

BURLEIGH DODDS SERIES IN AGRICULTURAL SCIENCE

# Achieving sustainable cultivation of tomatoes

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# Preface

Tomato is the second largest horticultural crop after potato, a worldwide industry valued at over \$50 billion. In addition to being a cash crop for farmers, tomato fruit is a significant dietary source of micronutrients, vitamins and antioxidants in maintaining and enhancing human health. It is important to consumers both as a product bought fresh and as a raw material in many processed foods.

As a horticultural crop, production cost per acre is high and profitable production is dependent on a large number of factors. In addition to the right cultivation methods, high-yielding tomato crops also require consistent pre- and post-harvest pest control, as well as appropriate post-harvest handling and effective storage. In the past few decades there has also been an increased emphasis on greenhouse production, greater sustainability and organic production.

High tomato yields also depend greatly on the development of improved cultivars with desirable fruit quality attributes and other agronomic traits such as water and nutrient use efficiency and the ability to cope with biotic and abiotic stresses. The emphasis on a stronger scientific foundation for adding desirable traits for crop production and tolerance to extreme environments has merged plant physiology and molecular breeding disciplines. The need of consumers for healthier products with potential nutraceutical properties has also encouraged improved breeding techniques and genetic engineering strategies including genome editing to further improve fruit quality attributes.

The need for a comprehensive treatise reviewing these important trends in research, with contributions by distinguished experts in their fields, is met by this book with chapters dealing with cultivation techniques in the field and in the greenhouse, together with molecular breeding and genetic engineering technologies for improving nutritional quality, flavour and shelf life, as well as weed and pest management including managing insects, viruses and other pathogens. Of particular importance is the emphasis on the sustainability of tomato productions in various parts of the world.

Part 1 has four chapters dedicated to cultivation practices including crop growth and yield modelling, good agricultural practices in tomato production, management of water and nutrient use efficiency, and sustainable and greenhouse tomato production. Part 2 has eight chapters discussing advances in understanding tomato plant physiology, maintaining tomato genetic diversity, responses to biotic and abiotic stresses, conventional tomato breeding, marker-assisted breeding, genetic engineering using molecular tools, improving flavour and desirability, and enhancing fruit shelf life. Part 3 has six chapters that focus on disease, pest and weeds during tomato cultivation and production, in particular, insect-transmitted diseases, the genetic basis of resistance to viruses, insect pests and integrated pest management, advances in developing pathogen-resistant tomato varieties, advances in insect resistance and integrated weed management during tomato cultivation.

The world today faces major challenges that include global climate change and the projected increase in human population to 10 billion by 2050. We are already witnessing serious pressures on water and other natural resources, particularly in developing countries. In some countries, there are already instances of using unclean water, even sewage water, for tomato production and post-harvest operations, seriously contributing to human health problems. To overcome these challenges in crop production, including tomato cultivation, there is more and more need for sustainable agricultural practices to achieve both higher

yields and safe, high-quality foods. The chapters in this book are designed to help achieve this goal. We sincerely thank all the authors for their outstanding contributions and the staff at BDS Publishing for diligently working with us to bring forth this volume in a timely manner. This book on tomato should prove an important reference source for researchers, students, growers and practitioners of sustainable agriculture.

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# Introduction

Tomato (*Solanum lycopersicum* L.) is the world's second largest horticultural crop after potato, with production valued at over \$50 billion. In the last twenty years, production has doubled to over 160 million metric tons. In addition to being a cash crop for farmers, tomato fruit is a significant dietary source of micronutrients, vitamins and antioxidants in maintaining and enhancing human health. It is important to consumers both as a product bought fresh and as a raw material in many processed foods.

As stated in the Preface, tomato cultivation, like other crops, faces a range of challenges. There is increasing competition for water, land, labour and other resources, requiring more efficient cultivation with fewer inputs. Cultivation must mitigate its impact on the environment which contributes to climate change whilst adapting to potentially more extreme weather associated with global warming. It must also deal with continuing pressure from insect pests and diseases. Finally, higher yields must be compatible with qualities such as flavour, shelf life and nutritional value (including preserving and enhancing the important nutraceutical properties of tomatoes). *Achieving sustainable cultivation of tomatoes* summarises key research addressing these challenges. This Introduction provides a more detailed review of the topics covered in each chapter.

