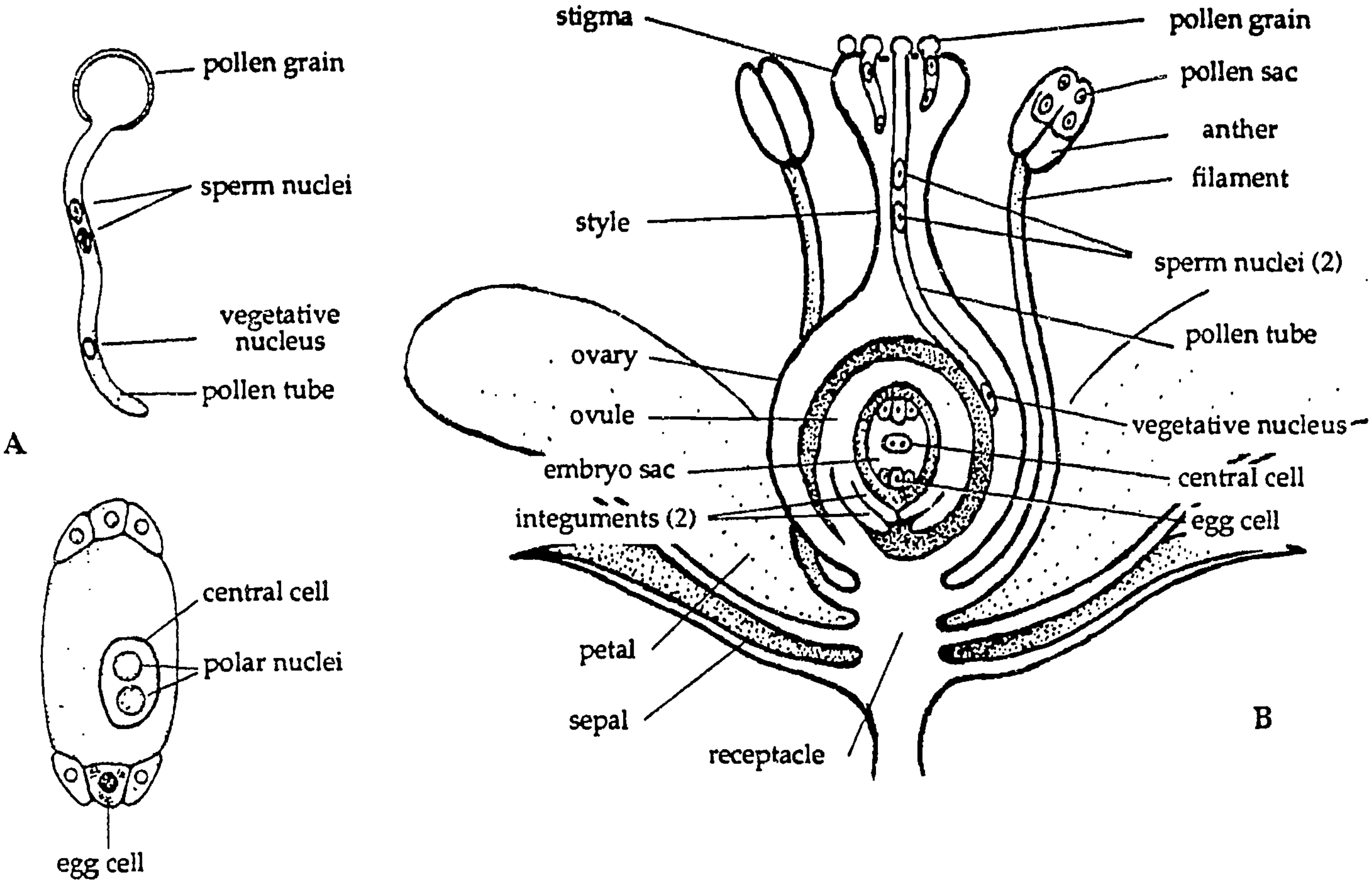


Figure 8. Gametophytes and gametes of an angiosperm. A, the male gametophyte, or pollen grain, is shown on the top, and the female gametophyte, or embryo sac, is on the bottom. B, gametophytes, gametes, and pollen tube growth in the context of floral structure.

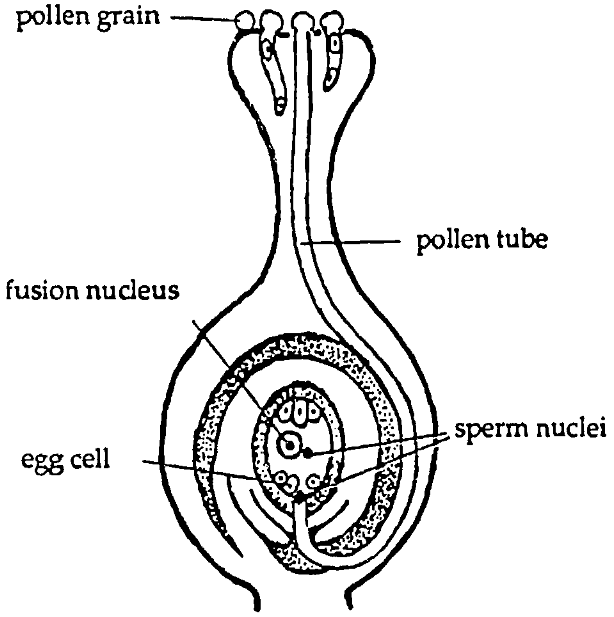


Figure 9. Fertilization. Pollen grains land on the stigma and give rise to pollen tubes that grow downward through the style. One of the pollen tubes shown here has reached the ovule in the ovary and discharged its sperm cells onto it. One sperm will fertilize the egg cell, and the other will unite with the diploid fusion nucleus (derived from the two polar nuclei) to form a triploid nucleus, which will give rise to endosperm.

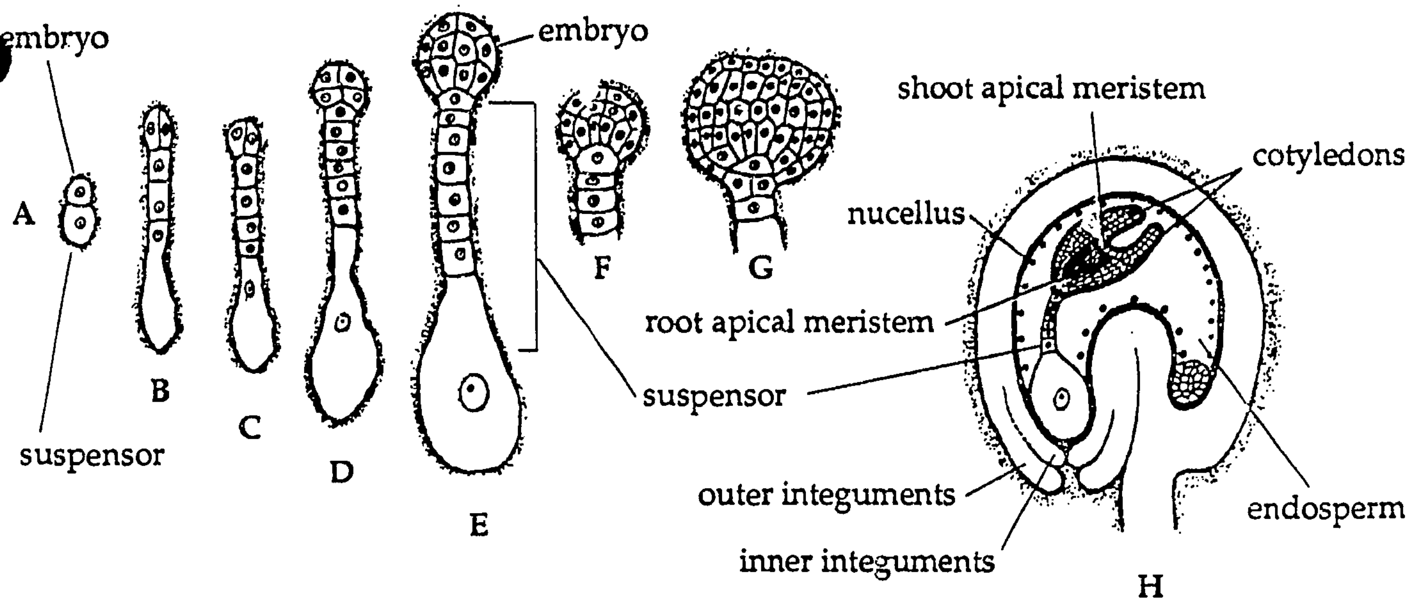


Figure 10. Embryo development in *Capsella bursa-pastoris* (shepherd's purse). A - G, early stages in embryo development, seen in median longitudinal section. H, the embryo at the time of cotyledon emergence, shown in the context of the ovule.

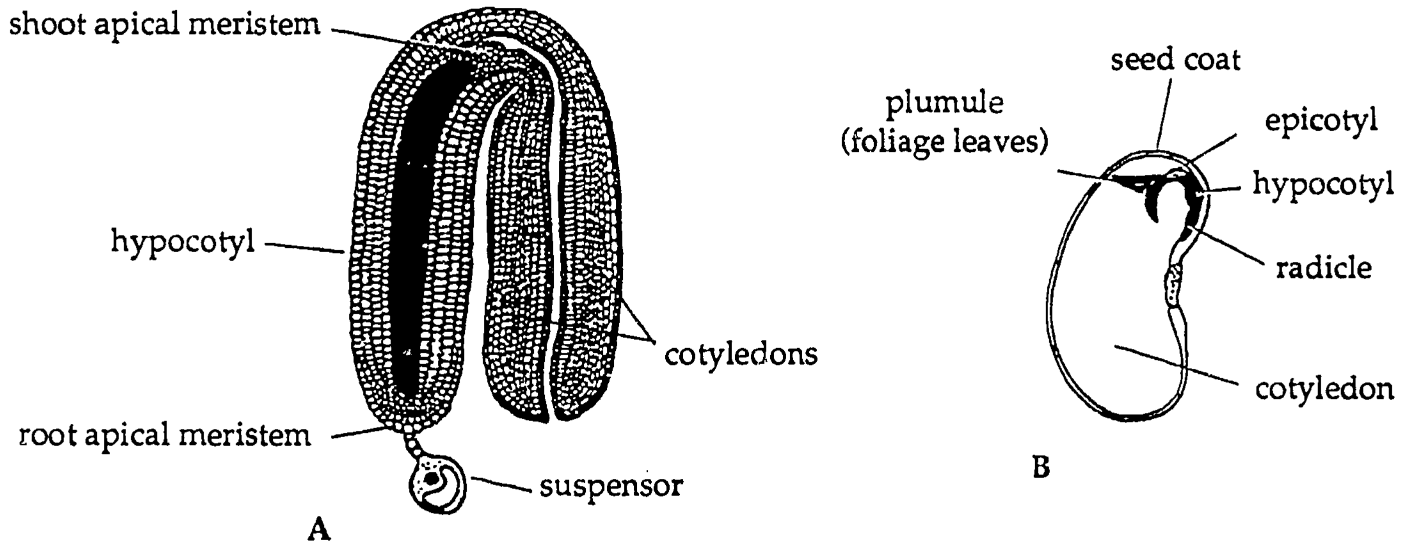


Figure 11. The mature dicot embryo. A, the *Capsella* embryo. In this dicot species, neither a plumule nor an elongated radicle is seen. B, a bean seed, with one cotyledon removed so that the embryo with its plumule and elongated radicle can be seen.

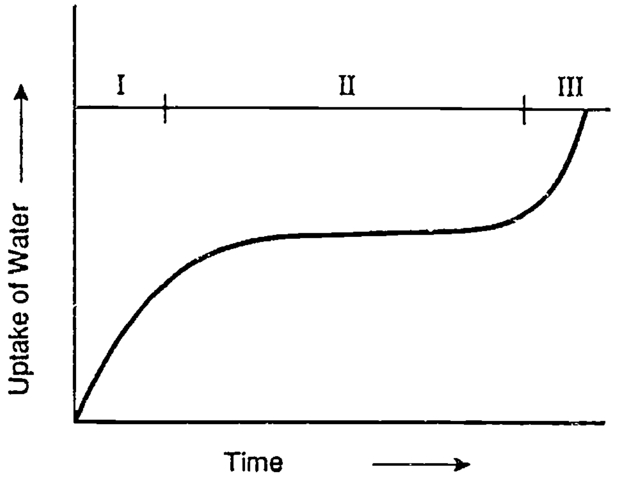


Figure 12. Stages of water uptake by a seed during germination. Stage I is *imbibition,* a physical process. Stage II occurs only in living seeds and comes about by a decreased osmotic potential. Stage III marks the beginning of visible germination.

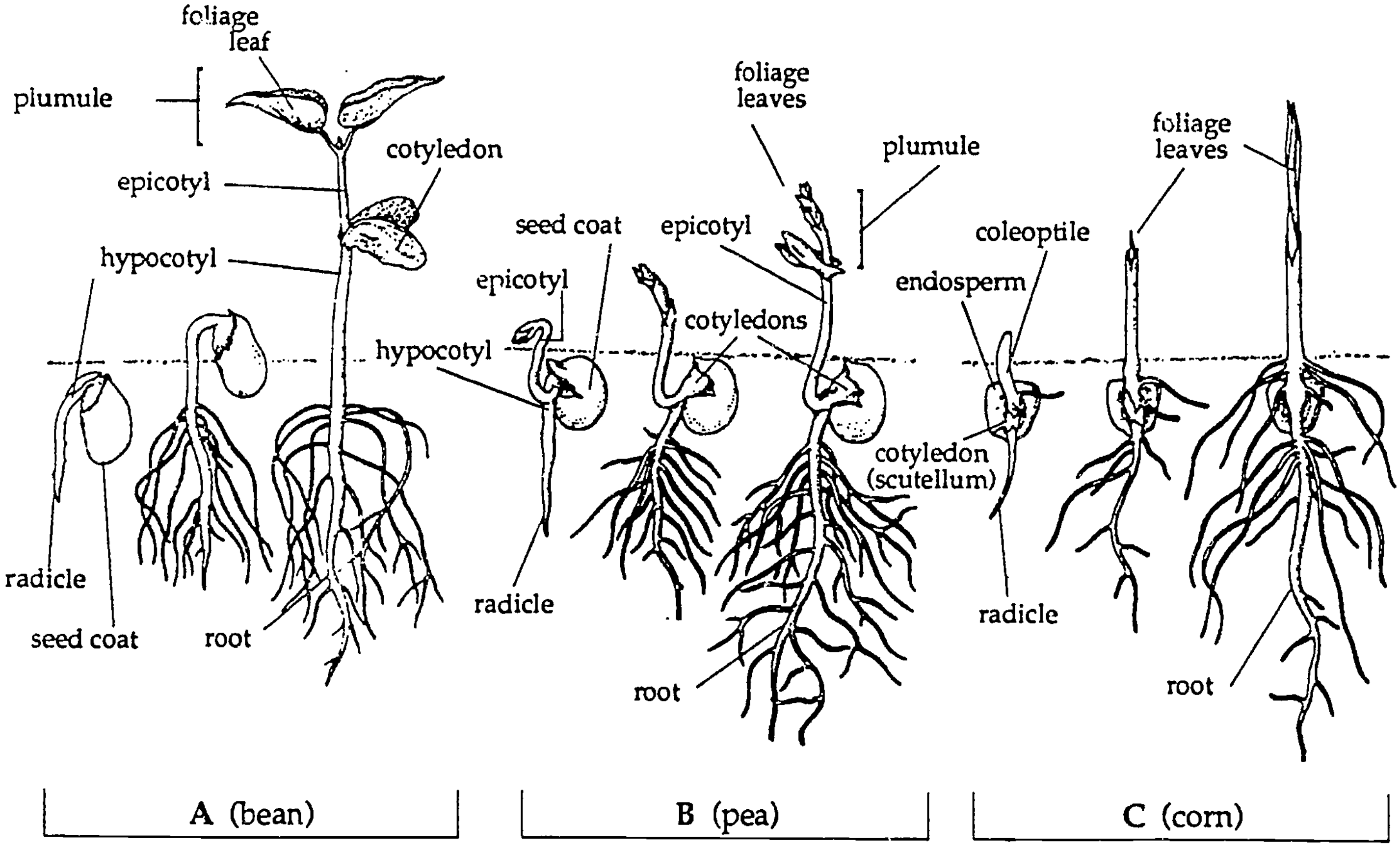


Figure 13. Strategies for seedling emergence. A, in the case of bean, seedling emergence is accomplished by elongation of the hypocotyl, such that the cotyledons emerge above ground. B, for the pea seedling, epicotyl elongation brings the plumule to the surface, leaving the cotyledons within the seed coat below ground. C, the corn seedling emerges by upward growth of the coleoptile and subsequent protrusion of the foliage leaves through the tip of the coleoptile.

