

BURLEIGH DODDS SERIES IN AGRICULTURAL SCIENCE

Achieving sustainable cultivation of temperate zone tree fruits and berries

Volume 1: Physiology, genetics and cultivation

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Introduction

Temperate fruits include stone/drupe fruits (such as peach), pome fruits (such as apple) and berries (such as strawberries). Like other crops, cultivation of these fruits faces a number of challenges. These include the need to optimize yields, sensory and nutritional quality; the dynamic threats from biotic and abiotic stresses in a changing climate; the increasing cost and decreasing availability of labour; and the need for more efficient use of resources to minimise environmental impact. Volume 1 of *Achieving sustainable cultivation of temperate zone tree fruits and berries* summarises the wealth of research addressing these challenges, focusing on key advances across the value chain, from breeding improved varieties to developing better techniques for cultivation and crop protection.

This volume reviews the latest research in tree fruit physiology, as well as discussing recent developments in genetics and their implications for improved breeding techniques. The volume also provides comprehensive coverage of key stages in cultivation, from nursery plants to water, nutrient and pest management.

Part 1 Physiology and genetics

The first part of the volume discusses current research on physiology and genetics. Chapter 1 is focussed on advances in understanding fruit tree root-rhizosphere relationships that enhance plant health. Host-microbe interactions in the rhizosphere influence numerous processes that determine plant productivity and health. The rhizo-microbiome influences functions ranging from protection of the plant from pathogen attack to enhanced nutrient availability and uptake. The chapter reviews the development of 'omics' technologies as a way to explore the effects of the rhizosphere microbiome on plant interactions with their environment. The chapter provides two case studies demonstrating ways to manipulate the rhizosphere microbiome to optimize crop production on orchard replant sites.

Moving from the soil to the root system, Chapter 2 discusses advances in development and utilization of rootstocks for fruit tree cultivation. In the previous century, apple rootstocks were chosen on the basis of suitability for a particular climate, required degree of vigour and plant availability, with only one or two choices available to growers in a particular location. However, with the proliferation of improved apple rootstocks, there is now a dizzying array of choices for apple growers. Advances in the development and utilization of fruit tree rootstocks are considered using apple as a case study. It starts by reviewing

the use of clonal rootstocks, followed by sections on rootstock improvement, propagation and evaluation. Rootstock effects on the scion and rootstock tolerance to both abiotic and biotic stresses are then considered. The chapter concludes with a discussion on trends in apple rootstock use. Although this chapter focuses mostly on apple, it exemplifies the various inherent rootstock properties and rootstock-induced effects on grafted scions that can be found in other temperate fruit species.

Adopting a broader focus, Chapter 3 looks at advances in understanding fruit tree growth in general. Owing to the importance of photosynthesis for the efficient functioning of plants as solar energy collectors, scientists have been intensively studying the process of photosynthesis for more than a century, with the hope of increasing its efficiency. There is substantial evidence that fruit trees distribute their nutrient resources to maximize photosynthetic competency, and adjust the angles of leaves in different parts of their canopy to optimize use of resources and sunlight as it passes through the canopy. The chapter examines the factors that influence photosynthesis in fruit trees, as well as the key principles governing the distribution and utilization of photosynthates. Finally, the chapter looks at the features of fruit tree canopy architecture which affect photosynthesis efficiency.

Chapter 4 examines advances in understanding reproductive development in fruit-bearing plants. In recent years, knowledge of the reproductive physiology of fruit trees has increased through numerous molecular and genetic studies. Beginning with an introductory overview, the chapter includes sections on the physiology and genetic analysis of reproductive meristem development, bud dormancy and flowering, sexual determination and development of flower structures. The physiology of pollination, fertilization and gametogenesis is discussed. The chapter concludes with sections on fruit development and phytohormones and, lastly, fruit maturation and ripening.

The first section of the volume concludes with Chapter 5 on advances in fruit genetics. Changing weather patterns, innovative production systems, increased pest and pathogen pressure, and fluctuating consumer preferences are forcing fruit producers to adjust at a higher pace than ever before. The chapter provides an overview of the advances in fruit genetics as they pertain to discoveries in fruit quality and disease resistance, and their application to the improvement of fruit production and sustainability. Genomic mapping, marker-assisted breeding and biotechnology are also explored, as are the genetics of fruit quality and disease resistance.