## Part 1 Cultivation techniques

Optimising inputs and improving yields needs benchmarks against which performance can be assessed. Crop growth simulation models have become important tools for researchers and growers in optimising production. Chapter 1 reviews existing models used for tomato cultivation, their strengths and weaknesses, before focusing on the CROPGRO-Tomato model. Through successive refinements, this model is able to simulate crop development, the effects of temperature and inputs such as nitrogen and water as well as potential yields. The authors show how the CROPGRO-Tomato model can be used by producers to manage their tomato crop in several ways: (1) predicting probable maturity date and yield, (2) optimising irrigation strategies, (3) optimising nitrogen fertiliser use and (4) predicting fruit size. It includes practical examples of the way the model has been used to optimise irrigation and fertiliser use.

Chapter 2 looks at how a better understanding of plant physiology can be used to optimise cultivation practices, focusing on the operation of leaf stomata. The opening and closing of the stomata affect a plant's photosynthesis, transpiration and respiration, which, in turn, affect plant and fruit development. The chapter reviews factors that affect stomata opening and closure such as soil water availability, light, relative air moisture and temperature. It then reviews cultivation practices such as plant spacing and pruning that support stomatal opening and thus boost yield and fruit quality. Chapter 2 can be read alongside Chapter 5. This chapter discusses how physiological mechanisms such as stomatal opening affect the way tomatoes manage water and how this understanding can then be used to develop more drought-resistant varieties.

Building on this understanding of the way plants manage resources, Chapter 3 reviews best practice in water and nutrient management. It looks at the shift in approach from optimising production to optimising input efficiency. It then discusses how to schedule

irrigation more effectively to minimise water use. The chapter goes on to review ways of optimising fertiliser use from soil sampling and testing, selection of the right kind of fertiliser, the use of cover crops, compost and manure to ways of determining appropriate nitrogen (N) rates.

Chapter 4 reviews a rapidly expanding sector in tomato production, organic greenhouse tomato cultivation. This production system endeavours to minimise system inputs and adverse environmental impacts through sustainable water and waste management, limited fossil energy use, nutrient-balanced approaches, and mechanical and biological control of pests. The chapter explores how this can be achieved through the use of appropriate types of greenhouse, cultivar and rootstock selection and seedling production; organic greenhouse production systems; fertilisation and water management; and plant protection methods.

## Part 2 Plant physiology and breeding

Since tomato is mainly cultivated under irrigated conditions, water use is of considerable significance for healthy plant growth and adequate yield. Indeed, water is the most limiting and yet essential resource needed by plants to grow and function efficiently. Chapter 5 starts by summarising what we know about genetic factors affecting the vegetative growth and flowering as well as the ways tomato plants regulate water intake to manage this growth. This chapter then looks at physiological mechanisms such as root–shoot ratios and the regulation of stomatal opening which affect water use efficiency (WUE) and drought resistance in tomato plants. It also reviews genetic variation in wild varieties such *Solanum pennellii* related to WUE and drought resistance and the genetic factors affecting desirable traits to optimise water use. Finally, it shows how this understanding can be used to breed more drought-resistant varieties.

The importance of wild varieties and genetic diversity discussed in Chapter 5 is picked up by Chapter 6. The exploitation of genetic diversity to develop crops with greater resistance to both biotic and abiotic stresses, or with enhanced phytonutrient content, is of strategic importance to combat the negative impact of climate change. Today, crop wild relatives that are threatened in the wild, and which are only partially conserved in genebanks, are being rediscovered as essential resources for crop improvement programmes. Accessibility and use of crop wild relatives for crop improvement is especially important in tomatoes, a crop where a cultivated variety contains less than 5% of the genetic diversity of its wild relative. Chapter 6 reviews current global *ex situ* conservation of tomato germplasm and the use of databases such as Genesys to search genebank collections. The chapter also deals with the policy framework for the conservation, access and benefit sharing mechanisms of plant genetic resources (PGR). It describes how the policy framework and stricter phytosanitary requirements affect the exchange and use of PGR. Ways to strengthen sharing of PGR for food and nutrition security and climate change adaptation are discussed.

Chapter 7 builds on Chapter 6 by showing how we can exploit tomato genetic resources. It also links to Chapters 2 and 5 in showing how we can make use of recent advances in understanding plant physiology. A major challenge in tomato production is to increase productivity by improving resistance and tolerance to crop stresses. Cultivar improvement depends on our ability to identify, study and leverage the genetic diversity present among tomato germplasm resources worldwide from which new resistance/tolerance traits can be selected and transferred via breeding and biotechnology. Chapter 7 summarises the

current status and advances in our understanding of tomato stress responses in tomato plants, including stress signalling and stress regulatory networks. It also discusses future trends in tomato stress biology and its potential implications for tomato improvement.

