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- Shoot tissues are derived from several discrete sets of apical initials 502
- Factors involved in auxin movement and responses influence SAM formation 503
- Embryonic SAM formation requires the coordinated expression of transcription factors 503
- A combination of positive and negative interactions determines apical meristem size 505
- KNOX class homeodomain genes help maintain the proliferative ability of the SAM through regulation of cytokinin and GA levels 506
- Localized zones of auxin accumulation promote leaf initiation 507

#### The Vascular Cambium 508

The maintenance of undetermined initials in various meristem types depends on similar mechanisms 508

# CHAPTER 18 Seed Dormancy, Germination, and Seedling Establishment 513

#### Seed Structure 514

Seed anatomy varies widely among different plant groups 514

#### Seed Dormancy 515

- Dormancy can be imposed on the embryo by the surrounding tissues 516
- Embryo dormancy may be caused by physiological or morphological factors 516
- Non-dormant seeds can exhibit vivipary and precocious germination 516
- The ABA:GA ratio is the primary determinant of seed dormancy 517

#### Release from Dormancy 519

- Light is an important signal that breaks dormancy in small seeds 519
- Some seeds require either chilling or after-ripening to break dormancy 519
- Seed dormancy can by broken by various chemical compounds 520

#### Seed Germination 520

Germination can be divided into three phases corresponding to the phases of water uptake 520

#### Mobilization of Stored Reserves 522

The cereal aleurone layer is a specialized digestive tissue surrounding the starchy endosperm 522

- Gibberellins enhance the transcription of  $\alpha$ -amylase mRNA 522
- The gibberellin receptor, GID1, promotes the degradation of negative regulators of the gibberellin response 523
- GA-MYB is a positive regulator of  $\alpha$ -amylase transcription 524
- DELLA repressor proteins are rapidly degraded 524
- ABA inhibits gibberellin-induced enzyme production 524

#### Seedling Growth and Establishment 526

- Auxin promotes growth in stems and coleoptiles, while inhibiting growth in roots 526
- The outer tissues of eudicot stems are the targets of auxin action 526
- The minimum lag time for auxin-induced elongation is 10 minutes 526
- Auxin-induced proton extrusion induces cell wall creep and cell elongation 528

#### Tropisms: Growth in Response to Directional Stimuli 528

- Gravitropism involves the lateral redistribution of auxin 528
- Polar auxin transport requires energy and is gravity independent 529
- According to the starch-statolith hypothesis, specialized amyloplasts serve as gravity sensors in root caps 530
- Auxin movements in the root are regulated by specific transporters 532
- The gravitropic stimulus perturbs the symmetric movement of auxin from the root tip 533
- Gravity perception in eudicot stems and stemlike organs occurs in the starch sheath 533
- Gravity sensing may involve pH and calcium ions (Ca<sup>2+</sup>) as second messengers 533

#### Phototropism 535

- Phototropism is mediated by the lateral redistribution of auxin 535
- Phototropism occurs in a series of posttranslational events 536

#### Photomorphogenesis 537

Gibberellins and brassinosteroids both suppress photomorphogenesis in the dark 538

- Hook opening is regulated by phytochrome and auxin 539
- Ethylene induces lateral cell expansion 539

#### Shade Avoidance 540

- Phytochrome enables plants to adapt to changes in light quality 540
- Decreasing the R:FR ratio causes elongation in sun plants 540

Reducing shade avoidance responses can improve crop yields 542

#### Vascular Tissue Differentiation 542

Auxin and cytokinin are required for normal vascular development 543

Zinnia suspension-cultured cells can be induced to undergo xylogenesis 544

Xylogenesis involves chemical signaling between neighboring cells 544

#### Root Growth and Differentiation 545

Root epidermal development follows three basic patterns 546

Auxin and other hormones regulate root hair development 546

Lateral root formation and emergence depend on endogenous and exogenous signals 547

- Regions of lateral root emergence correspond with regions of auxin maxima 548
- Lateral roots and shoots have gravitropic setpoint angles 549