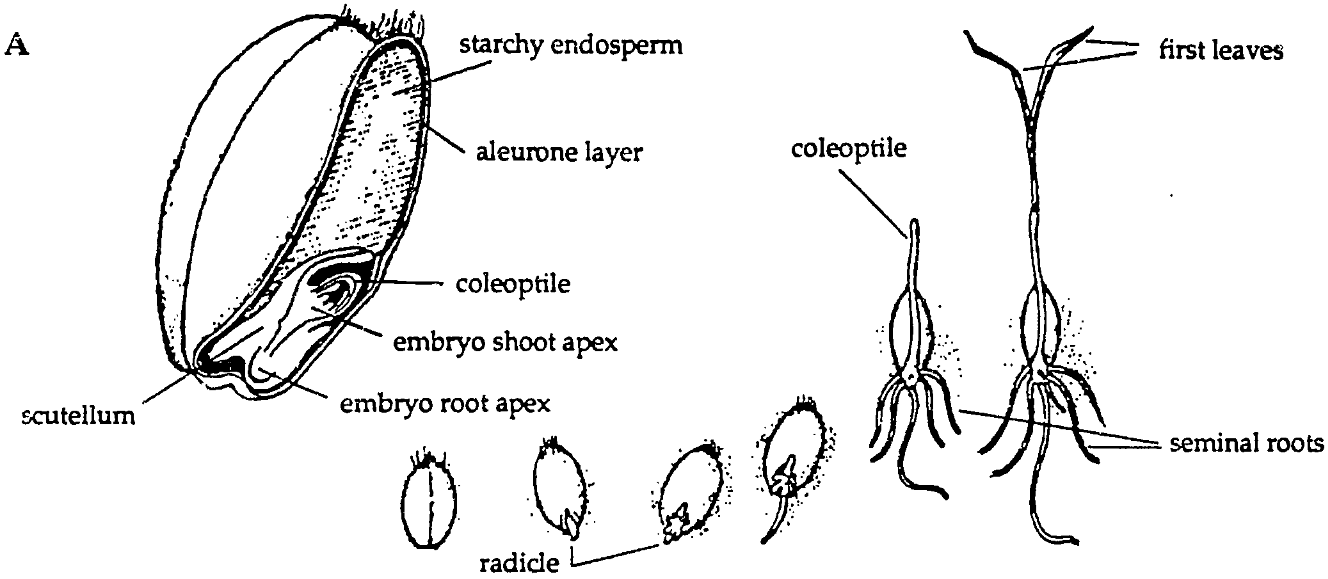
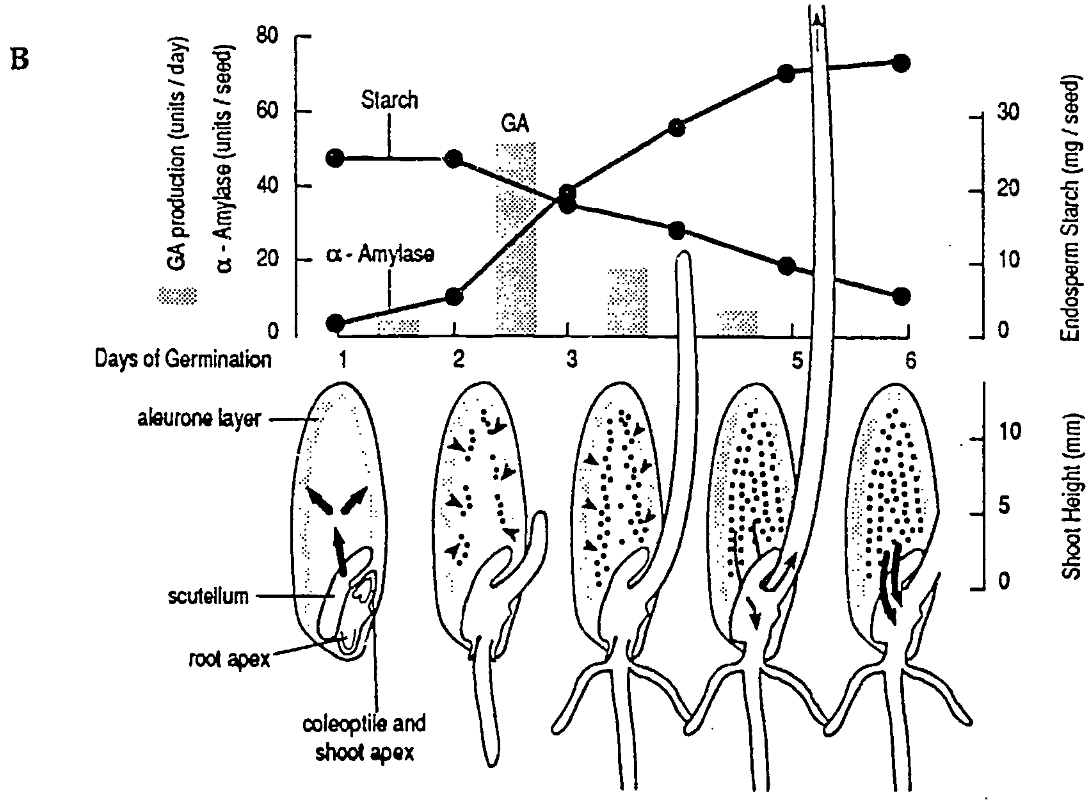


Figure 14. Role of gibberellin in the regulation of starch utilization during germination of barley.

A, structural details of the barley "seed" (really a fruit; the outermost layer is the fruit wall), and six stages in seed germination and seedling development.

B, levels of starch, α-amylase, and gibberellin (GA) during the first 6 days after germination of barley seeds, keyed to schematic diagrams illustrating the gibberellin-controlled formation of hydrolases that leads to release and translocation of nutrients from the endosperm. Data shown on the graph are for synthesis of GA by the embryo, for GA-dependent synthesis of α-amylase by the aleurone cells, and for breakdown of starch in the endosperm by amylase.



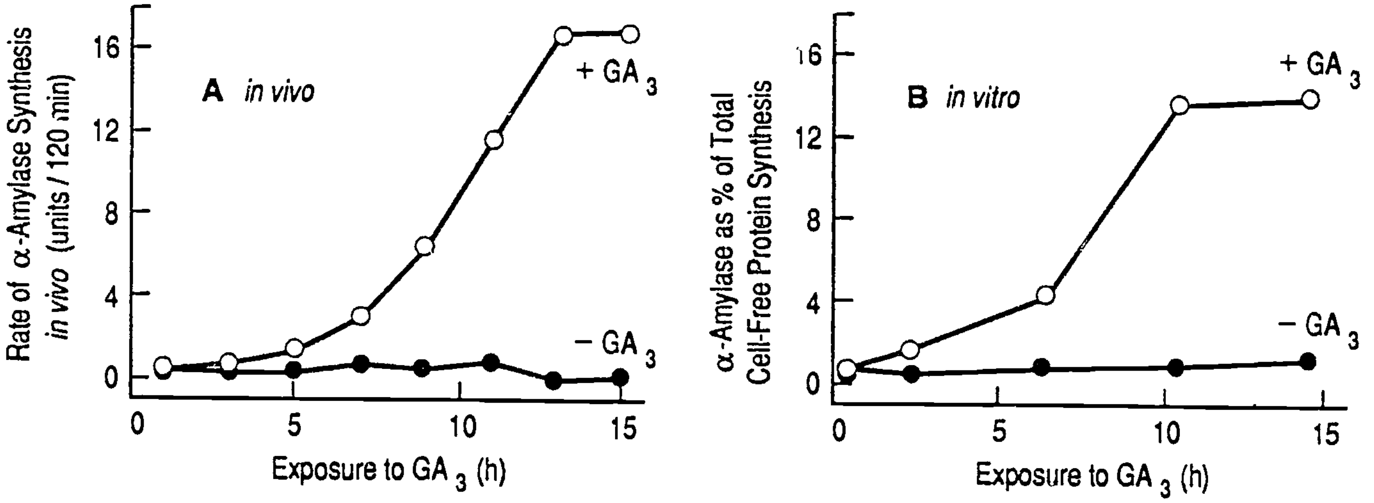


Figure 15. Evidence for the progressive appearance of the mRNA for amylase in barley aleurone cells in response to gibberellin (GA_3) treatment.

In A, the rate of amylase synthesis in isolated but intact aleurone layers is expressed as the increment in enzyme level (units of amylase activity) during successive 2-hour intervals following GA_3 treatment.

The data in B were obtained by isolating total RNA from aleurone layers at various times after hormone treatment, enriching for mRNA (poly[A]-containing RNA, actually) and then adding that mRNA to an *in vitro* protein-synthesizing system containing no other source of mRNA. (All polypeptides synthesized in this system become radioactively-labeled because ^{35}S-methionine is present). After a suitable period of incubation, α-amylase protein is specifically recovered from the other translation products by immunoprecipitation with antibody that has been prepared by injecting rabbits with barley α-amylase. The immunoprecipitated amylase is then quantified (by electrophoretic resolution of the amylase and autoradiographic detection of the ^{35}S) and expressed as a percent of the total *in vitro* protein synthesis attributable to amylase specifically at each time point. The increasing prominence of amylase synthesis *in vitro* shown in B is taken as an indication of the progressive appearance in the GA_3-treated aleurone cells of the mRNA for α-amylase.

The good agreement between the actual profile for α-amylase synthesis *in vivo* (A) and the increasing capacity for α-amylase synthesis *in vitro* (B) suggests that the stimulation of amylase appearance in aleurone cells by gibberellin involves an increase in amylase mRNA. This conclusion has since been confirmed by a technique called **Northern blotting**, in which an amylase-specific DNA clone was used to assay for mRNA molecules directly (data not shown; see *J. Biol. Chem.* 258:2370 or *Plant Mol. Biol.* 3:407 for details).

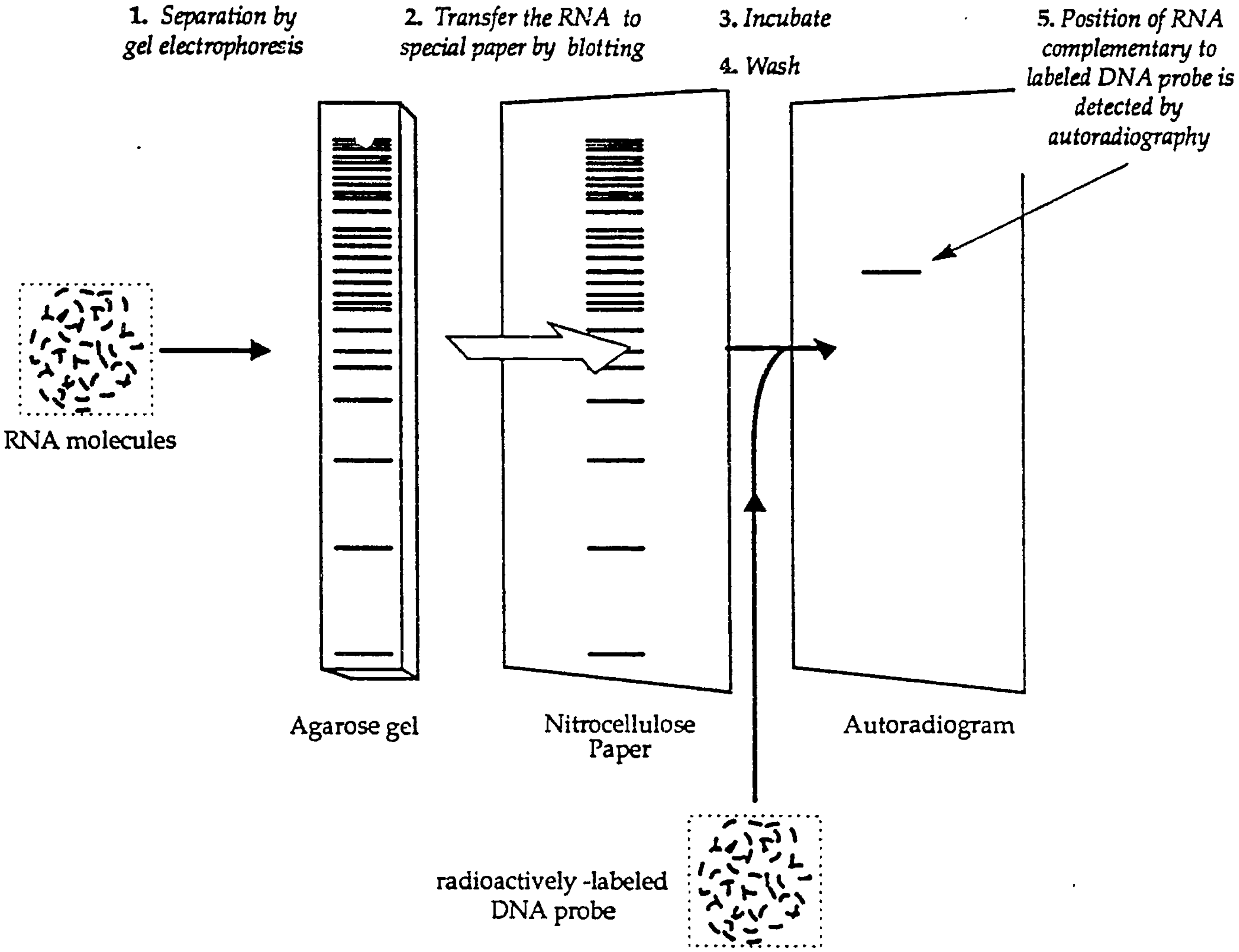


Figure 16. The Northern blot technique for identifying specific RNA molecules.

1. A mixture of RNA molecules is isolated from the tissue of interest and fractionated by electrophoresis through an agarose gel.

2. The many different RNA molecules, now separated along the length of the gel according to size, are transferred to nitrocellulose or nylon paper by blotting.

3. The paper sheet (or "blot") is then exposed to a radioactively-labeled DNA probe for a prolonged period of time under conditions that allow DNA molecules to hybridize to complementary RNA sequences on the blot.

4. The blot is then washed thoroughly to remove all non-hybridized DNA.

5. The positions of RNA molecules complementary to the DNA probe are determined by autoradiography; the hybridized (and radioactive) DNA causes such bands to "light up" on the autoradiogram.

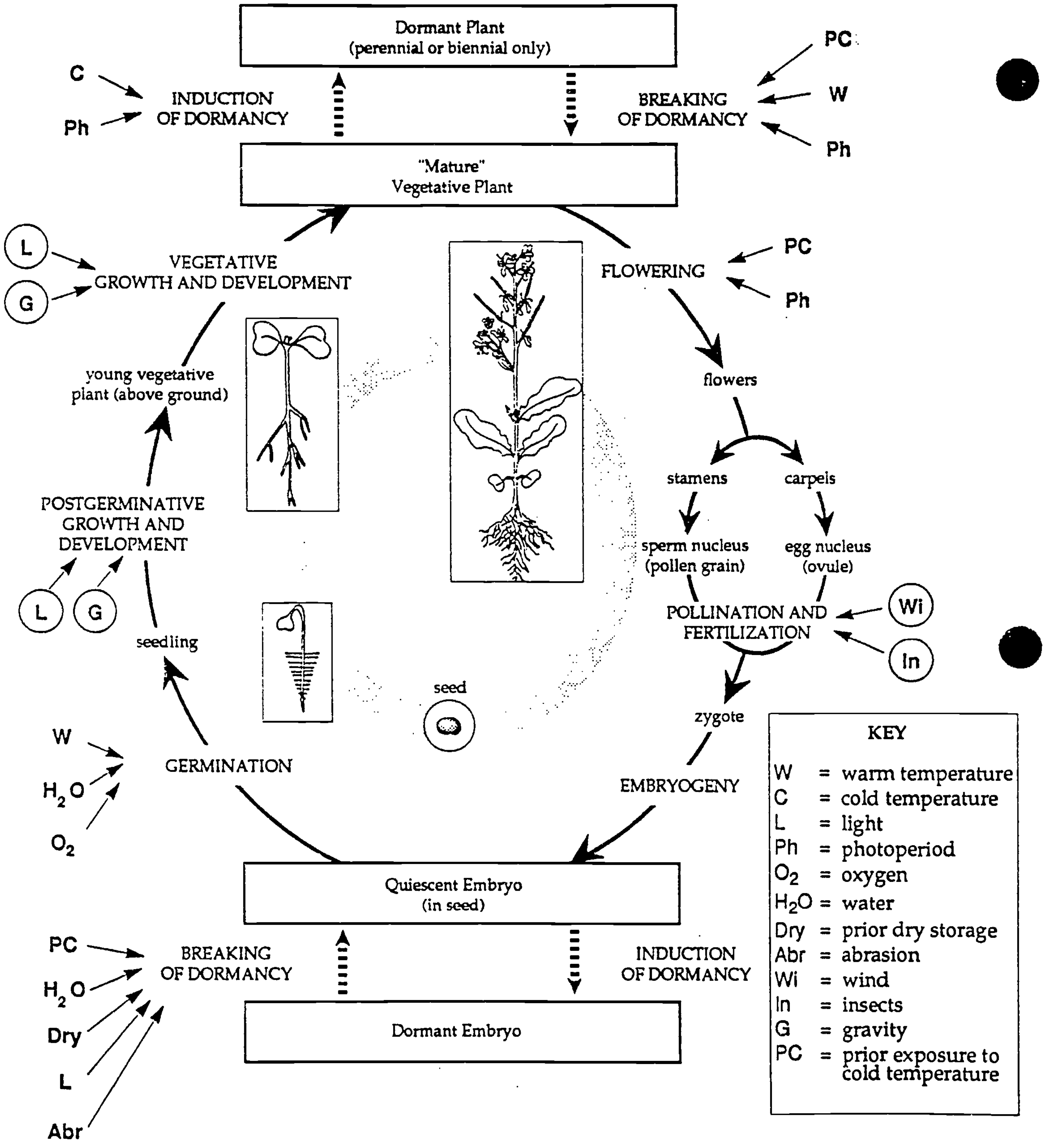


Figure 17. Effects of external factors on the growth and development of angiosperms. The life cycle of Figure 7 is reproduced here with shading to indicate the key "control points" of seed germination, flowering, and the induction and breaking of dormancy. The major external signals which influence growth and development are indicated by letter codes (see key).