Chapter 8 reviews developments in 'conventional' breeding, which is defined as the integrated application of classic genetics principles and genomics through visual and/or molecular selection with non-GM (genetic modification) tools. Chapter 8 discusses four conventional methods: true breeding, tomato hybrids, introgression breeding and mutagenesis. True breeding occurs mainly by selecting preferred genotypes in the existing germplasm, which have arisen from recombination, natural mutations and spontaneous outcrossing with wild relatives. To deal with the narrow genetic diversity in cultivated tomato, new traits from wild germplasm can be introduced into the cultivated tomato through recurrent backcrossing. Introgression of alien genes from wild relatives has played a major role in tomato hybrid breeding, for which molecular tools have been integrated with traditional breeding methods, crossing/backcrossing and visual selection. The chapter reviews ways of dealing with the breeding barriers that arise in interspecific crosses, including unilateral incompatibility, hybrid inviability, sterility and reduced recombination, chromosomal rearrangement and inversion. It also discusses the generation of genetic variation by mutagenesis treatments which have proven to be a powerful method for the unravelling of biological processes and the alteration of agronomical traits in plant species such as tomato. Finally, it reviews recent advances in sequencing technology and gene editing techniques which promise to revolutionise plant breeding.

Chapter 8 provides a foundation for Chapter 9, which describes the process of marker development and how this can be used to improve tomato breeding. Marker-assisted selection (MAS) makes selection independent of the phenotypic expression of the traits and enables fast, precise introgression of these desired traits. The chapter reviews marker development, populations for mapping, strategies for trait association and genome-wide association studies, mapping targeted traits in tomato (such as disease resistance, abiotic stress tolerance, fruit quality and yield-quality traits) and how they support MAS techniques such as marker-assisted backcrossing (MABC) and marker-assisted recurrent selection as well as genomic selection (GS). The chapter explores the reasons for the gap that still exists between gene/ quantitative trait loci (QTL) mapping and the implementation of MAS, and problems such as the need for better characterisation of available genetic resources, and suggests how the technique can be developed further.

Chapter 10 shows how genetic dissection using fruit ripening mutants, new transgenic plants and molecular breeding has created a road map for the further unravelling of the regulation of genes governing fruit quality attributes and fundamental metabolic processes. Precision in engineering plant genomes has enabled development of novel tomatoes with marketable traits such as enhanced quality and shelf life, abiotic and biotic stress tolerance as well as for non-food applications such as production of oral vaccines.

Tomato fruit quality is a complex trait involving a number of components including appearance, flavour, aroma and texture. A few major genetic mutations have been found to have a significant effect on fruit quality (notably the *rin* mutation). Chapter 11 examines the use of QTL mapping to identify favourable sensory characteristics such as flavour, exploring current technologies and suggesting future trends for research in this area. New approaches such as genome-wide association studies or MAGIC populations using genome information are allowing a higher precision of QTL location. The chapter looks at progress in moving from MAS to GS for flavour breeding.

The shelf life of tomatoes is regulated via myriad physiological, biochemical and environmental processes, including hormonal regulation and the activity of cell wall proteins. As Chapter 12 shows, ripening is associated with marked changes in gene expression, regulating the biosynthesis of a large number of catabolic enzymes, including cell wall hydrolases implicated in fruit softening. The chapter explores the advantages and disadvantages of cultivating ripening-impaired tomato mutants and genetically engineered genotypes characterised by inhibition of the ripening process.

## Part 3 Diseases, pests and weeds

As Chapter 13 describes, many viruses transmitted by insects cause great damage to tomato crops in the field and in the greenhouse. It has been estimated that pests and diseases contribute to about 40% of tomato yield loss in the field worldwide. Management of insect-transmitted tomato viruses is a race between the emergence of new viruses coupled with the proliferation of quickly adapting vectors and strategies that include physical and chemical protection from insects and development of virus-tolerant crops. The major insect-transmitted viruses infecting tomato are described in detail in this chapter, including viruses transmitted by aphids, thrips, whitefly and leafhoppers such as tomato spotted wilt virus, tomato yellow leaf curl virus, begomoviruses and RNA viruses. The chapter explores the potential of technologies such as genetic engineering to combat insect-transmitted viruses.