# CHAPTER 19 Vegetative Growth and Organogenesis 553

#### Leaf Development 553

#### The Establishment of Leaf Polarity 554

- Hormonal signals play key roles in regulating leaf primordia emergence 555
- A signal from the SAM initiates adaxial-abaxial polarity 555

ARP genes promote adaxial identity and repress the KNOX1 gene 556

Adaxial leaf development requires HD-ZIP III transcription factors 556

The expression of HD-ZIP III genes is antagonized by miR166 in abaxial regions of the leaf 558

Antagonism between KANADI and HD-ZIP III is a key determinant of adaxial-abaxial leaf polarity 558

Interactions between adaxial and abaxial tissues are required for blade outgrowth 558

Blade outgrowth is auxin dependent and regulated by the YABBY and WOX genes 558

Leaf proximal-distal polarity also depends on specific gene expression 559

In compound leaves, de-repression of the KNOX1 gene promotes leaflet formation 559

#### Differentiation of Epidermal Cell Types 561

Guard cell fate is ultimately determined by a specialized epidermal lineage 562

Two groups of bHLH transcription factors govern stomatal cell fate transitions 563

Peptide signals regulate stomatal patterning by interacting with cell surface receptors 563

Genetic screens have led to the identification of positive and negative regulators of trichome initiation 563

GLABRA2 acts downstream of the GL1–GL3–TTG1 complex to promote trichome formation 565

Jasmonic acid regulates Arabidopsis leaf trichome development 565

#### Venation Patterns in Leaves 565

The primary leaf vein is initiated discontinuously from the preexisting vascular system 566

- Auxin canalization initiates development of the leaf trace 566
- Basipetal auxin transport from the L1 layer of the leaf primordium initiates development of the leaf trace procambium 568

The existing vasculature guides the growth of the leaf trace 568

Higher-order leaf veins differentiate in a predictable hierarchical order 569

- Auxin canalization regulates higher-order vein formation 570
- Localized auxin biosynthesis is critical for higher-order venation patterns 571

#### Shoot Branching and Architecture 572

Axillary meristem initiation involves many of the same genes as leaf initiation and lamina outgrowth 573

- Auxin, cytokinins, and strigolactones regulate axillary bud outgrowth 573
- Auxin from the shoot tip maintains apical dominance 574
- Strigolactones act locally to repress axillary bud growth 574

Cytokinins antagonize the effects of strigolactones 576 The initial signal for axillary bud growth may be an

increase in sucrose availability to the bud 577

- Integration of environmental and hormonal branching signals is required for plant fitness 577
- Axillary bud dormancy in woody plants is affected by season, position, and age factors 578

#### Root System Architecture 579

Plants can modify their root system architecture to optimize water and nutrient uptake 579

- Monocots and eudicots differ in their root system architecture 580
- Root system architecture changes in response to phosphorous deficiencies 580

Root system architecture responses to phosphorus deficiency involve both local and systemic regulatory networks 582

Mycorrhizal networks augment root system architecture in all major terrestrial ecosystems 583

#### Secondary Growth 583

- The vascular cambium and cork cambium are the secondary meristems where secondary growth originates 584
- Secondary growth evolved early in the evolution of land plants 585
- Secondary growth from the vascular cambium gives rise to secondary xylem and phloem 585
- Phytohormones have important roles in regulating vascular cambium activity and differentiation of secondary xylem and phloem 585
- Genes involved in stem cell maintenance, proliferation, and differentiation regulate secondary growth 586
- Environmental factors influence vascular cambium activity and wood properties 587

# CHAPTER 20 The Control of Flowering and Floral Development 591

### Floral Evocation: Integrating Environmental Cues 592

#### The Shoot Apex and Phase Changes 592

Plant development has three phases 592

- Juvenile tissues are produced first and are located at the base of the shoot 592
- Phase changes can be influenced by nutrients, gibberellins, and other signals 593