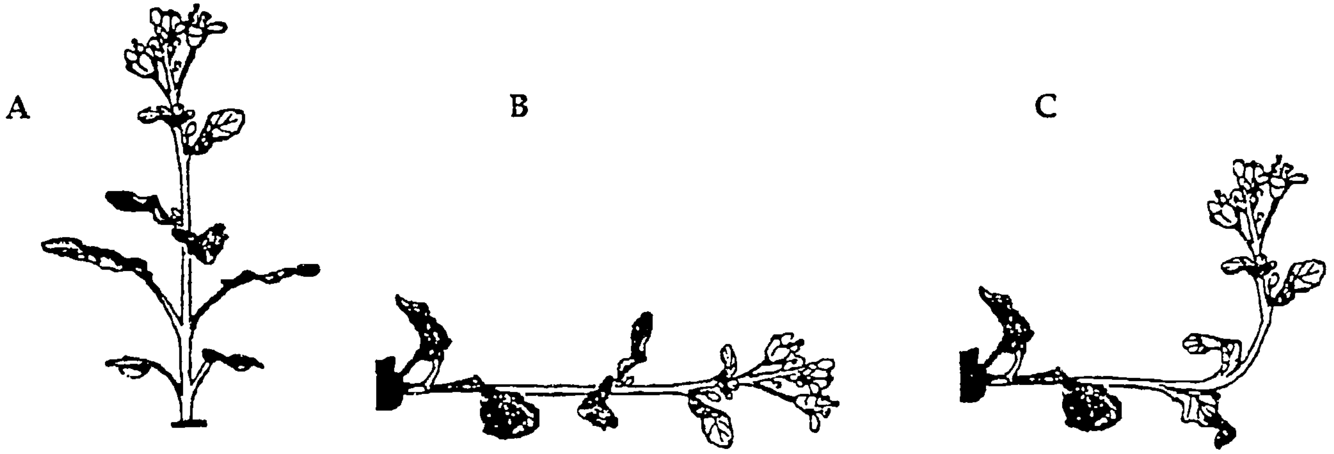


Figure 18. Gravitropism. The wild mustard plant shown in A was placed on its side (B). C, the same plant several hours later.

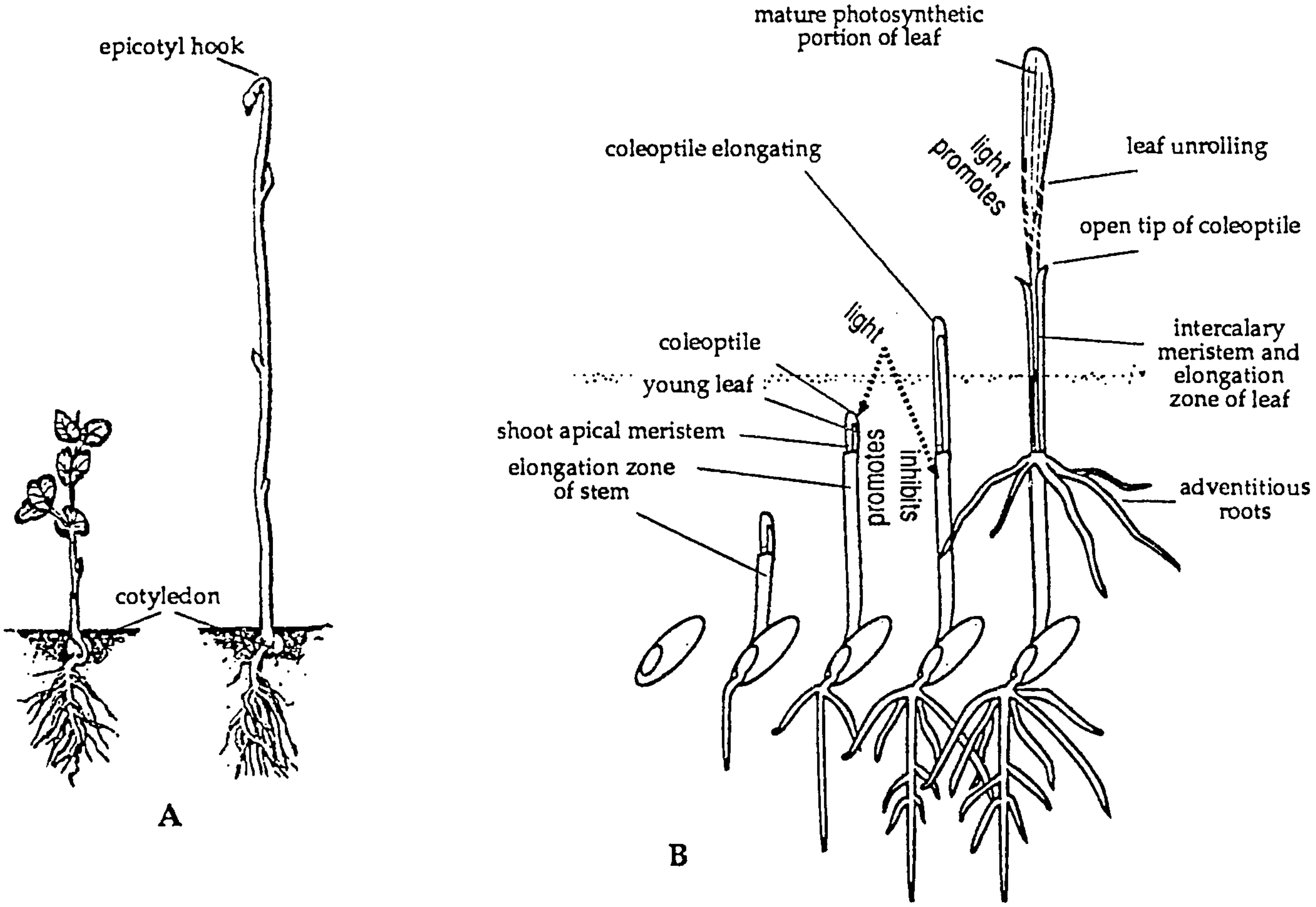


Figure 19. Effects of light on vegetative growth of emerging seedlings. A, the pea seedling on the left was grown for 9 days in the light, and the seedling on the right was grown for the same period in the dark (etiolated). Notice the extreme differences in leaf expansion, unbending of the epicotyl hook, and stem elongation. B, the effects of light on the emerging seedling of a monocot. Note that light inhibits elongation of the coleoptile, but promotes unfurling and development of the leaf. (For simplicity, only one leaf is shown, although several leaf primordia are actually developing around the apical meristem.)

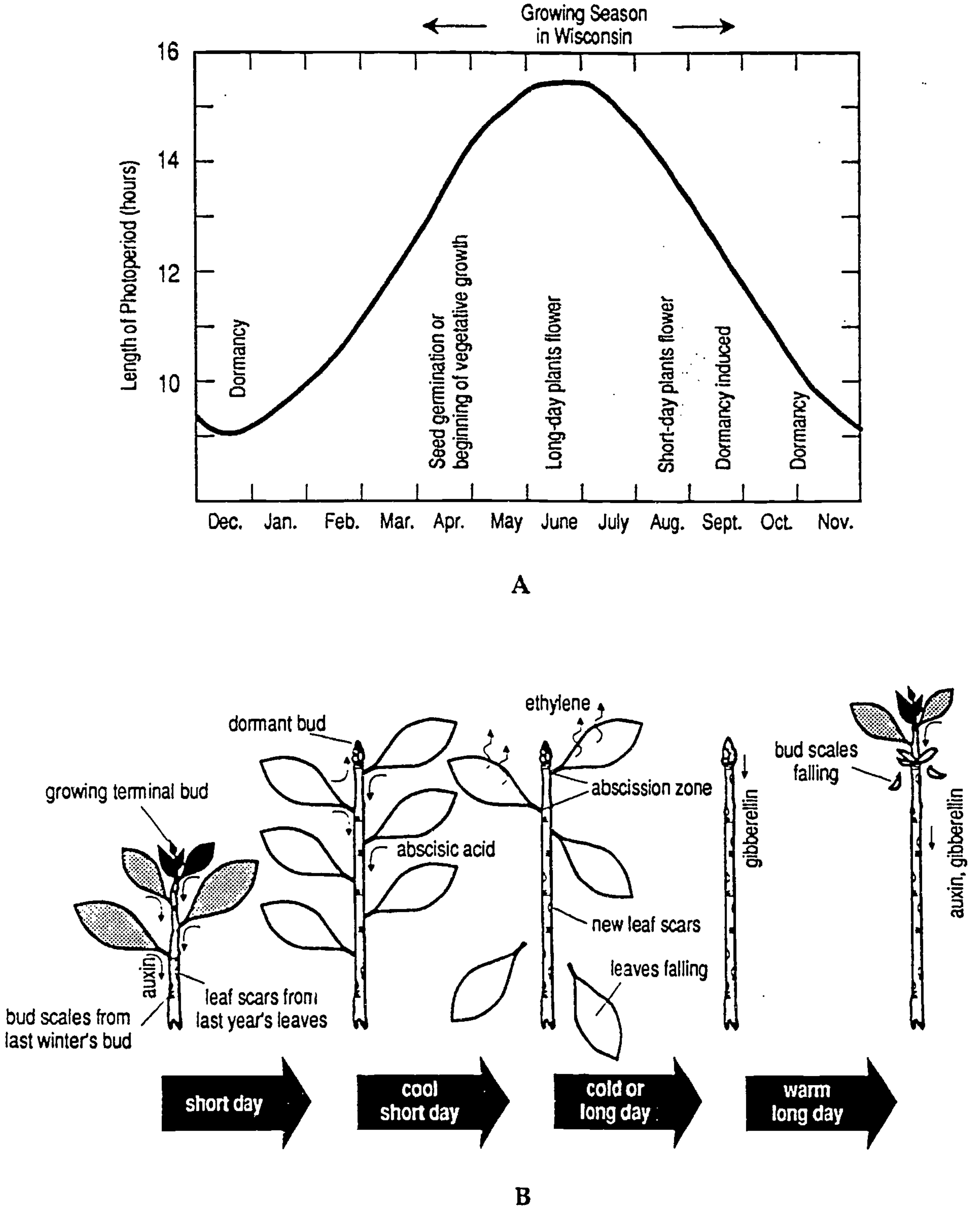


Figure 20. Effects of photoperiod on vegetative and reproductive growth. A, the effects of changing daylength on vegetative and reproductive development for a temperate-zone latitude with a growing season approximating that of Wisconsin. B, the typical seasonal cycle of growth and dormancy of a woody shoot in a climate such as ours, including a current interpretation of hormonal control of dormancy.

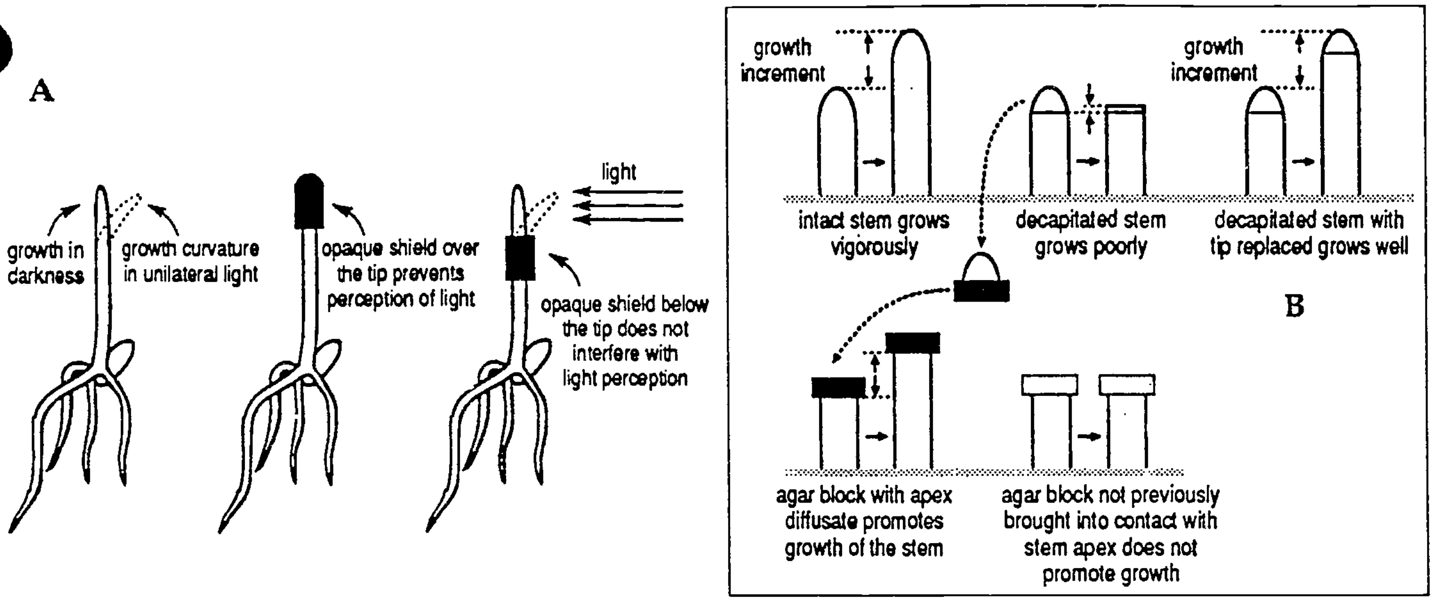


Figure 21. Experimental demonstration of the involvement of auxin in coleoptile growth and phototropism. A, the coleoptile tip is established as the region which is sensitive to the light, even though the response comes in the growing zone below the tip. B, the "influence" in the tip is shown to be diffusible into and transmissible by an agar block.

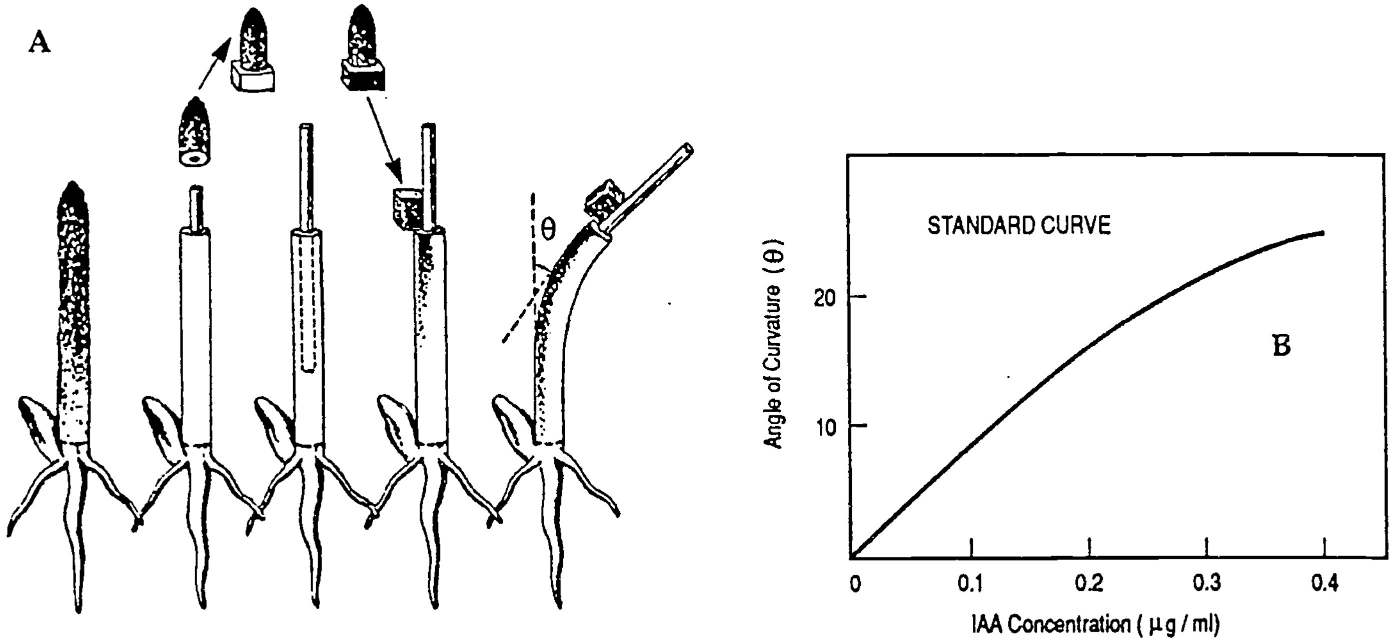
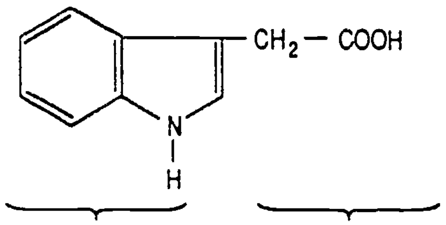
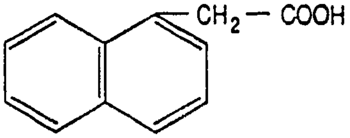


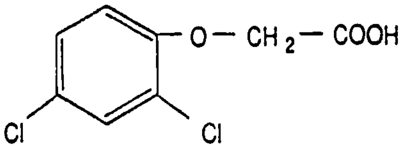
Figure 22. The oat coleoptile curvature test as a bioassay for auxin. A, the coleoptile bioassay for auxin depends on measurement of the angle of curvature θ to determine the amount of auxin in the agar block. B, by measuring θ for a variety of known IAA (auxin) concentrations, a standard curve can be plotted of θ vs. IAA concentration. The angle of curvature from an unknown sample contained in an agar block can then be determined and the IAA concentration read from the standard curve.



