Preface

In the 18th and 19th centuries experiments on bark ringing and tropisms indicated that plants contain a mobile signal, which was subsequently revealed to be the auxin indole-3-acetic acid (IAA). The first half of the last century saw the chemical identification of many of the major plant signaling molecules (hormones) and although progress in understanding their formation and mode of action was initially slow, recent advances in this field have been spectacular, including the identification of receptors for several hormone classes, with those for abscisic acid, IAA and gibberellin being identified within the last year (2005–2006) (see Chapters 1, 2 and 6, respectively). This would therefore appear to be an ideal time to highlight the recent progress in this field. This preface traces briefly the history of plant hormone discovery and identification, which occurred when methods of analysis were much less sensitive than those available today.

Although auxin was the first plant hormone to be recognised as such, when in 1926 Frits Went demonstrated the presence of a diffusible, growth-promoting substance in oat coleoptiles, the profound effects of ethylene on plant development had been observed and utilised well before this time. As related in Chapter 5, the induction of fruit ripening by ethylene has been unknowingly exploited since ancient times, through, for example, scratching the surface of fruit to induce wound ethylene, or by exposure to smoke, which contains ethylene. The accidental discovery in the Azores in 1874 that smoke from burning fields synchronised flowering in pineapples has been exploited in pineapple production ever since, the smoke being replaced by acetylene and later the ethylene-releasing compound ethephon or naphthalene acetic acid, which induces ethylene production, once the active ingredient had been identified. In 1901 Dimitry Neljubow showed that ethylene was the active component of coal gas that induced diageotropism in dark-grown pea seedlings. It might therefore be claimed that ethylene was the first plant hormone to be discovered, although evidence that plants actually produce this gas was not provided until 1934 and it took many more years for it to be accepted as a *bona fide* plant hormone. It may have been difficult to acknowledge that a gas could function as a hormone, although with the discovery of nitric oxide as a ubiquitous signaling molecule, this concept is now well accepted.

Following Went's discovery of auxin (initially referred to as growth accelerating substance and then as Wuchsstoff, the term auxin was introduced by Kögl in 1932) it took several years and some false trails (see Wildman, 1997 for a fascinating account of the early attempts to define the chemical identity of auxin) before IAA was identified as the active principal present in human urine, which was known to contain IAA already in 1885. IAA was also found to be responsible for the auxin activity present in extracts of yeast and *Rhizopus suinus*, and it was finally identified from a plant source, maize meal, in 1942.

It was a common theme that plant hormones were initially identified from non-plant sources, since their concentrations in plants are generally too low for them to have been chemically detectable from this source by the methods available at the time. Thus, the next class of hormones to be discovered, the gibberellins, were found as growth active secretions of the fungus *Gibberella fujikuroi*. Although crystalline substances, named gibberellins by Teijiro Yabuta, were obtained in the 1930s (see Chapter 6), the first chemical structure, that of GA_3, was not proposed until 1956. The ability of GA_3 and plant extracts to restore the growth of certain dwarf mutants and induce bolting in rosette plants led several groups to propose that GAs were endogenous plant growth regulators (see review by Phinney, 1983). Their presence in plants was confirmed by the identification of GA_1 in seeds of runner bean in 1958.

The fourth hormone class, the cytokinins, were also first identified from a non-plant source. Several plant and non-plant materials, including coconut milk and yeast extract, were found to stimulate division of plant cells in culture, with autoclaved herring sperm being particularly effective. The active ingredient from herring sperm, named kinetin, was identified in 1955 by Miller *et al.* (1955) as N^6-furfuryladenine, a rearrangement product of 2-deoxyribosyladenine. The first naturally occurring cytokinin was identified from maize in the early 1960s independently by Letham and Miller, who agreed on the name zeatin (Lethem & Miller, 1965). The term cytokinin for this class of hormones was introduced by Skoog *et al.* (1965). Recent advances in cytokinin signaling is described in Chapter 4.

The last of the so-called classical plant hormones, abscisic acid (see Chapter 1), was identified around the same time as zeatin, atypically directly from plant sources, although fungi are also known to produce this compound. Investigations of growth inhibiting substances were carried out in the 1950s and early 1960s, including the purification of compounds that apparently induced abscission of cotton fruit in the laboratory of Frederick Addicot, who named them abscisins, and of a substance (dormin) that induced bud dormancy in trees, by Wareing and co-workers. In 1965, Addicot's group reported the structure of Abscisin II, which was later shown to be identical to dormin. The name abscisic acid (ABA) was agreed by the two groups (Addicott *et al.*, 1968), yet it has become subsequently clear that ABA is not involved in abscission processes and its accumulation in abscising fruit may have been due to the stress associated with this process.