#### Circadian Rhythms: The Clock Within 594

Circadian rhythms exhibit characteristic features 595

- Phase shifting adjusts circadian rhythms to different day–night cycles 596
- Phytochromes and cryptochromes entrain the clock 596

### Photoperiodism: Monitoring Day Length 597

- Plants can be classified according to their photoperiodic responses 597
- The leaf is the site of perception of the photoperiodic signal 599
- Plants monitor day length by measuring the length of the night 599
- Night breaks can cancel the effect of the dark period 599
- Photoperiodic timekeeping during the night depends on a circadian clock 599
- The coincidence model is based on oscillating light sensitivity 600

- The coincidence of CONSTANS expression and light promotes flowering in LDPs 601
- SDPs use a coincidence mechanism to inhibit flowering in long days 603
- Phytochrome is the primary photoreceptor in photoperiodism 603
- A blue-light photoreceptor regulates flowering in some LDPs 604

### Vernalization: Promoting Flowering with Cold 605

Vernalization results in competence to flower at the shoot apical meristem 605

- Vernalization can involve epigenetic changes in gene expression 606
- A range of vernalization pathways may have evolved 607

#### Long-Distance Signaling Involved in Flowering 608

Grafting studies provided the first evidence for a transmissible floral stimulus 608

Florigen is translocated in the phloem 609

#### The Identification of Florigen 610

The Arabidopsis protein FLOWERING LOCUS T (FT) is florigen 610

Gibberellins and ethylene can induce flowering 610

The transition to flowering involves multiple factors and pathways 612

#### Floral Meristems and Floral Organ Development 612

The shoot apical meristem in Arabidopsis changes with development 613

The four different types of floral organs are initiated as separate whorls 613

Two major categories of genes regulate floral development 614

Floral meristem identity genes regulate meristem function 614

- Homeotic mutations led to the identification of floral organ identity genes 616
- The ABC model partially explains the determination of floral organ identity 616
- Arabidopsis Class E genes are required for the activities of the A, B, and C genes 618
- According to the Quartet Model, floral organ identity is regulated by tetrameric complexes of the ABCE proteins 618

Class D genes are required for ovule formation 619

Floral asymmetry in flowers is regulated by gene expression 620

# CHAPTER 21 Gametophytes, Pollination, Seeds, and Fruits 625

# Development of the Male and Female Gametophyte Generations 625

# Formation of Male Gametophytes in the Stamen 626

Pollen grain formation occurs in two successive stages 627

The multilayered pollen cell wall is surprisingly complex 628

### Female Gametophyte Development in the Ovule 630

The Arabidopsis gynoecium is an important model system for studying ovule development 630

- The vast majority of angiosperms exhibit *Polygonum*type embryo sac development 630
- Functional megaspores undergo a series of free nuclear mitotic divisions followed by cellularization 631
- Embryo sac development involves hormonal signaling between sporophytic and gametophytic generations 632

# Pollination and Fertilization in Flowering Plants 632

- Delivery of sperm cells to the female gametophyte by the pollen tube occurs in six phases 633
- Adhesion and hydration of a pollen grain on a compatible flower depend on recognition between pollen and stigma surfaces 634
- Ca<sup>2+</sup>-triggered polarization of the pollen grain precedes tube formation 635
- Pollen tubes grow by tip growth 635
- Receptor-like kinases are thought to regulate the ROP1 GTPase switch, a master regulator of tip growth 635
- Pollen tube tip growth in the pistil is directed by both physical and chemical cues 637
- Style tissue conditions the pollen tube to respond to attractants produced by the synergids of the embryo sac 637

Double fertilization occurs in three distinct stages 638

# Selfing versus Outcrossing 639

Hermaphroditic and monoecious species have evolved floral features to ensure outcrossing 639

- Cytoplasmic male sterility (CMS) occurs in the wild and is of great utility in agriculture 640
- Self-incompatibility (SI) is the primary mechanism that enforces outcrossing in angiosperms 640
- The Brassicaceae sporophytic SI system requires two S-locus genes 641