Indoleacteic acid (IAA)



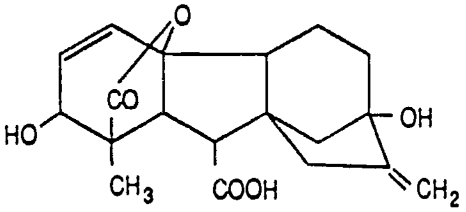
Naphthalenacetic acid (NAA)



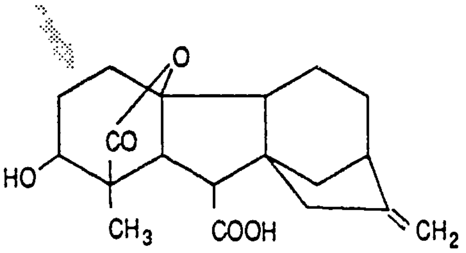
2,4-Dichlorophenoxyacetic acid (2,4-D)

A. Auxins

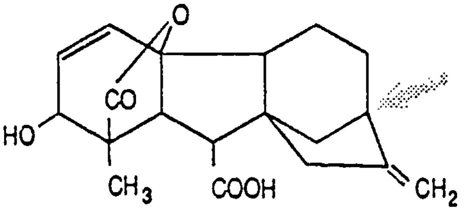
Indoleacetic acid (IAA) is the major naturally occurring auxin. **Naphthalenacetic acid** (NAA) is a synthetic auxin widely used in horticultural practice to induce roots on vegetative cuttings. **Dichlorophenoxyacetic acid** (2,4-D) and its trichloro analogue 2,4,5-T display auxin properties at low concentrations but have a herbicidal effect at high concentrations, presumably because they cannot be degraded by the plant or by soil microorganisms.



Gibberellic acid (GA_3)



GA_4

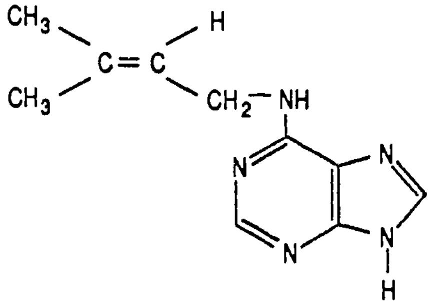


GA_7

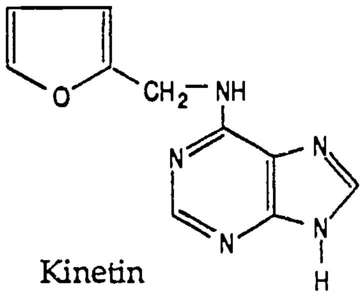
B. Gibberellins

Shown here are three of the more than 60 gibberellins that have been isolated from natural sources. **Gibberellic acid** (GA_3) is the most abundant in fungi. All known gibberellins have the same basic structure, but with minor differences such as those indicated for GA_4 and GA_7 by the arrows in the figure.

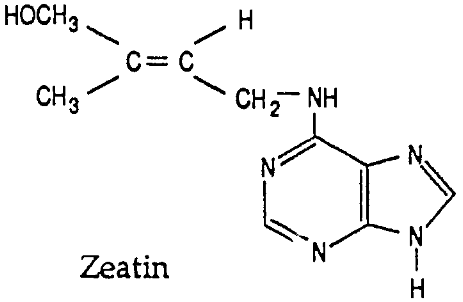
Figure 23. Structures of plant hormones.



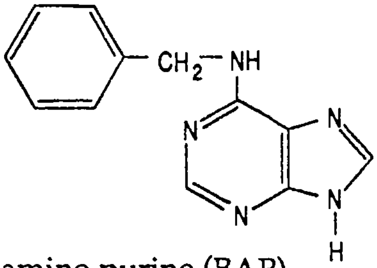
Isopentenyladenine (i^6Ade)



Kinetin



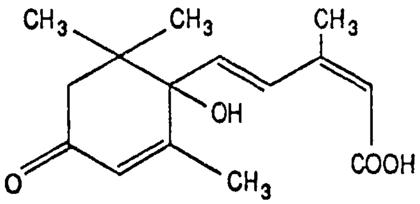
Zeatin



6-Benzylamino purine (BAP)

C. Cytokinins

Most cytokinins are derivatives of adenine. Shown on the left are the naturally occurring cytokinins **isopentenyladenine** (i^6Ade) and its hydroxylated analogue, **zeatin.** On the right are two synthetic cytokinins, **kinetin** and **6-benzylamino purine** (BAP). Natural cytokinins also occur *in vivo* as the riboside.



D. Abscisic Acid

This is the only known structure for this growth-inhibiting plant hormone, previously also known as abscisin and dormin.

Figure 23. Structures of plant hormones (continued).

Figure 24. Effect of gibberellin on stem elongation in the wild mustard, *Brassica rapa*. The plant on the right was treated with gibberellin, the one on the left was not.

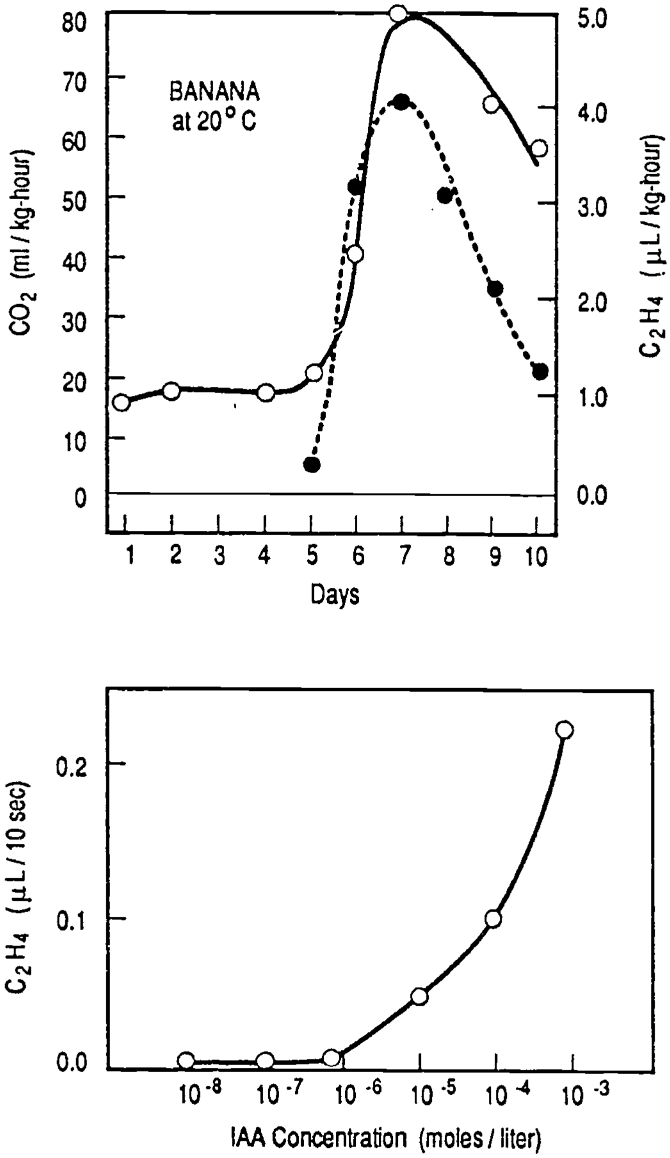


Figure 25. The role of ethylene in fruit ripening. **A**, the production of ethylene (C_2H_4) by ripening banana fruit. Note how closely ethylene generation parallels the burst of respiratory activity, marked by the high rate of CO_2 production. **B**, the production of ethylene gas by etiolated pea stems is greatly stimulated by auxin (IAA).

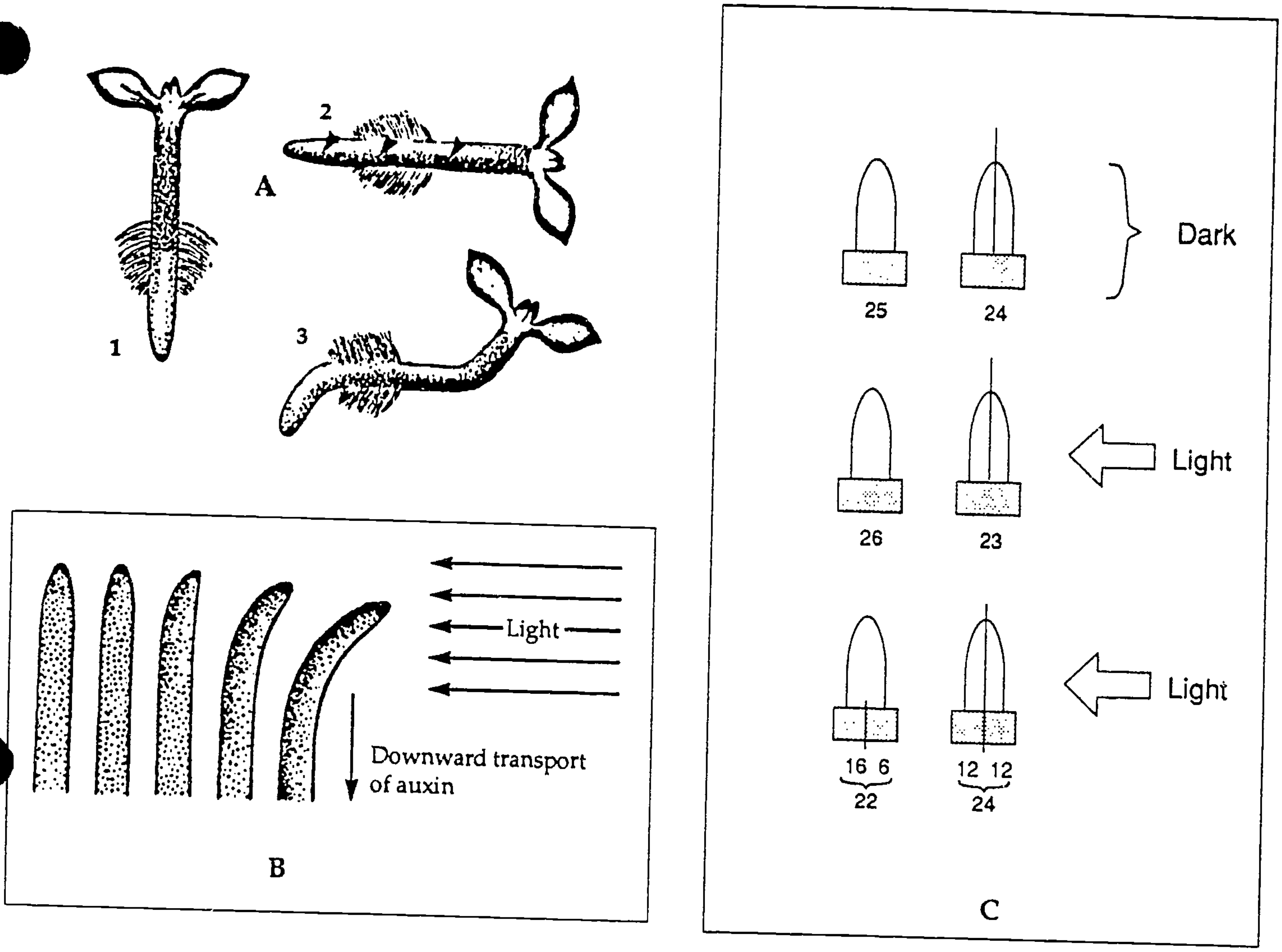


Figure 26. Role of auxin in gravitropism and phototropism. The response of root and shoot growth both to gravity (gravitropism) and to light (phototropism) is mediated by a differential lateral distribution of auxin, represented schematically by shading.

A. Gravitropism. When a seedling (1) is turned horizontally (2), auxin accumulation on the lower side promotes cell elongation in the shoot and inhibits elongation in root cells (3).

B. Phototropism. Illumination of a grass coleoptile with unidirectional light causes a lateral migration in auxin concentration across the coleoptile. Note that the difference in auxin concentration on the two sides arises at the light-sensitive tip and moves down the coleoptile as the auxin is transported away from the tip. As a result, curvature begins just below the tip and progresses toward the base. The events illustrated would occur in about 2 hours in a 2-centimeter oat coleoptile.

C. The results of an experiment designed to demonstrate light-dependent lateral migration of auxin in a coleoptile tip. The numbers represent the units of auxin (measured by the bioassay described in Figure 22) recovered in the agar block (or half-block) in each case.

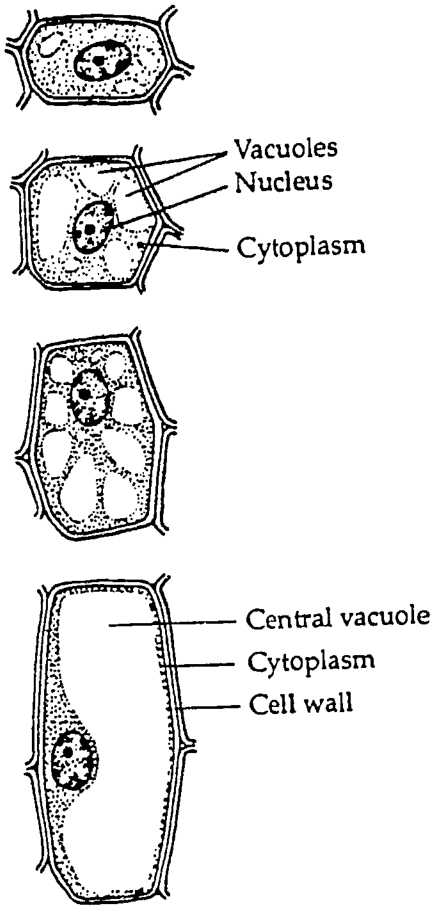


Figure 27. Cell expansion as a response to turgor pressure.

As more and more water moves into the cell vacuoles, the walls are stretched, but in only one dimension, because of the orientation of the cellulose microfibrils (see Figure 28). Almost no synthesis of new cytoplasm occurs during this kind of growth. The increased volume of the cell is taken up by the expanding vacuoles, which eventually fuse into a single large central vacuole. In the mature cell the thin band of peripheral cytoplasm may constitute less than 10 percent of the total volume of the cell.

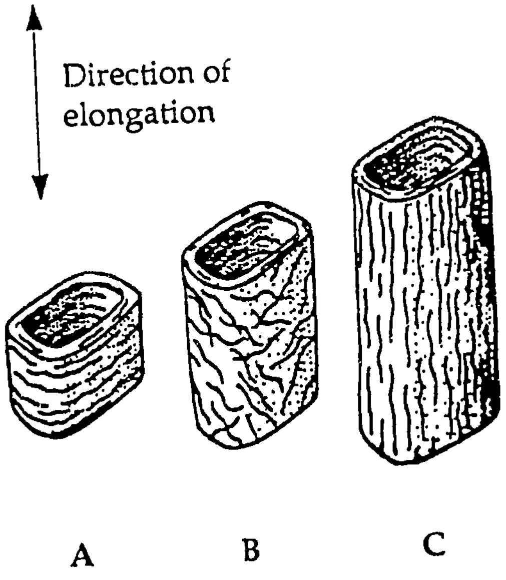


Figure 28. Change in the orientation of cellulose microfibrils of the cell wall as a plant cell elongates.

A. Before the start of elongation, the cellulose microfibrils are arranged horizontally.

B. As elongation begins and the wall is stretched, the microfibrils are displaced and tipped toward a more vertical alignment.

C. In the fully elongated cell, the microfibrils in the outer, older wall layers are oriented vertically. The recently deposited microfibrils in the inner new layers are horizontal.