Part 2 Optimizing sustainable cultivation and quality

The second part of the volume reviews advances in temperate zone fruit cultivation from orchard design to optimizing water and nutrient management

and harvesting operations. The subject of Chapter 6 is optimizing the production of quality nursery plants for fruit tree cultivation. It is now possible to purchase specific nursery tree types that are more compatible with an intended training system, improving planting efficiency and encouraging early production. Although single axis, well-feathered scions suitable for high-density spindle training systems have dominated nursery production over the past two decades, some nurseries increasingly produce double axis scions for pear, apple, and even stone fruits, helping growers obtain uniform and early-producing fruiting walls. The chapter summarizes current knowledge of the physiology of grafting and recent innovations in fruit tree nursery techniques. New approaches to regulating nursery plant growth and development are discussed, including *in vitro* propagation, which is becoming a more powerful technique for producing rootstocks and self-rooted varieties of several fruit species. The chapter covers scion grafting and budding techniques as well as the biochemical and physiological aspects of graft incompatibility. The chapter concludes with a section on tree production in the nursery.

Chapter 7 moves to tree fruit nutrition, focussing on optimizing precision in orchard irrigation and nutrient management. Precise resource management in fruit production systems has become a key area of study over recent years, not only due to the changing climate but also due to increased demand for fruit from a growing population as part of a healthy diet. Irrigated fruit production has proven to be both reliable and more efficient than rain-fed production, and the trend is towards high efficiency irrigated systems. The chapter examines both precision management of irrigation and nutrients in orchards (mainly apple, pear, sweet cherry and peach). Precision management of irrigation is detailed, including the use of efficient irrigation systems, matching water supply to plant demand, reducing evaporation from the soil surface and responding to drought. A further section on nutrient management covers both ferti-irrigation or fertigation, in which nutrients are delivered in irrigation water, and foliar application, in which nutrients are applied directly to the fruit tree in dilute water sprays.

The subject of Chapter 8 is the optimization of plant growth, yield and fruit quality with plant bioregulators (PBRs). Both natural and synthetic plant bioregulators are used extensively in tree fruit production. They influence many processes in plants, including shoot growth, branch angle, bud break, flower bud formation, and fruit abscission, ripening, shape and finish. As a result, they can be used to optimize not only plant growth but also fruit yield and quality. The chapter starts with a classification of PBRs, followed by a detailed discussion on the application of PBRs and their use in the development and maintenance of tree structure, including the control of vegetative growth. The chapter reviews the use of PBRs in crop load management and their influence on flowering and fruit set, concluding with sections on both the preharvest application of PBRs and their use in improving fruit shape and appearance.

Moving from plant growth to fruit production, Chapter 9 examines the challenge of optimizing fruit production efficiencies via mechanization. Many technological advances in farming have been adopted over the last century, transforming various tasks. However, some processes in fruit and vegetable production such as harvesting have changed little, and crops such as for fresh market apples, cherries, peaches, blueberries and strawberries are harvested manually, an operation that is highly labour intensive, demanding a huge seasonal workforce in rural areas around the world. Starting with an introductory section on challenges faced in tree fruit harvesting, the chapter goes on to discuss harvest aid (or labour assist) machines (or platforms), which as the name suggests, are designed to assist human fruit pickers. The chapter also covers mass and robotic harvesting systems, which are designed to remove the need for manual picking, with specific examples included. The chapter also discusses fruit conveyance and handling, as well as mechanical pruning.

Chapter 10 shifts to the theme of fruit pests and the importance of optimizing pest management in fruit cultivation. Tree fruit growers in temperate regions have faced challenges in managing the complex of arthropod pests present in these systems because of increasing pesticide regulatory restrictions, public concerns about food safety and environmental quality, and resistance to older pesticides by key pests. Growers are attempting to adopt newer tactics such as reduced-risk (more selective) pesticides and increased reliance on sampling and monitoring techniques plus pheromone-based mating disruption, but these are more expensive and require more time and precise use patterns. In addition, most previous integrated pest management protocols were designed for control programs based on the use of older conventional pesticides. As this chapter shows, a more current and practical approach stresses a basic understanding of pest biology and development, which can be used in predictive models to support the effective use of more selective crop protectants and other sustainable tactics, such as mating disruption and biological control.

Chapter 11 shifts the focus from pest to disease management in fruit cultivation, and discusses optimizing plant protection from diseases. Sustainable management of plant diseases is a perennial challenge for pome, stone, and berry fruit producers in humid regions throughout the world. Delayed orchard profitability, decreased orchard longevity, reduction in fruit quality, and unsalable fruit caused by fungal and bacterial diseases result in devastating economic losses annually. Globally, tree fruit growers are increasingly relying on an integrated management approach through the incorporation of predictive pathogen life-cycle modeling and biological, chemical, and cultural control methods to mitigate disease-associated losses. The chapter provides an introduction to general tree fruit production management paradigms, followed by a discussion of the main pre-harvest fungal and bacterial diseases, methods

of integrated disease management, and advances in technology for pathogen detection and disease management.