Gametophytic self-incompatibility (GSI) is mediated by cytotoxic S-RNases and F-box proteins 642

# Apomixis: Asexual Reproduction by Seed 643

# Endosperm Development 643

- Cellularization of coenocytic endosperm in Arabidopsis progresses from the micropylar to the chalazal region 645
- Cellularization of the coenocytic endosperm of cereals progresses centripetally 646
- Endosperm development and embryogenesis can occur autonomously 646

Many of the genes that control endosperm development are maternally expressed genes 647

- The FIS proteins are members of a Polycomb repressive complex (PRC2) that represses endosperm development 647
- Cells of the starchy endosperm and aleurone layer follow divergent developmental pathways 649
- Two genes, *DEK1* and *CR4*, have been implicated in aleurone layer differentiation 649

### Seed Coat Development 650

Seed coat development appears to be regulated by the endosperm 650

# Seed Maturation and Desiccation Tolerance 652

- Seed filling and desiccation tolerance phases overlap in most species 652
- The acquisition of desiccation tolerance involves many metabolic pathways 653
- During the acquisition of desiccation tolerance, the cells of the embryo acquire a glassy state 653
- LEA proteins and nonreducing sugars have been implicated in seed desiccation tolerance 653
- Specific LEA proteins have been implicated in desiccation tolerance in *Medicago truncatula* 653
- Abscisic acid plays a key role in seed maturation 654
- Coat-imposed dormancy is correlated with long-term seed-viability 654

# Fruit Development and Ripening 655

Arabidopsis and tomato are model systems for the study of fruit development 655

Fleshy fruits undergo ripening 657

- Ripening involves changes in the color of fruit 657
- Fruit softening involves the coordinated action of many cell wall-degrading enzymes 658
- Taste and flavor reflect changes in acids, sugars, and aroma compounds 658
- The causal link between ethylene and ripening was demonstrated in transgenic and mutant tomatoes 658
- Climacteric and non-climacteric fruit differ in their ethylene responses 658

The ripening process is transcriptionally regulated 660

Angiosperms share a range of common molecular mechanisms controlling fruit development and ripening 660

Fruit ripening is under epigenetic control 660

A mechanistic understanding of the ripening process has commercial applications 661

# CHAPTER 22 Plant Senescence and Cell Death 665

#### Programmed Cell Death and Autolysis 666

- PCD during normal development differs from that of the hypersensitive response 668
- The autophagy pathway captures and degrades cellular constituents within lytic compartments 669
- A subset of the autophagy-related genes controls the formation of the autophagosome 669
- The autophagy pathway plays a dual role in plant development 671

#### The Leaf Senescence Syndrome 671

- The developmental age of a leaf may differ from its chronological age 672
- Leaf senescence may be sequential, seasonal, or stressinduced 672
- Developmental leaf senescence consists of three distinct phases 673
- The earliest cellular changes during leaf senescence occur in the chloroplast 675
- The autolysis of chloroplast proteins occurs in multiple compartments 675
- The STAY-GREEN (SGR) protein is required for both LHCP II protein recycling and chlorophyll catabolism 676
- Leaf senescence is preceded by a massive reprogramming of gene expression 677

#### Leaf Senescence: The Regulatory Network 678

- The NAC and WRKY gene families are the most abundant transcription factors regulating leaf senescence 678
- ROS serve as internal signaling agents in leaf senescence 680
- Sugars accumulate during leaf senescence and may serve as a signal 681
- Plant hormones interact in the regulation of leaf senescence 681

#### Leaf Abscission 684

The timing of leaf abscission is regulated by the interaction of ethylene and auxin 685

#### Whole Plant Senescence 686

Angiosperm life cycles may be annual, biennial, or perennial 687

- Whole plant senescence differs from aging in animals 688
- The determinacy of shoot apical meristems is developmentally regulated 688
- Nutrient or hormonal redistribution may trigger senescence in monocarpic plants 689
- The rate of carbon accumulation in trees increases continuously with tree size 689