As Chapter 14 shows, genetic resistance requires the identification of resistance loci, typically in wild species. The advances made in recent years in the high-throughput sequencing and re-sequencing of whole-plant genomes have made the task of gene identification much easier, enabling fast identification of genes that control resistance and the development of recombination-free precision DNA markers. These whole-plant genome technologies are also invaluable in capturing elite susceptible recipient genomes during backcross breeding programmes designed to introgress genes of interest, including disease resistance genes (GS). These technologies will cumulatively enhance the pyramiding of genes into elite commercial hybrids. The advances made in recent years in genome editing technologies such as CRISPR-Cas are expected to accelerate the breeding of cultivars resistant to diseases such as fungal blights, bacterial spots, bacterial wilts, begomovirus and diseases caused by tospoviruses.

As shown in Chapter 13, tomato production in tropical countries, in particular, is severely constrained by insect and mite pests. As an example, the onset of whitefly early in the season can lead to complete crop loss because of its ability to transmit begomoviruses whilst fruit borers are a serious problem during the reproductive phase of the crop. The use of broad-spectrum chemical pesticides can make this problem worse, as it can encourage the build-up of resistance whilst damaging the natural enemies of these pests. Understanding the bioecology of these pests is therefore essential to developing effective strategies to manage them. Chapter 15 reviews recent research on the bioecology of the major insect and mite pests affecting tomato crops, including aphids, thrips, whitefly, leaf miners, fruit borers, armyworms and spider mites. In each case, the chapter considers pest ecology and how the pest affects the tomato plant. As the chapter shows, there are several natural enemies and disease-causing pathogens attacking these pests. It is possible to exploit species-specific natural enemies and entomopathogens, and integrate them with other components of integrated pest management (IPM) such as resistant cultivars and pheromones.

Understanding the ecology of insect pests is the foundation for the development of successful IPM strategies for dealing with them. This is the subject of Chapter 16, which reviews key aspects of IPM before, during and after the growing season, from the use of high-quality pest and pathogen-free seeds and transplants and effective monitoring systems to post-harvest sanitation techniques. The chapter demonstrates the considerable progress that has been made in the development and implementation of IPM packages for tomato production including improved diagnosis, an increase in the tactics available for inclusion in packages and development of packages for different production systems. A continuing challenge will be to develop effective IPM packages for smallholder farmers in tropical and subtropical regions where overlapping crops are grown throughout the year. It is in these situations where excessive pesticide use is most common and the potential for benefits from IPM programmes are the greatest.

As noted earlier, tomato is known to be afflicted by at least 200 different disease-causing organisms from most major pathogen classes – bacteria, fungi (including Oomycota), viruses and nematodes. Despite decades of conventional breeding and selection, there are still a large number of diseases caused by these pathogen classes that make tomato production challenging in various parts of the world. Current advances in tomato genetics and genomics can be combined with conventional plant breeding methods to introgress resistance genes and expedite the breeding process. Building on Chapter 14, Chapter 17 summarises current advances in the development of disease-resistant varieties. The chapter provides a systematic review of progress in tackling particular tomato diseases caused by bacteria, fungi, viruses and nematodes, showing that, with the incorporation of MAS, the rate of improvement has been significantly enhanced, even if many challenges remain.

Weeds have long been recognised as a source of considerable economic loss in agriculture. Weeds not only cause crop yield losses due to competition for resources but may also host pests and pathogens that can be detrimental to the crop. Chapter 18 reviews best practices in integrated weed management (IWM) which combines the use of indirect (i.e. preventive measures and agronomic practices) and direct (i.e. physical, mechanical, biological and chemical methods) weed control strategies. The chapter discusses topics such as competition thresholds, cultural control techniques from stale seedbeds to crop rotations, cover crops and mulches, physical control methods such as solarisation, thermal and mechanical weeding, and the continuing role for chemical treatments.

## Summary

The chapters in *Achieving sustainable cultivation of tomatoes* highlight a number of key themes in tomato research. These include how a greater understanding of plant physiology is informing improvements in both cultivation and breeding (Chapters 2, 5 and 7). A second theme is the critical importance of wild varieties (Chapters 5–7); the ways that breeding techniques are seeking to capitalise on this rich genetic resource (Chapters 8–10) to improve traits such as flavour, shelf life, drought and disease resistance (Chapters 7, 11, 12, 14 and 17); and the continuing challenges in fully tapping this potential. At the same time, improved varieties still need good cultivation techniques as well as effective IPM and IWM strategies (Chapters 1–4, 16 and 18), which themselves need to build on a deeper understanding of pest biology and ecology (Chapters 13 and 15).

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