Several more groups of compounds with biological activity on plants were subsequently discovered, but there was initially some resistance to according them full plant hormone status, partly because it was difficult to assign them a physiological function. The brassinosteroids provide a prime example of this. The first member of this group to be chemically identified was brassinolide, which was isolated from oilseed rape (*Brassica napus*) pollen in the 1970s (Grove *et al.*, 1979). Brassinolide and other brassinosteroids were shown to have activity in bioassays, but it was not until a number of severely dwarfed GA-insensitive mutants were found to contain lesions in brassinosteroid biosynthesis or response (see Chapter 3) could the claim of brassinosteroids as endogenous growth regulators be no longer ignored. The

brassinosteroid signaling pathway is now better understood than for some of the longer established hormones and its receptor was one of the first to be identified.

Jasmonic acid and related compounds such as cucurbic acid were identified as endogenous growth inhibitors in the 1970s and 1980s. Jasmonic acid has subsequently been shown to be involved in a number of physiological responses, particularly reproductive development and in resistance to insect herbivores and pathogens. There is also evidence that volatile metabolites of jasmonic acid, such as methyl jasmonate and *cis*-jasmone, may function in interplant or plant-insect communication (see Chapter 7). Pathogen resistance, particularly to biotrophic pathogens, is also mediated by salicyclic acid, a plant metabolite that is better known for its medicinal properties. Like jasmonic acid, salicyclic acid has been associated with a number of physiological processes in plants, the most spectacular of which is the induction of thermogenesis in the spadex of arum lily. However, its involvement in systemic acquired resistance has been the most extensively studied (see Chapter 8).

Lack of space prevents inclusion in this volume of a number of more recently discovered molecules, for which details of the signaling pathways are less advanced or for which hormonal activity is less clear. A signaling role for polyamines in plants was recognised recently but, although they participate in numerous developmental processes, their presence at relatively high concentrations suggests that they do not act strictly as hormones. The phytosulfokines, a group of sulphated pentapeptides, were isolated from rice cell suspension cultures and shown to stimulate cell division (Matsubayashi *et al.*, 1997), although their signal transduction pathway is unknown. Numerous other molecules from various sources have been shown to have often quite specific physiological effects. Recently the component of plant-derived smoke that stimulates seed germination was identified as a butenolide derivative with a striking structural similarity with strigol, a compound present in root exudates of many species that stimulates germination of the parasitic weeds *Striga* and *Orobanche* (Flematti *et al.*, 2004). This raises the possibility that related compounds may have a hormonal function. The existence of a potentially new group of unidentified hormones that control branching has been indicated by genetic studies (reviewed in Schmitz & Theres, 2005). Components of the biosynthetic and signal transduction pathway for these hormones are encoded by the *MORE AXILLARY GROWTH* (*MAX*) genes of *Arabidopsis* and the *RAMOSUS* (*RMS*) genes of pea.

The absence of appropriate technology meant that progress in understanding the function of the hormones was initially slow and relied on observations of the effects of exogenous hormone applications. In some cases, the availability of hormone-deficient mutants was extremely helpful in determining physiological function and in investigating the hormone biosynthetic and catabolic pathways. The advent of molecular genetics and plant transformation, together with the development of sensitive and high throughput analytical techniques has enabled rapid advances in our understanding of hormone signaling such that most details of the metabolic pathways are known for all the major hormones and substantial progress has been made in elucidating their signal transduction pathways. Receptors have now been identified

for seven of the eight hormone classes covered in this volume. While the first three receptors to be discovered, those for ethylene, brassinosteroids and cytokinins are located on the plasma membrane, soluble receptors have been identified for auxin, GA and ABA. The recently discovered auxin and GA receptors participate fairly directly in the ubiquitin ligase-mediated degradation of transcriptional regulators, bypassing the need for a complex signaling cascade. Time will tell whether or not the membrane receptors predicted for these hormones by numerous earlier studies also exist.

Protein degradation is proving to be a common theme in plant hormone signal transduction, the hormone signal resulting in removal or stabilisation of transcriptional regulators, depending on the pathway. Another common feature is the presence of feedback regulation, in which transduction of the hormone signal results in modification, usually repression, of biosynthesis at the transcript level, providing a mechanism for hormone homoeostasis. Moreover, it is also clear that there are complex interactions between the hormone pathways, acting on biosynthesis or signal transduction, that allow homeostasis at a higher level. Most developmental processes respond to several hormones, which mediate and integrate the different intrinsic and extrinsic cues that act on these processes. This volume includes chapters that consider the hormonal regulation of reproductive development (Chapter 10) and of seed development and germination (Chapter 11). A complete understanding of the hormonal control of development will need to take account of their interactions, the complexity of which may ultimately be fully understood only with the help of computer modelling.

This volume also includes a chapter on hormone distribution (Chapter 9), focusing on IAA, GAs and brassinosteroids, which differ considerably in their mobility. Among the hormones, only IAA is known to be actively transported, while other hormones may move by diffusion between cells or over longer distances in the vascular system. Some hormones undoubtedly act in some cases within the cell in which they are produced. Thus, as in animals, examples of autocrine, paracrine and even endocrine signaling can be found in plants. The debate about whether plant hormones can legitimately be called such on the basis of the original definition, which recognised only endocrine signals, has long since been abandoned as irrelevant. Plants have developed their own chemical signaling system, the importance of which for survival, development and response to the environment is becoming ever more apparent with increased understanding.

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