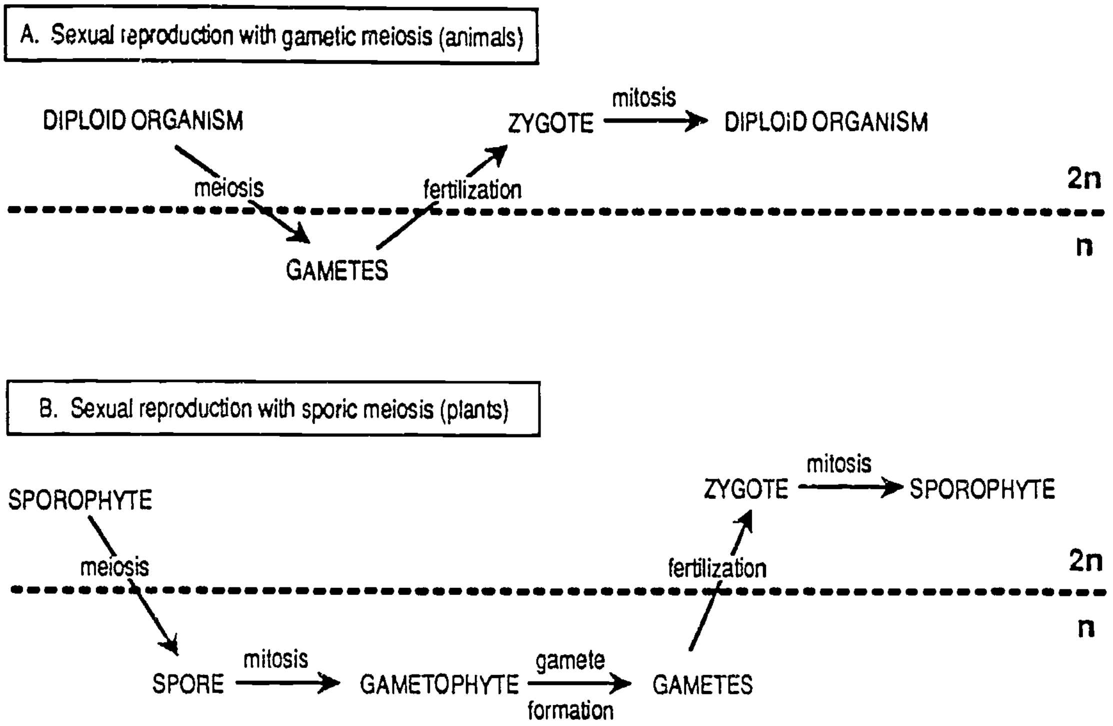


Figure 29. Alternation of diploid and haploid phases in the life cycle of plants and animals. In each case, the diploid (2n) phase is shown above the dashed line and the haploid (n) phase is shown below. A. In animals, meiosis results in the direct formation of gametes, which represent the only haploid phase of the life cycle. B. In plants, on the other hand, the immediate product of meiosis is always a haploid spore, from which arises a haploid organism (the gametophyte) and eventually the gametes necessary for restoration of the diploid state.

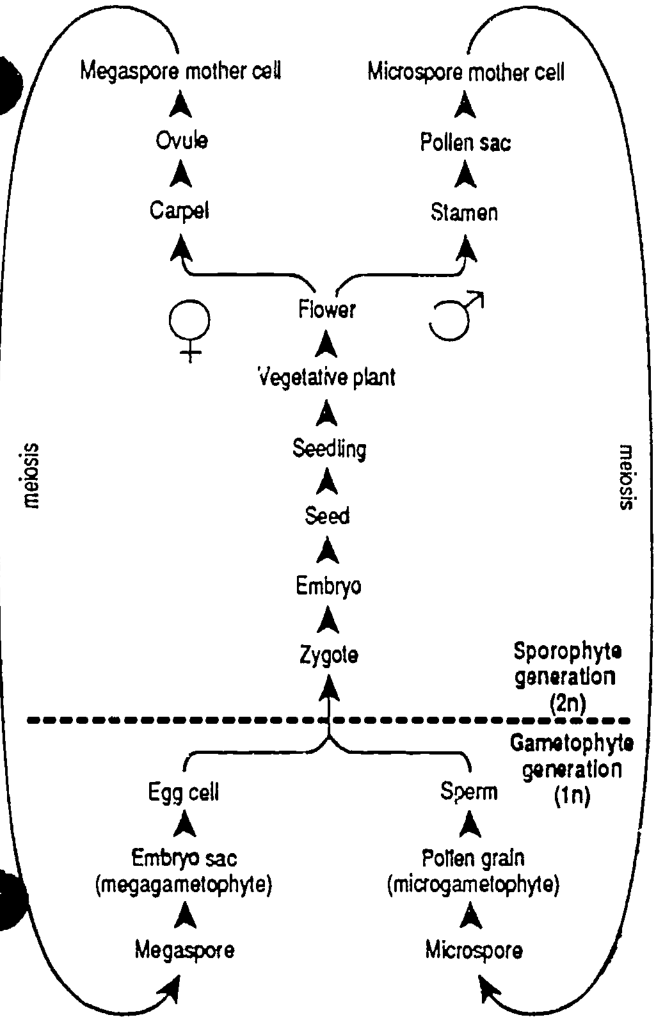


Figure 30. Alternation of generations in plants. The diploid (sporophyte) generation is shown above the dashed line and the haploid (gametophyte) generation is shown below. Floral structures and gametophyte generation are indicated on the right for the male, and on the left for the female.

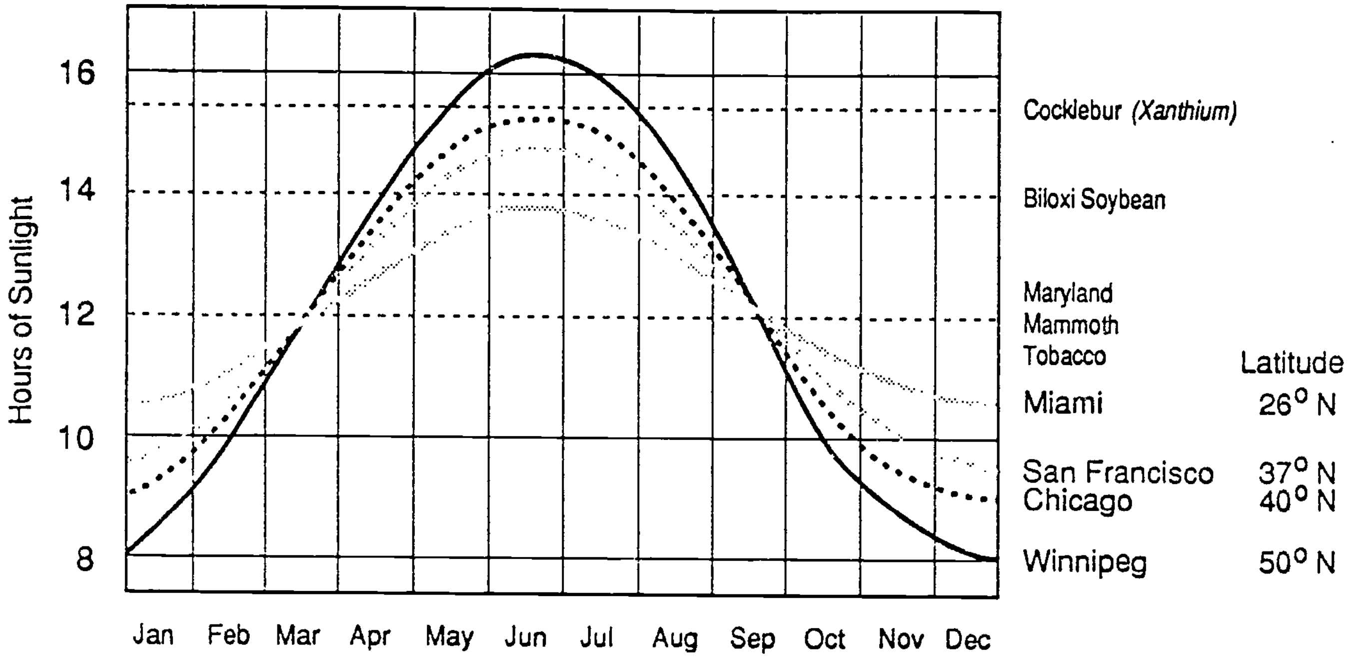
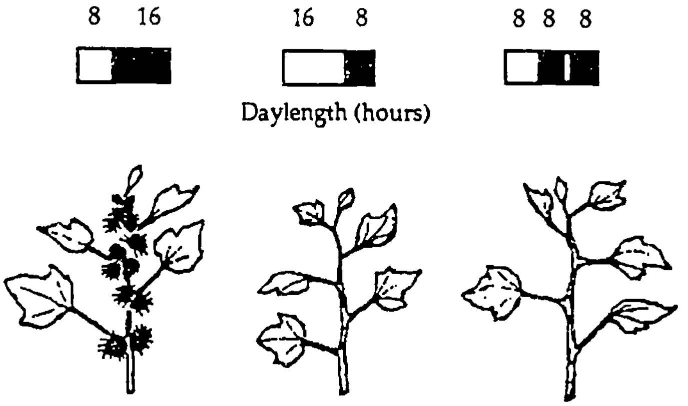


Figure 31. Seasonal changes in daylength at several different latitudes. The relative length of day and night determines when plants flower. The four curves depict the annual change of daylength in four North American cities at four different latitudes. (For comparison, Madison has a latitude of 42° N.) The horizontal dashed lines indicate the effective photoperiod of three different short-day plants.



A. Short-Day Plant
Xanthium strumarium

B. Long-Day Plant
Hyoscyamus niger

Figure 32. Flowering in short-day and long-day plants.

A. Short-day plants flower when the photoperiod is less than some critical value (15.6 hours for *Xanthium;* see Figure 31), but remain vegetative at longer daylengths. A flash of light in the middle of the dark period causes the plant to remain vegetative, despite the short day.

B. By contrast, long-day plants flower when the photoperiod exceeds some critical value (about 10 hours for *Hyoscyamus*), but remain vegetative at shorter daylengths. A flash of light in the middle of the dark period causes the plant to flower, even though the daylength remains short.

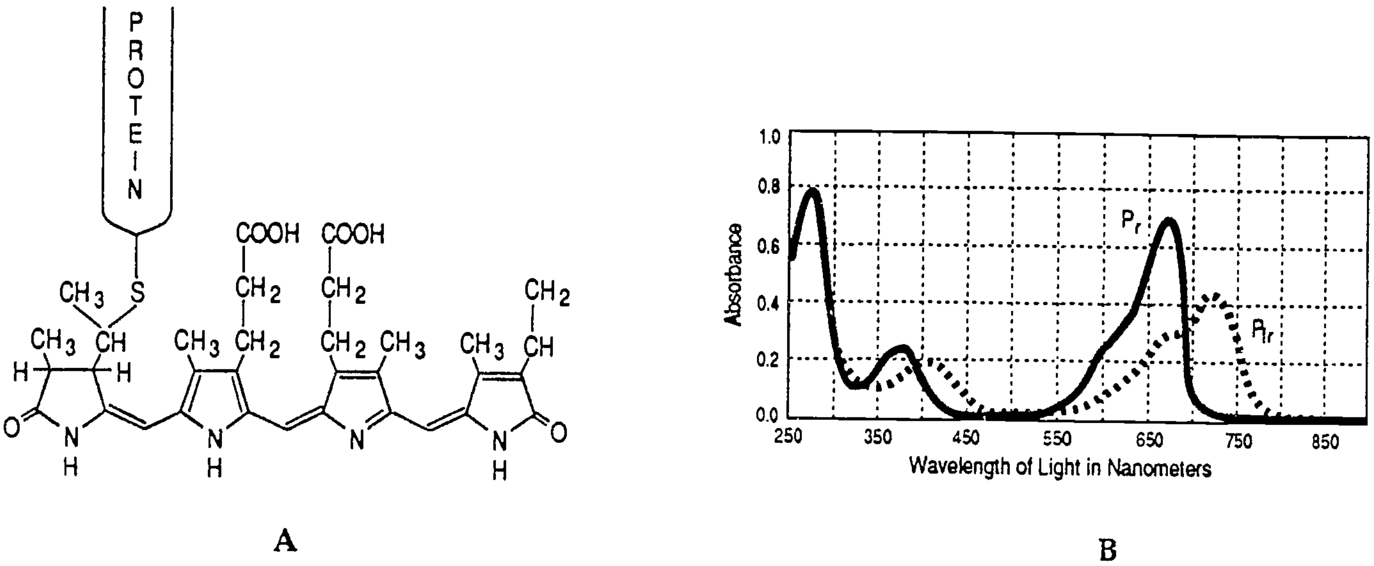


Figure 33. The chromophore and absorption spectra of phytochrome. A. The chromophore of phytochrome is a linear tetraphyrrole capable of undergoing a cis-trans isomerization in response to light. Note that the chromophore is attached to the protein through a sulfur atom. B. The absorption spectra of the P_r and P_{fr} forms of phytochrome.

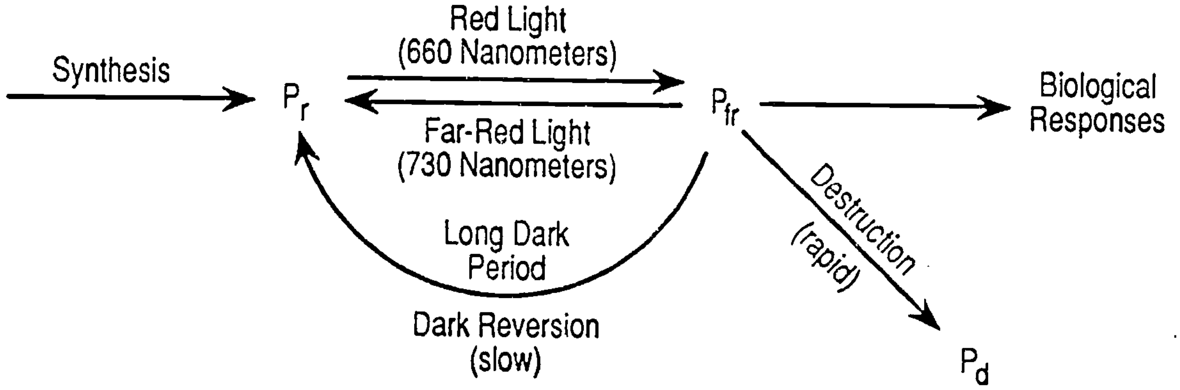
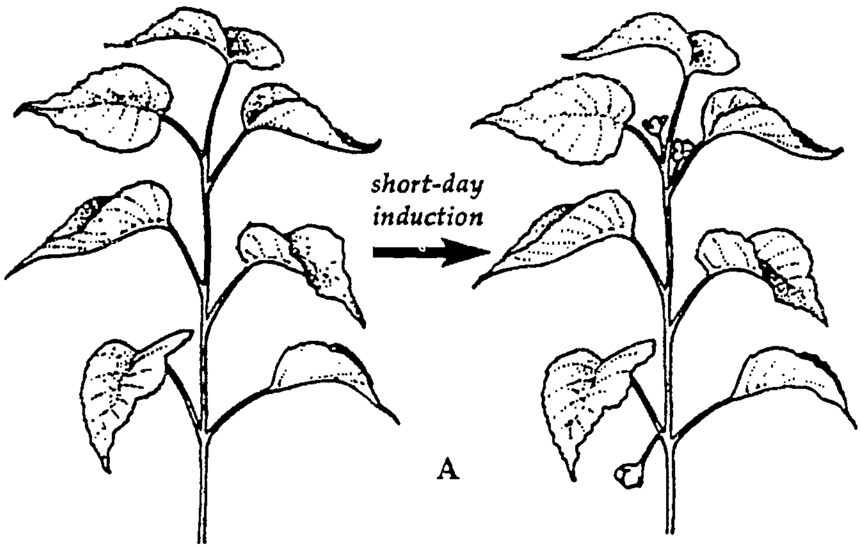
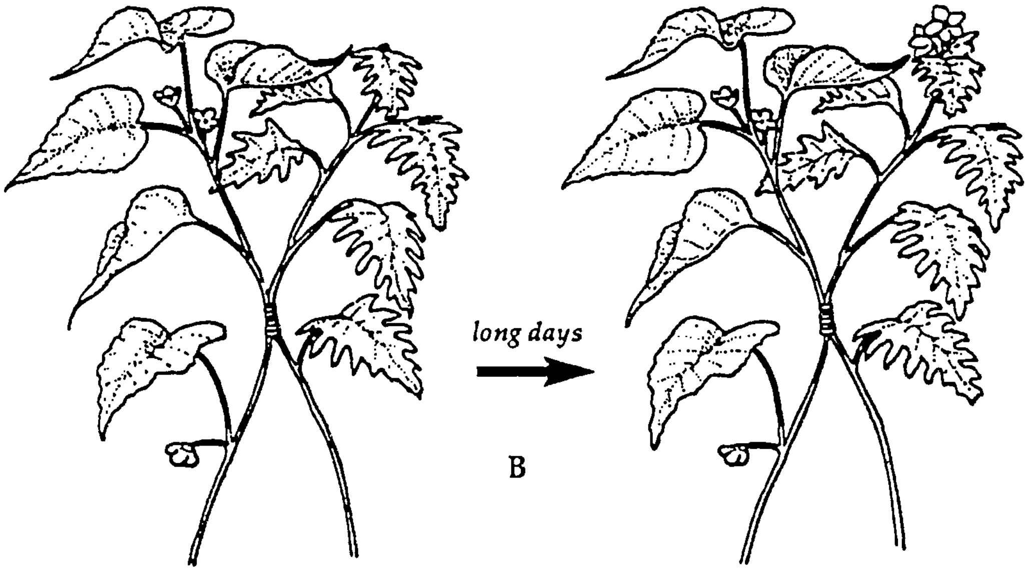


Figure 34. Synthesis, photoconversion, and degradation of phytochrome. Phytochrome is synthesized in the P_r form, which is converted into the P_{fr} form upon exposure to red light. P_{fr} is the active form that induces a variety of biological responses. P_{fr} can be photoconverted to P_r by exposure to far-red light. In darkness P_{fr} reverts slowly to P_r or is degraded rapidly to a series of degradation products (P_d).



