When guanine nucleotide-binding proteins (G proteins) bind GTP, they adopt an activated conformation that leads to activation of downstream signaling elements. In this capacity, G proteins couple, amplify, and integrate upstream signals to downstream cellular changes. One of the most fascinating aspects of G proteins is that they operate like a molecular timer because the GTP-bound, activated state converts to the GDP-bound, resting state after an inherently determined amount of time due to hydrolysis of GTP to GDP by the intrinsic GTPase. The cycling of activated to resting states, known as the G cycle, enables cellular signaling to occur within kinetics of seconds to hours. In eukaryotes, G proteins are divided into two major subgroups: the Ras superfamily of small G proteins and the heterotrimeric G proteins. The Ras superfamily is further divided into the Ras, Rho, Rab, Arf, and Ran subfamilies. The G$\alpha$ subunits of the heterotrimeric G-protein complex divide the complexes into four subclasses, G$_i$, G$_s$, G$_q$, and G$_{12/13}$. The Ras, Rho, and the heterotrimeric G proteins are implicated in regulation of signaling, while Rab, Arf, and Ran carry out other cellular functions and are not be covered in this book. Ras proteins have not been identified in plants. This leaves the small G protein from the Rho family, called ROPs or RACs (hereafter ROPs/RACs), and the heterotrimeric G proteins to comprise the two major groups of signaling G proteins in plants. This book summarizes a decade of research on ROPs/RACs and heterotrimeric G proteins in plants.

In the active state, the small GTPases interact with target proteins commonly referred to as effectors to initiate a signaling process. In most small G proteins, the GDP/GTP exchange is not spontaneous and requires accessory proteins known as G$\text{uanine nuc}$ leotide $\text{Ex}$change $\text{Factors}$ (GEFs). The inefficient GTPase activity is enhance by a second group of proteins known as GTPase Activating Proteins (GAPs). GEFs and GAPs provide a means to regulate the activity of the small GTPases in time and space. Subcellular distribution of proteins from Rho and Rab families is regulated by a third group of proteins designated G$\text{uanine nuc}$ leotide $\text{Dissociation Inhibitors}$ (GDIs).
Heterotrimeric G protein are composed of three subunits designated \(\alpha\), \(\beta\), and \(\gamma\). The \(\alpha\) subunit is a GTP-binding protein that contains one domain that resembles small GTPases. The \(\beta\) subunit has a seven-bladed propeller structure and forms a tight dimeric complex with the \(\gamma\) subunit. In metazoans, heterotrimeric G proteins are associated with membrane proteins known as G-Protein-Coupled Receptors (GPCRs) that are the ligand-regulated GEFs. Activation of GPCRs upon ligand binding leads to GDP/GTP exchange and activation of the \(G\alpha\). In turn, \(G\beta\)- and \(G\gamma\) dissociate from the subunit as a complex and signaling is induced by both the dissociated \(G\alpha\) and \(G\beta\gamma\) complex. Signaling terminates by GTP hydrolysis that leads to reassociation of \(G\beta\gamma\) with the \(G\alpha\). As discussed in the Chapter "Bioinformatics of Seven-Transmembrane Receptors in Plant Genomes," the existence of GPCRs in plants is questioned.

Furthermore, as discussed in the Chapter "Plant \(G\alpha\) Structure and Properties," while GDP release from the \(G\alpha\) subunit is the rate-limiting step in vertebrate G protein complexes, that does not seem to be the case for \textit{Arabidopsis}. The implications of this strange property are described.