# CHAPTER 23 Biotic Interactions 693

#### Beneficial Interactions between Plants and Microorganisms 695

Nod factors are recognized by the Nod factor receptor (NFR) in legumes 695

- Arbuscular mycorrhizal associations and nitrogenfixing symbioses involve related signaling pathways 695
- Rhizobacteria can increase nutrient availability, stimulate root branching, and protect against pathogens 697

#### Harmful Interactions between Plants, Pathogens, and Herbivores 697

- Mechanical barriers provide a first line of defense against insect pests and pathogens 698
- Plant secondary metabolites can deter insect herbivores 700
- Plants store constitutive toxic compounds in specialized structures 701
- Plants often store defensive chemicals as nontoxic water-soluble sugar conjugates in the vacuole 703
- Constitutive levels of secondary compounds are higher in young developing leaves than in older tissues 705

#### Inducible Defense Responses to Insect Herbivores 705

- Plants can recognize specific components of insect saliva 706
- Modified fatty acids secreted by grasshoppers act as elicitors of jasmonic acid accumulation and ethylene emission 706
- Phloem feeders activate defense signaling pathways similar to those activated by pathogen infections 707
- Calcium signaling and activation of the MAP kinase pathway are early events associated with insect herbivory 707
- Jasmonic acid activates defense responses against insect herbivores 708
- Jasmonic acid acts through a conserved ubiquitin ligase signaling mechanism 709
- Hormonal interactions contribute to plant-insect herbivore interactions 709

- JA initiates the production of defense proteins that inhibit herbivore digestion 710
- Herbivore damage induces systemic defenses 710
- Glutamate receptor-like (GLR) genes are required for long-distance electrical signaling during herbivory 712
- Herbivore-induced volatiles can repel herbivores and attract natural enemies 712
- Herbivore-induced volatiles can serve as long-distance signals between plants 713
- Herbivore-induced volatiles can also act as systemic signals within a plant 714
- Defense responses to herbivores and pathogens are regulated by circadian rhythms 714
- Insects have evolved mechanisms to defeat plant defenses 715

# Plant Defenses against Pathogens 715

- Microbial pathogens have evolved various strategies to invade host plants 715
- Pathogens produce effector molecules that aid in the colonization of their plant host cells 716
- Pathogen infection can give rise to molecular "danger signals" that are perceived by cell surface pattern recognition receptors (PRRs) 717
- *R* genes provide resistance to individual pathogens by recognizing strain-specific effectors 718
- Exposure to elicitors induces a signal transduction cascade 719
- Effectors released by phloem-feeding insects also activate NBS-LRR receptors 719
- The hypersensitive response is a common defense against pathogens 720
- Phytoalexins with antimicrobial activity accumulate after pathogen attack 721
- A single encounter with a pathogen may increase resistance to future attacks 721
- The main components of the salicylic acid signaling pathway for SAR have been identified 723
- Interactions of plants with nonpathogenic bacteria can trigger systemic resistance through a process called induced systemic resistance (ISR) 723

# Plant Defenses against Other Organisms 724

- Some plant parasitic nematodes form specific associations through the formation of distinct feeding structures 724
- Plants compete with other plants by secreting allelopathic secondary metabolites into the soil 725
- Some plants are biotrophic pathogens of other plants 726

# CHAPTER 24 Abiotic Stress 731

# Defining Plant Stress 732

Physiological adjustment to abiotic stress involves trade-offs between vegetative and reproductive development 732

# Acclimation and Adaptation 733

- Adaptation to stress involves genetic modification over many generations 733
- Acclimation allows plants to respond to environmental fluctuations 733

### Environmental Factors and Their Biological Impacts on Plants 734

Water deficit decreases turgor pressure, increases ion toxicity, and inhibits photosynthesis 735