The challenges of prolonging the life of harvested fruit are reviewed in Chapter 12, including pre- and post-harvest strategies to optimize fruit quality and shelf-life. The adoption of new, non-destructive quality assessment technologies is important for quantifying, evaluating, and managing fruit quality in postharvest systems. The chapter examines the challenge of managing biological variance to improve the success of postharvest technologies, and describes ways of measuring harvest maturity and improving sorting operations, as well as postharvest technologies and temperature control. The chapter includes a detailed case study of post-harvest strategies in cherry cultivation in British Columbia.

The volume's final chapter, Chapter 13, addresses research on bioactive/nutraceutical compounds in fruit that optimize human health benefits. In the past decade, numerous reports demonstrate that high consumption of fruits and vegetables is beneficial for health, being associated with a reduced risk of degenerative diseases. The chapter provides a brief description of the chemistry of bioactive compounds (BCs), including polyphenols, carotenoids, and Vitamin C, their presence in temperate fruits, production practices that influence BC synthesis, and discusses recent advances in strategies toward improving sustainable crop production for nutraceuticals.

Chapter 1

Advances in understanding tree fruit-rhizosphere microbiome relationships for enhanced plant health

Mark Mazzola and Shashika S. Hewavitharana, USDA-ARS, USA

- 1 Introduction
- 2 Contribution of the microbiome in directing plant responses to their environment
- 3 Case studies: manipulation of the rhizosphere microbiome to optimize crop production on orchard replant sites
- 4 Conclusion
- 5 Future trends
- 6 Where to look for further information
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1 Introduction

The plant microbiome influences a spectrum of outcomes in terms of plant growth, development, resilience to abiotic stress and overall health and productivity. Contribution of the microbiome in directing plant responses to its environment and the instrumental role of host species or genotype in determining functional composition of the microbiome have been established (Berendsen et al., 2012; Mendes et al., 2013). The rhizosphere microbiome, in particular, may regulate important physiological and developmental processes that will directly determine plant productivity, some of which may be described as unanticipated. For instance, Panke-Buisse et al. (2015) demonstrated that the rhizosphere microbiome can modulate flowering time of a plant host and that flowering phenotype can be altered through manipulation of the rhizosphere microbiome. The rhizosphere microbiome clearly influences other qualities such as plant nutrient status through various processes such as nitrogen fixation, phosphorous acquisition via mycorrhizal fungi (Gianinazzi et al., 2010) and uptake of trace elements (Lemanceau et al., 2009).

There exists expansive study of the rhizosphere microbiome as it relates to plant health and soil-borne disease suppression. The microbial community

inhabiting the rhizosphere can serve as a first line of plant defense against deleterious organisms, including plant pathogens, that inhabit the soil system. Historically, exploitation of microbial resources to address yield-limiting aspects of a crop production system has relied upon the introduction of specific microbes possessing a known functional trait (Raaijmakers and Mazzola, 2016). Interest in understanding how the indigenous soil microbiome can be managed to the benefit of plant production systems is of rather recent occurrence (Mazzola and Freilich, 2017). However, although there exists abundant information regarding a limited number of taxonomic groups that function in the rhizosphere to limit disease development, a vast portion of this microbial resource remains to be defined. There exists a need to not only identify composition of the microbiome in the rhizosphere environment, but also establish the role these microbes may have as determinants of plant health.

Various tactics may be implemented that strategically amplify functional components of the soil microbiome with the goal of subsequent crop plant rhizosphere colonization. Such strategies commonly involve the application of specific soil inputs that select for microbial consortia or traits that act to suppress soil-borne plant pathogens (Mazzola et al., 2015; Inderbitzin et al., 2017). Alternatively, management practices such as altering plant spatial patterns in an orchard system (Rumberger et al., 2007) or maintenance of a living tree row understory (Wardle et al., 2001; Hoagland et al., 2008) have been employed to expose the plant to a soil microbiome that will either directly improve plant production or minimize potential exposure to pathogenic microorganisms. Successful use of this approach will clearly rely upon intimate knowledge of microbial groups regulating the desired plant response and a highly directed protocol that amplifies the targeted functional group.

Significant interest also resides in potential to use the crop plant itself as a means to recruit a rhizosphere microbiome that will optimize crop performance. Composition of the rhizosphere microbial community may differ in a plant genotype-dependent manner (Micallef et al., 2009), and this selection may operate to the level of determining genotype of a functional microbial attribute. For instance, wheat (*Triticum aestivum*) cultivar influenced both the density and genotype of the 2,4-diacetylphloroglucinol (2,4-DAPG)-producing fluorescent *Pseudomonas* spp. population detected in the rhizosphere (Mazzola et al., 2004). Production of 2,4-DAPG by fluorescent pseudomonads contributes to the biological disease control potential of these bacteria towards a diversity of plant pathogens (Weller et al., 2007). Drivers determining plant recruitment of the rhizosphere microbiome are likely multifaceted including root architecture, metabolic composition of root exudates (Micallef et al., 2009) and multitrophic interactions that occur in this habitat. Composition of the apple (*Malus domestica*) rhizosphere microbiome also was shown to differ in a rootstock genotype-dependent manner (Reed and Mazzola, 2015). An understanding

of the factors that influence differential composition of the apple rhizosphere microbiome and its effect on tree health could be utilized to develop improved rootstocks with enhanced capacity to withstand biotic and abiotic stresses.