The book begins with a chapter from Janice Jones describing these and other G protein signaling principles and then describes the unique properties of plant heterotrimeric G proteins. The chapter "\textit{Structure and function of ROPs and their GEFs}," by Christoph Thomas and Antje Berken takes a similar approach with the small G proteins and thus, these two chapters provide an interesting comparison of the \(G\alpha\) subunit of the heterotrimeric G protein complex and the small G proteins in plants. Physiological aspects are taken up in later chapters. For example, in the Chapter "Heterotrimeric G Proteins and Plant Hormone Signaling in Rice," by Yukimoto Iwasaki and coworkers, evidence is presented that the G protein in rice is mediating fundamentally different signaling than in \textit{Arabidopsis}. Jin-Gui Chen in the Chapter "Heterotrimeric G-Proteins and Cell Division in Plants," builds the case that the heterotrimeric G protein complex controls the rate of the plant cell cycle and consequently cell proliferation. Two chapters ("The Role of Seven Transmembrane Domain MLO Proteins, Heterotrimeric G-Proteins and Monomeric RAC/ROPs in Plant Defense" and "G Proteins and Plant Innate Immunity") by Justine Lorek et al. and Yuri Trusov et al., respectively, deal with the role of small and heterotrimeric G proteins in plant defense against different pathogens. Whether or not G proteins couple multiple plant hormones and environmental signals remains an open question but is a theme throughout the book. As mentioned earlier, the receptors that activate the heterotrimeric G protein complex are poorly conserved at the primary sequence level. Therefore, in the Chapter "Bioinformatics of Seven-Transmembrane Receptors in Plant Genomes," Etsuyko Moriyma and Stephen Opiyo provide strategies to identify 7-transmembrane proteins from divergent genomes. They then apply these tools to 18 genomes of the bikonts, the group that includes higher plants and the algae. The chapter "Evolution of the ROP GTPase Signaling Module" is about the bizaar; Lei Ding and coworkers discuss
proteins that share limited sequence similarity to canonical Gα subunits of the heterotrimeric G protein complex.

ROPs/RACs are master regulators of cell polarity, similar to their homologs in yeast and animal cells. Remarkably, these studies showed that regardless of the evolutionary-conserved functions, many of the ROPs/RACs effectors are unique to plants. The chapter “ROP GTPases and the cytoskeleton” by Ying Fu focuses on the function of ROPs/RACs in cytoskeleton organization, highlighting the role of a plant-unique group of proteins designated RICs (ROP Interacting CRIB containing) as well as by the evolutionary-conserved WAVE and Arp2/3 complexes. In the absence of other signaling small GTPases, ROPs/RACs were suggested to function in diverse signaling cascades. The chapter “ROP GTPases in the Regulation of Polarity and Polar Cell Growth” by He-Ming Wu and Alice Cheung describes the role of ROPs/RACs in cell polarity, hormonal, and reactive oxygen species signaling. The chapter highlights how conserved mechanisms involving proteins such as ADF/cofilins and formins together with plant-unique proteins such as the RICs and ICR1 (Interactor of Constitutive active ROP1) orchestrate polar cell growth. The chapter “The Role of Seven Transmembrane Domain MLO Proteins, Heterotrimeric G-Proteins and Monomeric RAC/ROPs in Plant Defense” by Justine Lorek et al. discusses the role of ROPs/RACs MLO proteins and heterotrimeric G proteins in plant defense responses and how they interface with cell polarity, complementing the discussion in the chapter “G proteins and plant innate immunity.” Two types of ROP/RAC GEFs are currently known in plants: an evolutionary-conserved Dock180 protein called SPIKE1, which may be associated with the WAVE complex and a family of proteins designated PRONE GEFs that can activate ROPs/RACs but not non-plant Rho proteins. In the chapter “Structure and Function of ROPs and Their GEFs,” Christoph Thomas and Antje Berken discuss the structure and function of ROPs/RACs and the PRONE ROPGEFs, highlighting the common and plant-unique features. GAPs and RhoGDIls play pivotal roles in regulation of signaling by Rho GTPases. The chapter “Regulatory and Cellular Functions of Plant RhoGAPs and RhoGDIs” by Benedikt Kost highlights studies showing how spatial distribution of certain GAPs and function of RhoGDIs regulate polar cell growth. The chapter “Evolution of the ROP GTPase Signaling Module” by John Fowler discusses the origin and evolution of ROPs/RACs. ROP/RACs and heterotrimeric G proteins function at the plasma membrane to which they attach by virtue of posttranslational lipid modifications and polybasic region comprised of lysine and arginine residues. In the chapter “Protein–lipid Modifications and Targeting of ROP/RAC and Heterotrimeric G Proteins,” Nadav Sorek and Shaul Yalovsky describe the lipid modifications and their regulatory roles in function of ROP/RACs and heterotrimeric G proteins. Each chapter of this book offers a different perspective of the state-of-the-art in the field, presenting a well-balanced and an up-to-date description of the current knowledge on G protein signaling in plants. The breadth of the book offers a thorough introduction, and at the same time, a detailed in-depth discussion to those who are new to the field. Thus, we hope to draw the
interest of both new and advanced students to this relatively young but fast-progressing and fascinating field of plant cell biology

Tel Aviv, June 2009
Shaul Yalovsky
Bonn, June 2009
František Baluška
Chapel Hill, June 2009
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