- Salinity stress has both osmotic and cytotoxic effects 736
- Light stress can occur when shade-adapted or shadeacclimated plants are subjected to full sunlight 736
- Temperature stress affects a broad spectrum of physiological processes 736
- Flooding results in anaerobic stress to the root 737
- During freezing stress, extracellular ice crystal formation causes cell dehydration 737
- Heavy metals can both mimic essential mineral nutrients and generate ROS 737
- Mineral nutrient deficiencies are a cause of stress 737
- Ozone and ultraviolet light generate ROS that cause lesions and induce PCD 737
- Combinations of abiotic stresses can induce unique signaling and metabolic pathways 738
- Sequential exposure to different abiotic stresses sometimes confers cross-protection 739

# Stress-Sensing Mechanisms in Plants 739

Early-acting stress sensors provide the initial signal for the stress response 740

# Signaling Pathways Activated in Response to Abiotic Stress 740

- The signaling intermediates of many stress-response pathways can interact 740
- Acclimation to stress involves transcriptional regulatory networks called *regulons* 743
- Chloroplast genes respond to high-intensity light by sending stress signals to the nucleus 744
- A self-propagating wave of ROS mediates systemic acquired acclimation 745
- Epigenetic mechanisms and small RNAs provide additional protection against stress 745

Hormonal interactions regulate normal development and abiotic stress responses 745

# Developmental and Physiological Mechanisms That Protect Plants against Abiotic Stress 747

Plants adjust osmotically to drying soil by accumulating solutes 748

- Submerged organs develop aerenchyma tissue in response to hypoxia 749
- Antioxidants and ROS-scavenging pathways protect cells from oxidative stress 750
- Molecular chaperones and molecular shields protect proteins and membranes during abiotic stress 751
- Plants can alter their membrane lipids in response to temperature and other abiotic stresses 752
- Exclusion and internal tolerance mechanisms allow plants to cope with toxic ions 753

- Phytochelatins and other chelators contribute to internal tolerance of toxic metal ions 754
- Plants use cryoprotectant molecules and antifreeze proteins to prevent ice crystal formation 754
- ABA signaling during water stress causes the massive efflux of K<sup>+</sup> and anions from guard cells 755
- Plants can alter their morphology in response to abiotic stress 757
- Metabolic shifts enable plants to cope with a variety of abiotic stresses 759
- The process of recovery from stress can be dangerous to the plant and requires a coordinated adjustment of plant metabolism and physiology 759
- Developing crops with enhanced tolerance to abiotic stress conditions is a major goal of agricultural research 759

Glossary G–1 Illustration Credits IC–1 Photo Credits PC–1 Subject Index SI–1 gas exchange in the leaf, water conduction in the wier, pho inthesis in the chloroplast, ich transport across membranes, gnal transduction pathways involving light and hormones, or jene expression during development, all of these functions depend emittely on structures.

Function derives from structures interacting atomery level of scale, it occurs when this molecules recognise and bind each other to produce a complex with new functions. It occurs as a new leaf unfolds, as cells and fisques interact during the process of plant development. It occurs when huge organisms shade, noutish, or mate with each other. At every level, from legules to organisms, structure and function represent different mes of reference of a biological unity.

The fundamental organizational unit of plants, and of alkilving organisms, is the call. The term call is derived from the Latin calls, meaning "storercom" or "chamber." It was first used in biology in 1955 by the English colentist Robert Hooke to describe the individual units of the honeycomb-like structure he observed in conunder a compound microscope. The cork "calls" Hogke observed were actually the empty lumans of dead calls surrounded by call walls, but the term is an apt one, because calls are the basic building blocks that define plant structure.

Moving outward from the cell, groups of specialized cells form specific titrues, and specific tistues arranged in particular patterns are the basis of time-dimensional organs dust as plant anatomy, the study of the matroacopic arrangements of cells and tissues within organs, mostlyed its initial impetus from improvements to the light microacopic in the seventeenth century, so plant cell biology the study of the immior of cells, was stimulated by the first application of the descent microacope to piological material in the.