PREFACE

The complexity of biological systems has a striking example in the interaction of plants with sedentary endoparasitic nematodes. The statement that *the sum of the parts is not equal to the whole* underlying biological research turns fully meaningful when looking at these perfectly designed nematode-feeding cells inside plant roots, the giant cells and the syncytia. These cells still constitute an open and intriguing world that researchers are continuously revisiting: a micro-world where nematodes negotiate with the plant cells in a continuous cross talk and debate that are full of surprises. The capacity of nematodes to induce the generation of new cell functionalities and their subtle interloping with molecular transduction pathways already established in other plant programs to develop non-previously planned new cells are captivating processes that makes us aware of the flexibility of plant cells. We would like this book to be a guide for the personal discovery of one of the most complex molecular dialogues between the animal and plant kingdoms: a guidance to discover yet the limitations of cell biology, biochemistry, genomics and genetic techniques for the full study of the underlying mechanisms and processes leading this fascinating plant-pathogen interplay. Finally, we would like this book to be also an inspiration for your own enthrallment on the open fields of research in continuous dynamism facing compatible plant–nematode interactions.

This book provides an updated view of some of the processes subjacent to compatible plant–nematode interactions, particularly focussed in sedentary endoparasitic nematodes. This knowledge constitutes the starting point in the search for new control strategies for these agricultural pests. Among the most damaging groups of plant parasitic nematodes for agriculture are the root-knot nematodes (RKNs; *Meloidogyne* spp.) and the cyst nematodes (CNs; *Heterodera* spp. and *Globodera* spp.), receiving their names from the characteristic structures formed within the roots after their infection (the galls or knots and the cysts, respectively). These sedentary parasites induce the formation of their feeding sites by directing the transdifferentiation of normal plant root cells into nematode feeding cells, named giant cells for RKNs, and syncytia for CNs. They show a sophisticated parasitism behaviour, as they develop an intimate relationship with their hosts, inducing highly specialized "pseudo-organs" to provide them with a continuous source of food. Plant damage caused by these parasites is mostly due to the reduced availability of water and nutrients caused by nematode

feeding and disruption of root anatomy. Cyst nematodes also produce wounding, particularly during migration, that predisposes the plant to other soil pathogens attack, such as pathogenic bacteria or fungi, sometimes carried by the nematode itself. Therefore, endoparasitic nematodes pose a major threat to many crops worldwide.

The volume starts with two introductory chapters that provide an overview of the parasitism mode of RKNs and CNs, the two major groups of sedentary endoparasitic nematodes, presenting general features of their feeding sites. Dramatic rearrangements in the cell wall and cytoskeleton, alteration of cell cycle mechanisms such endoreduplication and/or mitosis, readjustment of enzymes involved in carbohydrate synthesis and degradation and alteration of lipid metabolism are among the main processes modified during the plant–nematode interaction that are revised in Chapters 3 to 6. These processes are especially relevant to allow the feeding cells act as sinks to provide nutrients for nematode life cycle completion. Several evidences show that nematodes induce their feeding sites by interfering with developmental mechanisms present in the plant. The molecular mechanisms used by microorganisms to interfere with plant processes are surprisingly subtle but can effectively modify predefined plant developmental patterns. Hence, nematodes may partially 'hijack' fundamental mechanisms of plant development, such as those described for molecular transducers common to lateral root (LR) and gall formation in RKNs (revised in Chapter 7).

Most of the research revised in these chapters was conducted in a few plant species, particularly *Arabidopsis thaliana*, all of them dicotiledoneus. However, sedentary endoparasitic nematodes are also major pests of important monocotiledoneus crops, thus the study of the compatible interactions with species such as maize or rice is an emerging field that is revised in Chapter 8. The above chapters review how tools such as transcriptomic analyses combined with genetics and molecular cell biology revealed dramatic and specific changes in gene expression in syncytia and giant cells. Nevertheless, to date, only a few players of the complex regulatory networks taking place during feeding cells development have emerged, and the understanding of the subtle interaction with their hosts and their necessary cross talk is still fragmentary. Yet, integrative analysis of proteomic and transcriptomics together with genetics and molecular and cell biology tools are facilitating its comprehension. Host endogenous small RNAs and RNA-silencing pathways appear also to play key roles in regulating gene expression changes and reprogramming cells in infected roots into specific syncytial or giant-cell types. Through massive sequencing

approaches, different types of transcriptional and post-transcriptional small RNA-mediated gene silencing in the feeding sites are starting to be deciphered. Furthermore, two artificial RNA interference systems, host-induced gene silencing and virus-induced gene silencing are shown as powerful tools for functional genomics of plant–nematode interactions, and all discussed in Chapter 9.

The mechanisms that nematodes use to invade roots and to induce and maintain their feeding sites are unclear, but some seem to involve nematode effector molecules secreted from their oesophageal glands, which play various roles during the parasitism. Comparative genomics analysis tools from the sequenced plant-parasitic nematode genomes helped to identify gene candidates for playing a role in the compatible and incompatible parasitic interaction. Additionally, it confirmed information obtained from EST sequencing and increased our understanding regarding the extent of Horizontal Gene Transfer as a source of novelty during the evolution of parasitism (reviewed in Chapter 10). The advances in the study of nematode effectors such as the *CLE*-like and the *CEP* peptides and their functions during the interaction are reviewed in detail in Chapters 11, 12 and 13. The induction of feeding sites by nematode secretions constitutes one of the most remarkable examples of cell morphogenesis directed by pathogen effectors in plants. Besides, one of the effective strategies of these nematodes to alter the plant responses for their benefit is a battery of molecular effectors that potentially suppress or decrease plant defenses during migration and establishment.

Nowadays, nematode control strategies in agriculture include chemicals (nematicides and fumigants), biological control with nematode antagonists, physical methods such as solarisation and fallowing, cultural methods as crop rotation, as well as the use of resistant plants. The use of chemicals is gradually vanishing due to their environmental risks and toxicity, as effective pesticides against these complex eukaryotes will mostly be potentially harmful to other organisms. Biological control has resulted in a low efficiency unless applied in combination with other techniques. Crop rotation with non-host species or resistant cultivars has provided locally good results, and the use of resistant cultivars combined with classical inbreed programs is probably the most extended economically viable and less contaminant control system. However, the increasing isolation of virulent nematode populations to those resistant plants seriously question their durability, and scientists have now the responsibility to lay a creative ground to developing new tools for nematode control. In this context, nematode control strategies

based on biotechnology are called to play an increasingly important role on sustainable crop production (discussed in Chapter 14).

There are still many challenges in understanding the complexity of these interactions. For instance, most research concentrates in examining feeding sites at a few selected times after infection, but feeding site cell status is continuously changing as it differentiates, possibly controlled by nematode nutritional needs. Therefore, inferred conclusions from the analysis of nematode-induced feeding sites at a few selected infection points should be taken cautiously. Holistic functional approaches on the nematode and the plant sides, combined with genetics and cell biology techniques, are generating vast lists of differentially expressed genes as candidates to play roles in the compatible interactions of sedentary endoparasitic nematodes with their hosts. The understanding of the mechanisms subjacent to root penetration and feeding site differentiation and maintenance, as well as a deeper knowledge of the nematodes modes of parasitism, is providing a variety of tools for the design of new control methods of these devastating agricultural pests. The further development of meaningful mega data analyses will contribute to integrated systemic views of the different events in this complex process.

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