Short-day plant previously exposed only to long days (non-flowering).

Plant flowers in response to short days



Flowering short-day plant (left) grafted to short-day plant exposed only to long days

Both plants flower while maintained on long days

Figure 35. Experimental evidence for the role of the leaves in the detection of daylength effects on flowering of a short-day plant. A. A short-day plant that has been previously exposed only to long days is induced to flower when shifted to a short-day regimen. B. When such an induced short-day plant (smooth-edged leaves) is then grafted to an uninduced (vegetative) short-day plant (jagged-edged leaves), the uninduced plant flowers. Evidently the flowering hormone "florigen" is transmitted from the induced flowering plant to the noninduced plant, causing flowering in the latter.

APPENDIX B

Plant Structure, Growth, and Development: Question Set for the Unit

W. M. Becker

Provided here is a set of questions intended to assist you in your study and understanding of this unit on plant growth and development. I offer them to you as an expression of my confidence in the old adage,

> "To hear is to forget,
> To see is to remember,
> To do is to understand."

I clearly don't expect you to look at all of these questions in detail, but I hope you will try a fair number, to convince yourself that you have indeed come to grips with the material in this unit. (That most of these questions come from old exams may be perceived in some quarters as an added incentive for taking a look at them!)

I very much hope that you will discern in these questions a concern on my part not just for the subject matter of the unit, but also for the way in which you think about the material. Because, quite frankly, I don't care what fraction of the current "facts" in this area you retain five years (or even five weeks) from now, but I care terribly much about whether you are developing some facility for thinking about questions in biology (the thinking is what's really important; the biology is just a convenient context). For the facts we teach today are almost certain to be superceded and eclipsed by the findings of tomorrow, but the ability to think about facts and findings is something I fervently hope might linger on. So please don't tell me that it's somehow "unfair" to ask you to think about things, whether in question sets or on exams. In the final analysis, it's the only "fair" and lasting thing we have to offer you.

-- wmb

I. Basic Plant Development

1. Floral Structure and Gametophyte Development. Figure A illustrates the formation of the male (micro) and female (mega) gametophytes for a simple perfect flower. With a bit of help from your textbook, you should be able to handle the following:

   (a) Label the following parts of the floral structure shown in the upper right-hand corner of the figure:

   anther
   carpel
   filament
   ovary
   petals
   receptacle
   sepals
   stamen
   stigma
   style

   (b) Describe the process of microgametophyte (pollen grain) development, following the arrows from the stamen at the top to the germinating pollen grain in the lower right-hand corner. Indicate the point at which meiosis occurs to give rise to the haploid microspore from which the microgametophyte develops. The following terms are appropriate to your discussion:

   anther
   filament
   stamen
   pollen sac
   microspore mother cell
   microspore
   pollen grain (microgametophyte)
   vegetative (tube) nucleus
   generative cell
   pollen tube
   sperm nuclei (2)

   (c) Describe the process of megagametophyte (embryo sac) development, following the arrows from the carpel at the top to the mature embryo sac at the end of the sequence. Indicate the point at which meiosis occurs to give rise to the haploid megaspore from which the megagametophyte develops. Terms appropriate to your discussion include:

   carpel
   ovule
   integuments
   micropyle
   megaspore mother cell
   degenerating megaspores (3)
   functional megaspore (1)
   mitotic divisions (3 in succession)
   linear tetrad of megaspores
   embryo sac (megagametophyte)
   antipodal cells (3)
   polar nuclei (2)
   1 egg cell + 2 synergids

2. Pollination and Fertilization. Figure B illustrates the processes of pollination and fertilization. Again, you may need some help from your textbook, but you should be able to describe the sequence of events beginning with the arrival of a pollen grain on a compatible stigma and terminating in so-called double fertilization (i.e., fertilization of the haploid egg nucleus with a haploid sperm nucleus to form the diploid zygote and fusion of the two haploid polar nuclei with the second haploid sperm nucleus to form the triploid endosperm nucleus). What is the eventual fate of the diploid zygote? What is the eventual fate of the triploid endosperm nucleus?

3. Embryogenesis and Germination. You should also be able to diagram the seed of a typical dicot (e.g., bean) and monocot (e.g., corn), distinguishing between testae, embryo, and endosperm (if still present), and identifying the several parts of the embryo.

II. Some Food for Thought

4. The Plant Body. The adult plant body is said to be a combination of mature and juvenile tissues.

    (a) What is meant by this statement?

    (b) Could the same be said of the mature animal body? Why or why not?

5. Whereas growth of stems and roots is characterized as "indeterminate", that of the leaf or fruit is "determinate".

    (a) What is meant by these terms?

    (b) Can you think of any tissues of the mature animal body which display an "indeterminate" growth mode?

6. Plant Hormones. What evidence can you cite to show that at least two of the plant hormones also occur in organisms other than higher plants?

7. Herbicides. Which is likely to be more deleterious to the environment if administered in equal doses, indoleacetic acid or 2,4-dichlorophenoxyacetic acid? Explain!

8. Chemical Nature of Plant Hormones. The plant hormones tend to be rather small organic molecules, in contrast to the animal hormones which are either proteins, oligopeptides or steriods. Can you think of any possible rationale for this?

III. The Plant Hormones: Experimental Analysis

9. Auxin and Tropisms. Figure C is a diagram from an experiment on geotropism published in 1961 by Gillespie and Briggs (Plant Physiol. 36: 364). In their Methods section the authors mention their use of the Went oat curvature test.

    (a) Explain briefly why the experiment was done (i.e., what it was designed to determine).

    (b) Describe in outline form how you think the experiment was done.

    (c) Describe the results which they probably obtained and summarize in a sentence or two what the experiment proved.

    (d) Suggest and describe an experiment which would extend or add to the findings of the above experiment.

10. Gibberellic Acid. Reproduced as Figure D is a graph which appeared originally in an article published in 1966 by van Overbeek (Science 152: 721). Using his data, answer parts (a) through (d) of question 9 for the van Overbeek experiment.

11. More Gibberellic Acid. The graph of Figure E was published in 1967 as part of the early work which linked gibberellin to the induction of amylase in the germinating barley seed. Study the graph and then answer the following questions.

(a) Formulate as succinctly as possible the specific question(s) which the investigators sought to answer by this experiment demonstrating the effect of gibberellin on the appearance of reducing sugars during the incubation of embryoless half-seeds of barley.

(b) Why is an assay for "reducing sugar" relevant to the germinating barley seed?

(c) Describe the experimental manipulations by which these results were most likely obtained. Start with ungerminated barley seeds and include each step necessary to arrive at the data shown in the figure.

(d) For each statement below, circle V if the statement is a valid conclusion from the data shown on the graph and circle N if the statement is not a valid conclusion from these data.

(1) Gibberellic acid at a concentration of 3 x 10^{-8} M causes the synthesis of the enzyme α-amylase in the cells of the aleurone layer.
V N

(2) The embryo of the barley seed secretes and releases gibberellic acid, which then causes the appearance of reducing sugar in the endosperm. V N

(3) The endosperm of an embryo-less half-seed of barley responds to 3 x 10^{-8} M gibberellic acid by degrading starch to glucose.
V N

(e) Inhibitor studies.

(1) On the graph, draw a dotted line to indicate the results you would expect if an embryo-less half-seed of barley is exposed to 3 x 10^{-8} M gibberellic acid but in the continuous presence (i.e., from imbibition through 48 hours) of actinomycin D at a concentration sufficient to suppress virtually all RNA synthesis. Explain why you drew the line as you did.

(2) On the graph, draw a solid line to indicate the results you would expect if an embryo-less half-seed of barley is exposed to 3 x 10^{-8} M gibberellic acid, but with the addition after 24 hours of cycloheximide at a concentration sufficient to suppress all further protein synthesis (i.e., cycloheximide not added until after 24 hours of germination, but continuously present thereafter). Explain why you drew the line as you did.

12. Effect of Hormones on Lettuce Seed Germination. Figure F is a graph showing the results of experiments designed to elucidate possible hormonal interactions in the control of seed germination. When added exogenously to the germination medium, gibberellic acid is known to overcome the requirement which some seeds (such as lettuce) normally have for red light. All of the effects shown below are for lettuce seed germinated in the dark, except for the line labeled "light control", which simply illustrates that in the

presence of red light, 100% of the seeds germinate regardless of the level of gibberellic acid. Using the data of this graph, answer parts (a) through (d) of question 9 for this experiment. GA = gibberellic acid; KIN = 0.05 mM kinetin; ABA = 0.04 mM abscisic acid.

13. Lettuce Seed Germination Again. Vidaver and Hsiao have recently reported (Plant Physiol. 53: 266, 1974) a series of experiments involving the effects of red light (RL) and gibberellic acid (GA) on germination of lettuce seeds. Figure G is reproduced from their paper. For this experiment, lettuce seeds were imbibed in distilled water in the dark and then held in the dark (still in distilled water) for up to 10 days. At 2-day intervals, seeds were subjected to one of four treatments: (1) ten-minute irradiation with RL; (2) transfer to a solution containing 0.5 mM GA; (3) both transferred to GA and irradiated for 10 minutes with RL; or (4) left undisturbed in distilled water in the dark. All such seeds were then scored for germination 48 hours later, and percentage germination was plotted as a function of the day on which the treatment was begun for a particular batch of seeds.

(a) Needed background information. From the six statements below, select the three which represent the most important background information required for the above experiment:

(1) Gibberellic acid stimulates the synthesis of α-amylase during germination of barley seeds.

(2) Phytochrome-mediated effects are dependent upon absorption of red light (660 nm).

(3) Lettuce seeds take up about 60% of their weight in water during imbibition.

(4) Lettuce seeds are small and must germinate near the soil surface.

(5) Lettuce seeds normally do not germinate in the dark.

(6) The light requirement of some dormant seeds can be overcome by exposure to gibberellic acid.

(b) Rationale. State as concisely as possible the specific question(s) which these investigators sought to answer by this experiment.

(c) Results. Briefly summarize the main results (results, not conclusions!) of the experiment.

(d) Interpretation. Each of the statements below represents a potential interpretation of the results of this experiment. For each statement, decide whether you agree or disagree that it is a logical interpretation of the data and indicate why.

(1) The rapid decrease in effectiveness of GA (line 2) could be due to the degradation or metabolism of the GA by the imbibed seeds.

(2) Red light probably stimulates germination by activating gibberellic acid synthesis.

(3) A possible explanation for the difference between lines 1 and 3 is that extended dark storage of imbibed seeds results in a reduction of endogenous gibberellins to levels below which the phytochrome-mediated process is able to support germination.

(e) Predicting results. Indicate with a dotted line on the graph the results you would expect if treatment (3) were repeated, but with the RL followed immediately by a 10-min irradiation with far-red (730 nm) light. Explain why you drew your line as you did.

V. Photobiology

14. Photobiology. Since light is one of the major environmental signals to which plants respond, photobiology is an inescapable component of plant development.

    (a) Cite at least three different ways in which plants use pigments (without using a given pigment more than once!).

    (b) Why does a plant physiologist use a green safelight when working in the dark with etiolated seedlings, but switch to a red safelight for experiments on phototropism?

    (c) Would a plant from earth be at any disadvantage if it were grown on a planet with an atmosphere that filtered out all wavelengths of light below 500 nm? Explain.

15. Photoperiodism. Indicated on the graph of Figure H are the seasonal changes in daylength in four North American cities at different latitudes. Ragweed is a short-day plant with a critical photoperiod of about 14½ hours.

    (a) If you were allergic to ragweed pollen, would you be safer in Winnepeg or Miami? Why?

    (b) Approximately when would you expect floral induction to occur in ragweed growing in the Madison area?

    (c) Suppose that for experimental purposes you wish to delay for a month the flowering of ragweed grown in a greenhouse here on campus. Describe two methods by which this might be accomplished and explain the rationale behind each.

16. More Photoperiodism. If you were raising spinach to sell leaf spinach to a supermarket chain, a farm near Miami, Florida, might be an ideal location; but if you intended instead to sell spinach seed to a seed company, you would be better off with a farm near Chicago, Illinois. Explain, using Figure H if necessary. (And keep markets, economics, etc. out of it; this is a question on biology!)

17. Still More Photoperiodism. Suppose you planted test plots of Species A and B in a greenhouse in the Chicago area and that artificial light was not used to extend daylength. Use the data below to determine to which group of plants (long-day, short-day, day-neutral) each species belongs, and estimate its approximate critical photoperiod, if it has one. Refer to Figure H, if necessary.

Experiment 1: Species A and B planted on June 1. Results: both species flowered toward the end of August.

Experiment 2: Species A and B planted on Nov. 1. Results: Species A flowered toward the end of January; species B had not flowered when the experiment was terminated on March 1.

Experiment 3: As for Experiment 2, except that each night was interrupted by a 10-minute period of illumination during the last two weeks of December. Results: Species A flowered toward the end of January regardless of when during the night the 10-minute illumination came; species B flowered also, but only if the 10-minute illumination came between 8 p.m. and 4 a.m.

18. Floral Induction. A Russian plant physiologist, Chailakhyan, has shown that a short-day plant like Chrysanthemum will not flower if the shoot apex is exposed to a short-day regime while the leaves are maintained on a long-day regime. Similarly, the plant will not flower if all the leaves are stripped from the plant prior to transfer from a long-day to a short-day regime.

    (a) How would you interpret these findings?

    (b) What further experiments can you suggest to test your interpretation?

    (c) What evidence would you consider necessary to prove your interpretation?

VI. Practical Applications

19. Why do horticulturists interested in vegetative propagation of plants frequently treat shoot or leaf cuttings with the synthetic auxin indolebutyric acid?

20. Why does a package of spinach seed read as follows on the back: "Plant seeds as early in spring as the ground can be worked"?

21. What is vernalization, and why is it essential to agriculture in Siberia?

22. Why doesn't spinach grow endogenously in the tropics?

23. Why do peach trees not grow in southern California?

24. Why can farmers who grow soybeans not spread out the work of harvest in fall by planting a portion of their crop every week or two during spring?

25. What is stratification, and how does it represent a practical application of a basic consideration in plant development?

26. Why are apples sold in bushel baskets with slats rather than in solid-walled containers?

27. Why don't tomato seeds germinate while still within the tomato fruit?

28. Why do morning glories planted around the base of a street light not flower, while those on the dark side of your garage do flower?

29. Your neighbor with the green thumb explains to you that by pinching off the tops of certain species of plants, he gets bushier plants with a lot more flowers. How would you explain what's happening?

VII. Multiple Choice

For each of the following, choose the single best answer.

30. The only one of the following which is not involved in the breaking of seed dormancy is

(a) leaching out of inhibitors
(b) exposure to warm temperature
(c) red light
(d) prior exposure to low temperature
(e) abrasion of the seed coat

31. Geotropism

(a) involves differential cell enlargement
(b) is a response to blue light (400-500 nm)
(c) involves differential auxin degradation
(d) is caused by a change in cytokinin concentration
(e) none of the above

32. The effect of auxin on cell wall expansion

(a) requires light in the blue region of the spectrum
(b) is to increase the elasticity (reversible extension) of the wall
(c) involves a temporary "softening" of the wall structure
(d) is mediated by microtubules embedded in the cell wall matrix
(e) depends upon hormone-induced synthesis of α-amylase

VIII. Relationships

Each set of words in this section has been chosen to establish a specific relationship between the 2 words on the left which is intended to be matched by a parellel kind of relationship between the two words on the right. From the choices provided in each case, select the word which best completes the pair on the right to reflect the desired parallelism in relationship. (If that sounds complicated, look at the example!)

Ex: Darwin : Auxin / Kurosawa : c

(a) Cytokinin (b) Foolish Seedling Disease (c) Gibberellin (d) Photoperiodism

33. Animal : Gamete / Plant : _____

(a) Spore (b) Seed (c) Megaspore Mother Cell (d) Sporophyte (e) Carpels & Stamens

34. Went : Oat Coleoptile / Skoog : _____

(a) Steward (b) Phototropism (c) Cytokinin (d) Coconut Endosperm (e) Tobacco Pith Tissue

35. IAA : 2,4-D / Zeatin : _____

(a) Bioassay (b) Kinetin (c) Adenine (d) Ethylene (e) Herbicide

36. Abscisin : Abscisic Acid / Dormin : _____

(a) Dormancy (b) Cotton Boll (c) Abscisic Acid (d) Wareing (e) Bud

37. Stratification : Germination / Vernalization : _____

(a) Induction of Dormancy (b) Winter Rye (c) Seedling Emergence (d) Flowering (e) Pollination

38. Chemical Inhibitor : Rainfall / Impermeable Seed Coat : _____

(a) Fungal Symbiont (b) Prairie Fire (c) Dessication (d) Integument (e) Desert Plant

39. Coleoptile Tip : Auxin / Leaf : _____

(a) Phytochrome (b) Photosynthesis (c) Cytokinin (d) Florigen

40. Protein : Protease / Starch : _____

(a) Amylase (b) Glycolysis (c) Cereal Grain (d) Maltose (e) Endosperm

41. Florigen : Apical Bud / Gibberellin : _____

(a) Lateral Bud (b) Barley Embryo (c) *Gibberella fujikuroi* (d) Tobacco Pith (e) Aleurone Layer

IX. True, False, or Eeny Meeny

Choose the appropriate letter (T, F, or E) for each question, using E for statements which could be either true or false, but for which inadequate information is provided to decide. In each case, comment briefly on the reasoning behind your answer. (An insightful defense can sometimes earn partial credit for a "wrong" answer.)

42. In all of nature, photoperiodic regulation os sexual reproduction appears to be unique to the flowering plants.

43. Darwin would not have noted a phototropic response if he had illuminated his canary grass coleoptiles unilaterally with red light.

44. Accumulation of auxin on the lower side of a horizontally-oriented plant axis stimulate cell elongation differentially on that side and causes bending in an upward direction.

45. A megaspore mother cell is a haploic (n) cell located in the ovule.

46. Soaking the seeds in strong mineral acid prior to germination is an accepted commercial practice for some kinds of seeds which have hard, otherwise impermeable seed coats.

47. A short-day plant will flower if a 16-hour period of darkness is interrupted by 5-10 minutes of white light given four hours after the onset of the dark period.

48. The normal requirement of some dormant seeds for exposure to red light can be circumvented by application of exogenous gibberellic acid because the effect of the red light is to stimulate endogenous synthesis of this hormone.

49. In many dicot species, seedling emergence is accomplished by hypocotyl elongation, resulting in the cotyledons remaining behind in the soil.

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50. Complete the following set in the same way as above, but using a phrase of your own choosing.

Animal : group of cells clustered around a G-I tract and dedicated to the task of keeping that gut full / Plant :

X. Experimental Analysis

50. The Acid Growth Hypothesis. Shown in Figure I are the results of an experiment in which the rate of coleoptile elongation was measured during continuous treatment (a) with auxin (solid line); (b) with the same level of auxin but in the presence of cycloheximide, a known inhibitor of eukaryotic protein synthesis (dashed line); and (c) with dilute mineral acid (dotted line). For each of the statements below, decide into which of the following categories the statement falls and indicate your choice by circling the appropriate letter to the left of the statement.

B: background information -- information of which the investigators were almost certainly aware at the time the experiment was planned

R: result -- an experimental finding readily apparent from the data shown in Fig. I

H: hypothesis -- a reasonable experimental hypothesis that can be postulated based on the data of Fig. I

F: false conclusion -- a conclusion that is not supported by the data of Fig. I

B R H F 0. Auxin causes coleoptile elongation by a mechanism that involves acidification of the cell wall.

B R H F 1. Dilute acid mimics the initial, but not the longer-term, effect of auxin on the coleoptile cells.

B R H F 2. Regardless of treatment, coleoptile elongation is essentially complete within 15-20 minutes; no significant elongation occurs thereafter.

B R H F 3. Coleoptile cells are permeable to cycloheximide.

B R H F 4. Auxin stimulates elongation by two different mechanisms, with an initial acid-induced passive phase followed by a longer-term response that requires protein synthesis.

B R H F 5. The initial phase of auxin-induced elongation can occur in the absence of protein synthesis.

B R H F 6. Auxin-induced acidification of the cell wall causes inhibition of protein synthesis *in vivo*.

B R H F 7. Auxin-induced acidification of the cell wall does not require protein synthesis.

51. The Frilly-Leafed Fandango. Two ambitious UW students recently returned from the Amazon River Basin with specimens of the frilly-leafed fandango (Locus hokus), a previously undescribed tropical plant species found growing in the dense underbrush of the jungle. Each of the following observations was made either on location in Brazil or in the laboratory upon their return. In each case, a) formulate a reasonable hypothesis to explain their observation, and, b) suggest a specific experiment that could be conducted to test the hypothesis.

(a) The axillary buds (located at the base of each leaf, where the leaf joins the stem) of frilly-leafed fandango plants do not usually develop, but if the top of the plant is cut off, the uppermost axillary bud will grow out and form the new growing tip of the plant.

(b) Frilly-leafed fandango plants were shown to grow toward a dim light (50-watt incandescant bulb), but away from a bright light (500-watt incandescant bulb).

(c) Fandango plants carrying the "stunted" (st) mutation usually have short, bushy stems, but will grow to normal height if the mold Fungus amungus is growing on its leaves, as is often the case in the jungle.

(d) The small subunit of ribulose-1,5-bisphosphate carboxylase (RuBPCase) was isolated from fandango leaves and used to prepare antibody. When poly(A)-rich RNA was isolated from fandango leaves and used to program an in vitro protein-synthesizing system, the antibody was found to precipitate a single polypeptide, with a molecular weight of 21,000 daltons. However, when leaf extracts were treated with the antibody, a polypeptide with a molecular weight of 16,000 daltons was precipated along with a proportionately smaller amount of a 21,000 dalton polypeptide.

(e) The mRNA for RuBPCase was isolated and cDNA (complementary DNA) molecule was synthesized by reverse transcription and cloned in a suitable vector. Radioactive cDNA was then used as a probe to test for hybridizable RNA molecules in preparations of poly(A)-rich RNA from both light-grown seedlings (L-RNA) and dark-grown seedlings (D-RNA) after electrophoresis of the RNA in polyacrylamide gels. Autoradiography revealed that labeled cDNA hybridized to a specific RNA band in the case of L-RNA, but not with D-RNA. However, when the dark-grown seedlings were exposed to two minutes of white light 60 minutes before the RNA was extracted, a band "lights up" on the autoradiogram at the same place (i.e., the same molecular weight) as for the L-RNA.

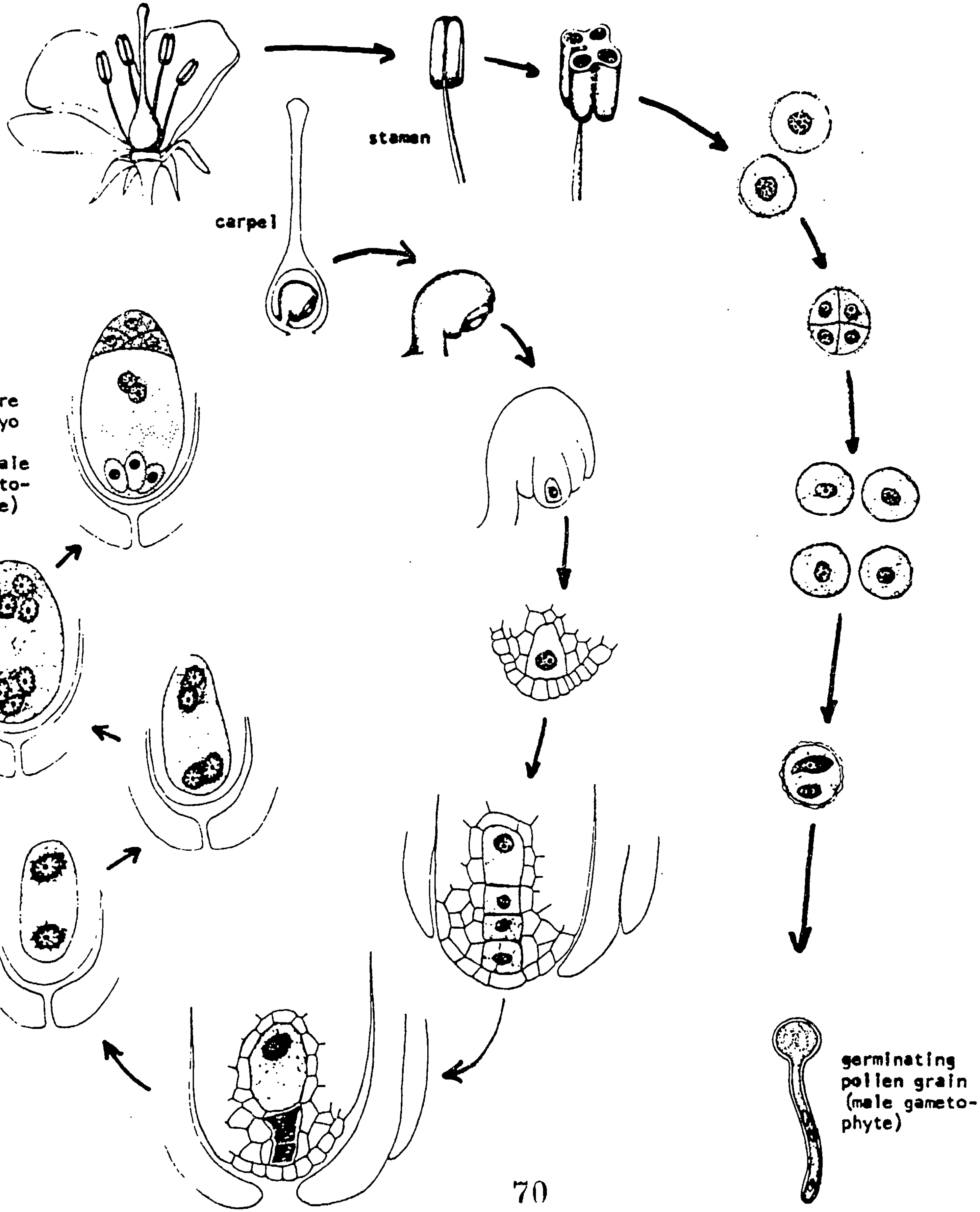
stamen
carpel
mature embryo sac (female gametophyte)
germinating pollen grain (male gametophyte)

Figure A

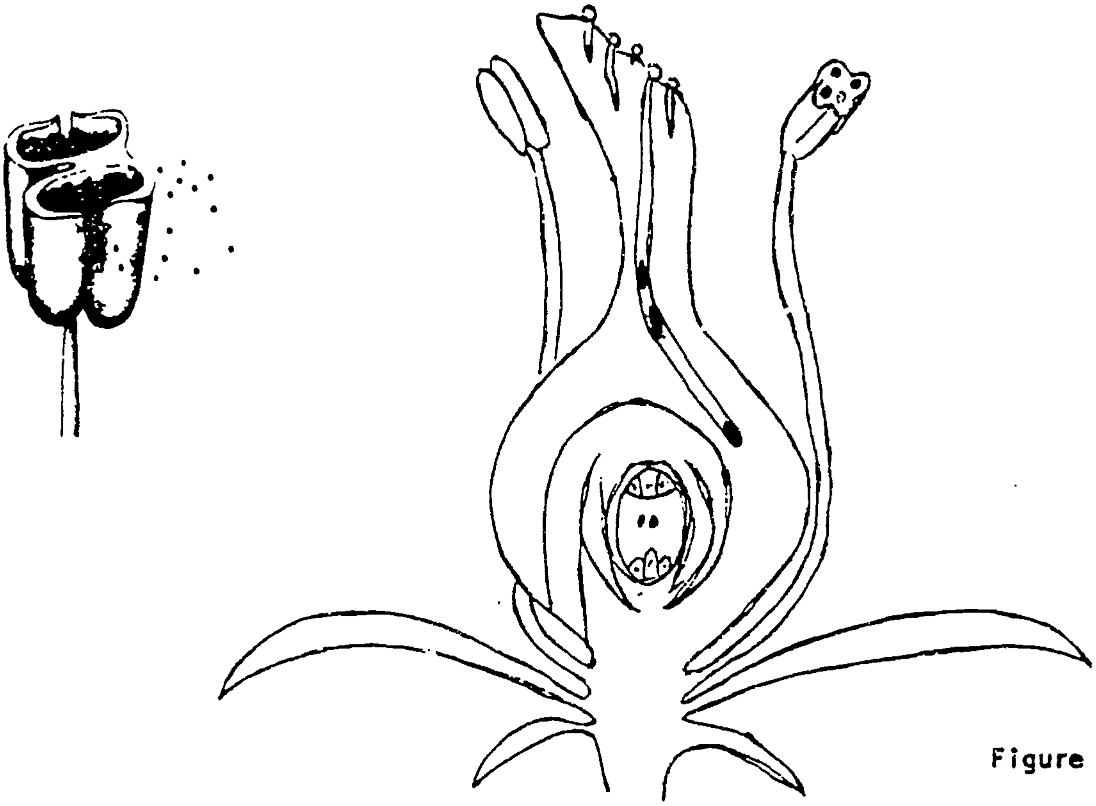

Figure B

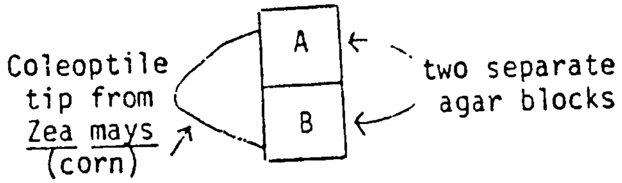

Figure C

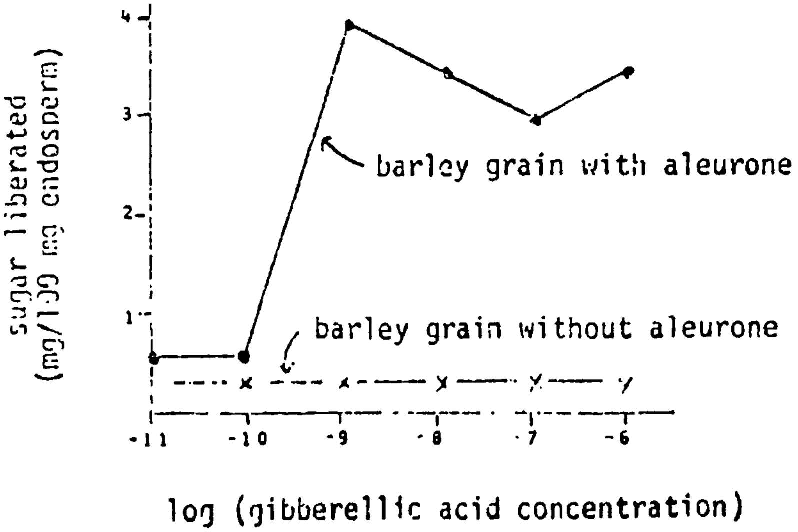

Figure D

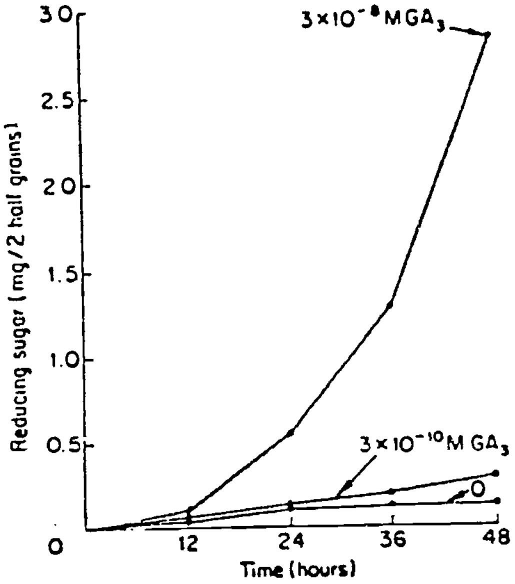

Figure E

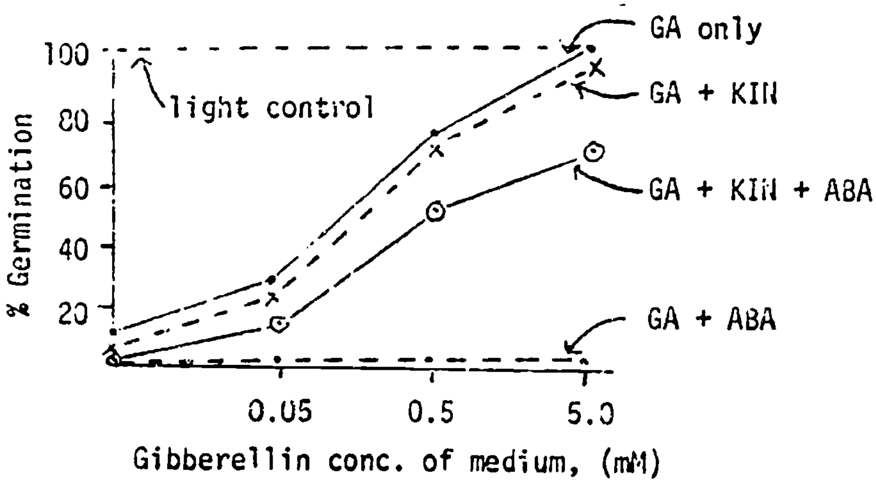

Figure F

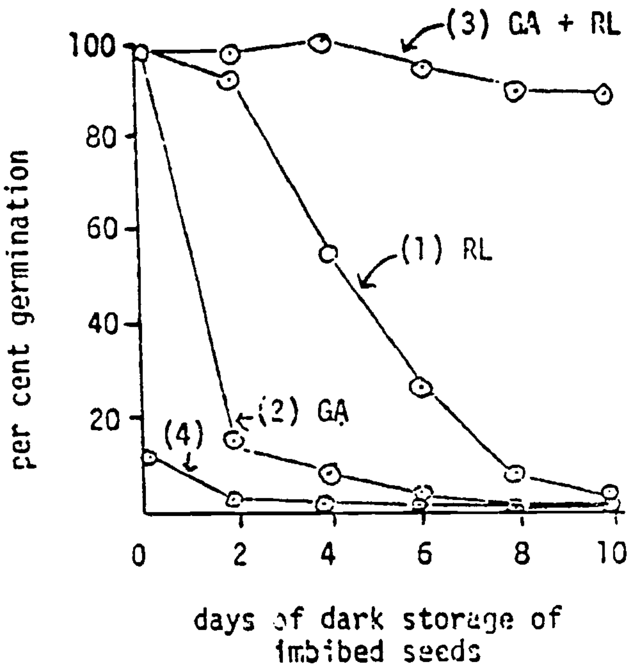

Figure G

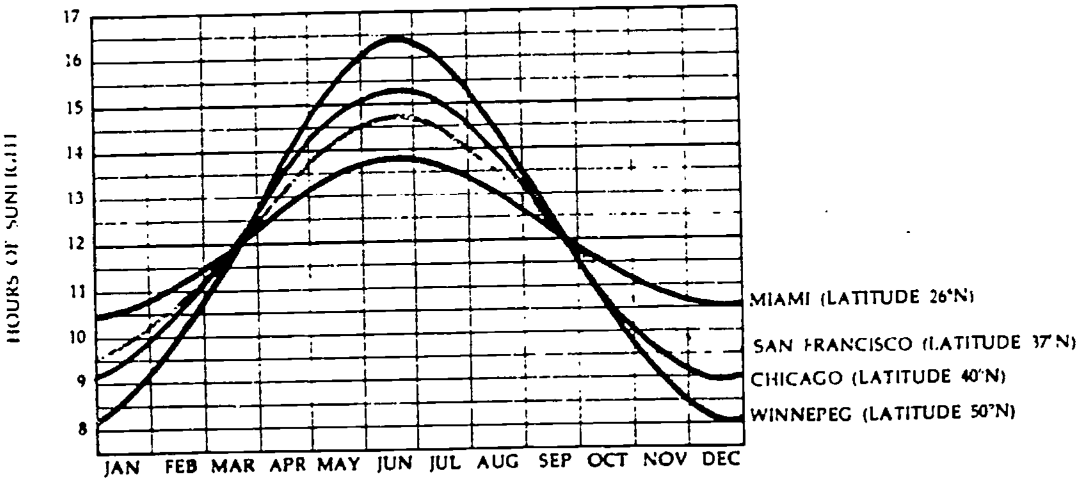

Figure H

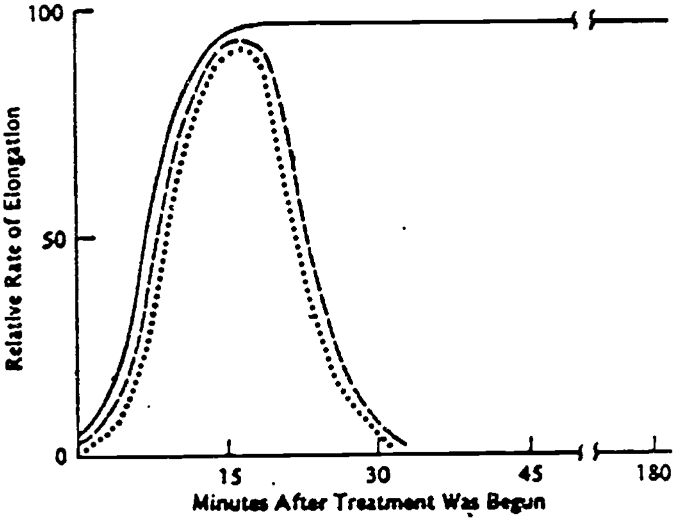
100
50
0
Relative Rate of Elongation
15
30
45
180
Minutes After Treatment Was Begun

Figure I

APPENDIX C

What it Means to be a Plant:
Some Musings on the Comparative Biology of Plants and Animals

W. M. Becker

As we come to a discussion of several aspects of plant organismal biology, a good way to begin might be to look briefly at plants and animals in a comparative sense, since in so doing we may come to appreciate some of the fundamental differences between the two kingdoms, especially in the ways they have solved a variety of problems common to all organisms. In the process, we may well also discover why some topics in organismal biology are common to plants and animals, while other topics are emphasized only for one or the other of the two kingdoms.

Unity and Diversity. In all biology, there is at every level a complementary interplay of unity and diversity -- everywhere we look in the biological world, we see that things are alike in some ways, and different in others.

Applied to plants and animals, it is easy to appreciate the unity, since we can readily identify a number of properties that are common to all multicellular organisms. For example, all face common problems of survival, including the acquisition and utilization of food, maintenance of water balance, provision for reproduction, and a need for integration of body function. In terms of development, both plants and animals are made up of parts which undergo progressive diversification and specialization as the organism grows and develops from the fertilized egg. In all cases, the developmental process involves orderly, predictable changes in time and space to give rise to the final adult organism. On a physiological basis, plants and animals face the common challenge of maintaining and integrating all the various functions they carry out and of responding appropriately to changes in their environment.

Equally important, however, is the diversity aspect, for plants and animals are fundamentally really quite different. The single most obvious difference lies of course in the basic body plan.

Plants and animals have, in fact, radically different structural strategies that can probably best be understood as the logical consequence of two quite different solutions to a common nutritional problem. In terms of your study of biology, the most profound implications of these basic differences between the two kingdoms are felt right here at the organismal level, where the emphasis is on structure, function, and development of individual organism, such that the contrasts between plants and animals become most acute.

The Nutritional Distinction. Thus, it is the diversity component of biological unity and diversity that takes on special significance for us at the organismal level. To develop this theme, I'd like to reach back to the unit on energy metabolism in our preceding course on cellular biology, and to assert that the all-important distinction between plants and animals is that of nutritional mode, and that all other differences can be seen as consequences of this basic nutritional difference. First, consider plants. Plants are autotrophs ("self-feeders"). They can manufacture the entire spectrum of needed organic compounds from CO_2, water, inorganic salts, and solar energy (sunlight). Animals, on the other hand, are heterotrophs ("other feeders"). They require their carbon, nitrogen, and energy in form of prefabricated organic food molecules and are in a sense "parasitic" upon autotrophs for their continued existence.

Why all this emphasis upon nutritional distinction? Because, as I see it, the "rules" turn out to be really quite different for autotrophs and heterotrophs, and these differences in turn have profound effects upon the structure, function, and development of organisms, and hence on the kinds of topics that are relevant to consider when looking at the organismal biology of plants and animals, respectively.

First, let's consider the heterotrophs. Heterotrophs are utterly dependent upon supplies of prefabricated food, such that the search for food, the ingestion, absorption, and assimilation of food, and the eventual excretion of unused materials loom large in the heterotrophic repertoire of physiological activities. With a bit of license, one can perhaps even view an animal as nothing more than a group of cells clustered around a gastro-intestinal tract, differentiated for and dedicated to the task of keeping that gut full. Critical to the survival of the heterotroph, then, is the ability to search out its own food, and high on the list of adaptive features for heterotrophs are those which aid in food gathering, including:

(1) motility -- to seek out food;
(2) flexible body -- to make that motility possible;
(3) sensory system -- to allow efficient and intelligent use of the motility; and
(4) hormonal and neural system -- to regulate and coordinate all of these activities.

But now consider the autotrophs. For these organisms, the need is for CO_2 and sunlight from the atmosphere and for water and mineral salts from the soil. The need for water and mineral salts was almost certainly one of the most difficult adaptive problems that land plants had to solve, since these two nutrients are much less readily available on land than they are in the oceans. The anatomical solution came in form of an elaborate subterranean root system capable of collecting water and inorganic salts from the soil; and a vascular system to get the water and minerals from the roots to the leaves and to move the products of photosynthesis from the leaves back down to the regions of the plant which never see the light. But consider what happened in the process: the same root system which gives the plant access to water and minerals also renders it non-motile. This non-motility is almost certainly one of the most fundamental consequences of autotrophy and has in turn far-reaching effects on what it means to be a plant.

On the other hand, the other two nutrients for autotrophs, sunlight and CO_2, are more readily available on the land than in the water, and presumably were the drawing cards that inexorably enticed the autotrophs onto the dry land in the first place. And with the transition from aquatic to terrestrial environment came an expanded foliage system with a large surface area exposed to the atmosphere to maximize the absorption of CO_2 and light. That expanded foliage system, in contrast to layers of cells simply spread out on the surface of water, demanded a rigid support system, which was conveniently met by encasing cells in rigid cell walls and mortaring them together almost like bricks in a wall. That would never have worked for animals with their heavy dependence upon motility, but turns out to be entirely compatible with the non-motility already conferred upon plants by their root system. Thus, rigid cell walls and non-motility go hand in hand and are probably the two most fundamental consequences of autotrophy.

Consequences of Autotrophy. We see, then, a growing catalogue of the consequences of autotrophy. At the structural level, it manifests itself in terms of:

(1) an extensive root system -- to ensure uptake of adequate water and minerals;
(2) a maximized surface area of leaves -- to ensure uptake of CO_2 and sunlight;
(3) rigid cell walls -- to make support of the foliar system possible; and
(4) a lack of motility -- since motility is neither necessary nor possible.

At the physiological level, you will see in several coming discussions in this course that autotrophy and its consequences have a profound influence on organismal function -- on water balance, on energy acquisition, on translocation of substances within the organism, and on release of waste products. This means that a physiological consideration of plants invariably involves topics or emphases quite different from the corresponding discussions for animals.

In terms of developmental phenomena, the consequences of autotrophy for the organism are if anything even more profound than at the physiological level. Consider first the consequence of non-motility. An animal is motile and can therefore react to its environment by modifying its behavior. This may involve seeking out shade, hibernating, building a dam, looking for a new waterhole, or buying an air-conditioner. A plant, however, is permanently rooted to one spot and must therefore interact intimately with and adapt to an environment from which it cannot escape:

> "Upon whose bosom snow has lain
> Who intimately lives with rain"

Unable to escape from its environment, a plant is profoundly influenced in its growth and development by environmental factors such as light, temperature, or moisture, which in animals are much more likely to elicit behavioral responses. In fact, plants make extensive use of environmental signals such as daylength or temperature changes to initiate and direct almost all aspects of their development.

Given that plants respond developmentally rather than behaviorally to changes in the environment then an inevitable, third consequence of non-motility is that development, rather than being limited to an early embryonic phase of the life cycle, must be possible throughout the life cycle. And indeed, it is a distinctive characteristic of plants that development occurs throughout the life cycle, as we'll be seeing shortly. We can therefore summarize the consequences of non-motility as follows:

(1) Plants adapt developmentally to an environment from which they cannot escape;
(2) plants use signals from their environment to initiate developmental changes; and
(3) in order to be able to do so, development must be possible throughout the life cycle rather than restricted to an early, embryonic portion or the life cycle.

Equally significant for the topic of plant growth and development is the impact of the rigid cell wall. In higher animals, growth can occur anywhere in the organism by increase in cell size or cell number. But not so in plants, where cells have rigid walls and are firmly stacked and cemented together. Here, growth is limited to increases in cell number at localized growing regions called meristems.

If you want to talk about morphogenesis (generation of form) instead of simply growth, again the differences are striking. In animals, morphogenesis involves considerable movement of cells within the developing embryo. Thus, any discussion of animal embryo genesis is rich in cell movements -- processes such as gastrulation, epibolization, or germ cell migration, each of which is critical to embryo development in animals. None of these movements can occur in plants due to the presence of a rigid cell wall. Instead, plant morphogenesis occurs by the differential addition of tissues at the meristems in a characteristic and usually final pattern.

Furthermore, since each meristem is capable of generating new tissue continuously and perpetually, we can add a third, somewhat more indirect consequence of autotrophy--an indeterminate pattern of growth. By this, we mean that the ultimate size and shape of a plant, resulting as it does from meristematic growth and development, is much less predictble and much more developmentally flexible than the determinate growth pattern of animals.

The consequences of rigid cell walls can therefore be summarized by noting that:

(1) Growth is restricted to an increase in cell number at localized growing points called meristems;
(2) morphogenesis occurs by differential addition and enlargment of cells at meristems, in the absence of long-distance cell movements; and
(3) growth at meristems is indeterminate.

In summary, a consideration of plant growth and development involves a variety of topics for which comparable phenomena simply do not exist in animals. These include:

(1) a rigid cell wall and all the restrictions it imposes;
(2) an indeterminate form of growth restricted to meristems;
(3) morphogenesis by differential cell addition rather than cell movement; and
(4) A profound influence of environmental factors from which the plant cannot escape and which it therefore interacts with and even anticipates in a manner that involves alterations in its pattern of growth and development.

Hence, plants cannot be thought of simply as "green animals", nor can their physiology and development be approached or studied strictly in animal terms.

Plants and animals have in many cases come up with distinctly different answers to common problems and these different answers in turn greatly influence their structure, their function, and their pattern of development. Plants must therefore be approached on their own terms. To attempt to understand their function or their development as subcases of phenomena characteristic of animals is to misunderstand profoundly what it means to be a plant and to disregard a number of physiological and developmental phenomena which are unique to plants and therefore essential to a well-rounded appreciation of organismal biology.

APPENDIX D

The Cycle of Life: The Concept of a Life Cycle

Life on Earth comprises populations of individuals whose life span varies from a few hours (bacteria) to hundreds or even thousands of years (some trees). It is through the cycle of life of individuals, repeated from one generation to the next, that life of a group of organisms or species is continued on earth. Life, for many organisms, begins with fertilization, the time when specialized reproductive cells representing the contributions of a single egg (female) and a sperm (male) join to form the **zygote** (first cell of the new generation). In higher organisms the zygote divides repeatedly, progressing through stages of growth and development. It eventually becomes a mature adult, producing reproductive cells which contribute to yet another generation. The ways in which various organisms complete their life cycles is extremely varied and a fascinating part of biology.

The growing of rapid cycling *Brassica rapa*, RCBr, through a life cycle from seed to seed can provide the basis for learning many aspects of biology that are relevant to the students' understanding of themselves as individual organisms among the many others inhabiting the planet Earth.

The following table on Concepts in the Life Cycle of Fast Plants should provide you with different ways of understanding of the Cycle of Life. By looking at the life cycle of Fast Plants from the perspective of the stages of growth and development from seed to seed, a framework can be developed for understanding the nature of the dependency between organisms and their environment.

Concepts in the Life Cycle of Fast Plants

Stage	State	Condition	Dependency
A. Seed	• quiescence (dormant embryo)	• suspended growth of embryo	• independent of the parent and many components of the environment
B. Germinating Seed	• germination	• awakening of growth	• dependent on environment and health of the individual
C. Vegetative Growth	• growth and development	• roots, stems, leaves grow rapidly, plant is sexually immature	• dependent on environment
D. Immature Plant	• flower bud development	• gametogenesis — reproductive [male (pollen) and female (egg)] cell production	• dependent on healthy vegetative plant
E. Mature Plant	• flowering • mating	• pollination — attracting or capturing pollen	• dependent on pollen carriers; bees and other insects
F. Mature Plant	• pollen growth	• gamete maturation • germination and growth of pollen tube	• dependent on compatibility of pollen with stigma and style
G. Mature Plant	• double fertilization	• union of gametes • union of sperm (n) and egg (n) to produce zygote (2n) • union of sperm (n) and fusion nucleus (2n) to produce endosperm (3n)	• dependent on compatibility and healthy plant
H. Mature Parent Plant *plus* Embryo	• developing fruit • developing endosperm • developing embryo	• embryogenesis — growth and development of endosperm and embryo • growth of supporting parental tissue of the fruit (pod)	• interdependency among developing embryo, endosperm, developing pod and supporting mature parental plant
I. Aging Parent Plant *plus* Maturing Embryo	• senescence of parent • maturation of fruit • seed development	• withering of leaves of parent plant • yellowing pods, drying embryo • suspension of embryo growth, development of seed coat	• seed is becoming independent of the parent
J. Dead Parent Plant *plus* Seed	• death, desiccation, • seed quiescence	• drying of all plant parts, dry pods will disperse seeds	• seed (embryo) is independent of parent, but is dependent on the pod and the environment for dispersal