2 Contribution of the microbiome in directing plant responses to their environment

2.1 Role of host species or genotype in determining rhizosphere microbiome functional composition

Plant fitness and crop productivity are a function of the plant as such and its attendant microbiota, which in total comprise the plant holobiont (Vandenkoornhuysen et al., 2015). All plant tissues act as host to microbial communities and support distinct consortia that interact to optimize plant function. For instance, the rhizosphere, phyllosphere and endosphere provide unique ecological niches to host different microbial communities that are adapted to environmental and nutritional conditions available. As these microbiomes are highly dependent on the plant genome, they form a second genome or pan-genome (Turner et al., 2013).

The most adjacent layer of soil influenced by plant roots via processes such as rhizodeposition of exudates, mucilage and sloughed cells is defined as the rhizosphere. The plant root may release 5–20% of plant photosynthate into the rhizosphere (Marschner, 1995) with the elevated substrate availability promoting increases in microbial biomass and activity. Interaction between the rhizosphere microbiome and different factors of the host plant is bidirectional. Root exudates are composed of chemically and functionally diverse compounds including organic acids, sugars, amino acids, fatty acids, vitamins, growth factors, hormones and antimicrobials (Bertin et al., 2003). Plant species, cultivars (Mark et al., 2005), age and developmental stage (Micallef et al., 2009) are all determinants of root exudate composition. Root exudates initiate and may modify the interaction between roots and soil microorganisms, and certain metabolites are known to function as signals to prompt symbiotic or pathogenic relationships (Bais et al., 2006; Bertin et al., 2003). The comprehensive root/rhizosphere metabolite profile (metabolome) will also be influenced by the microbiome through microbial transformations or altered exudation patterns. The observation of differential phenolic compound profiles between roots cultivated in field soil and roots cultivated in pasteurized soil indicated a role for the microbiome in altering the metabolic profile from apple roots (Emmett et al., 2014).

Tree fruit root exudates may function to directly promote or limit colonization of the rhizosphere and plant roots. Genotype-specific phenolic concentrations were detected in fine distal roots of apple (Emmett et al., 2014), and a number of compounds were associated with higher or lower root colonization by plant

pathogenic fungi and oomycetes. A recent study employed an untargeted metabolomics approach to assess the potential role of apple rootstock genotype-dependent exudates contributing to apple replant disease field tolerance (Leisso et al., 2017). Findings of the study revealed that the four rootstock genotypes assayed (G.935, G.41, M.9Nic29 and M.26) differed significantly based on the water-soluble phenolic rhizodeposits collected from water percolated through rhizosphere planted in pasteurized quartz sand. The G.935 rootstock, which demonstrates higher field tolerance to soil-borne plant pathogens, generated higher levels of benzoic acid in root exudates. Abundance of this metabolite in the tolerant genotype was linked to a higher population of *Burkholderia* spp. relative to susceptible genotypes. Members of this bacterial genus are known for elevated abundance in the rhizosphere of tolerant apple rootstock genotypes and providing biological control against soil-borne plant pathogens (Mazzola et al., 2015; St Laurent et al., 2010). The preference of *Burkholderia* spp. towards benzoic acid as a substrate (Pumphrey and Madsen, 2008) supports the hypothesis of genotype-specific selection of the rhizosphere microbiome. Malic acid is a significant metabolite in apple root exudates and was shown to selectively signal and recruit the plant beneficial rhizobacterium *Bacillus subtilis* FB17 to the rhizosphere of *Arabidopsis thaliana* in a dose-dependent manner (Rudrappa et al., 2008). It could be speculated that differential metabolite production by tree fruit rootstocks may be exploited to selectively recruit or support specific microbial consortia to limit the activity of plant root pathogens.

2.2 Rhizosphere microbiome influence on nutrient acquisition and growth promotion

The capacity of any genotype to acquire essential nutrients from the soil relies essentially on two factors: (1) nutrient interception, which is dependent on root size and architecture and (2) the acquisition process as affected by efficient uptake of available nutrients and retention or loss of plant nutrients through various microbial transformations (Hinsinger et al., 2005; Ismail et al., 2007; Lambers et al., 2006). Several root-structure-related traits may also offer possibilities for improving nutrient acquisition. These include enhancing density or length of root hairs (Gahoonia and Nielsen, 2004), adjusting root to shoot ratio to balance acquisition of limiting nutrients and modifying root architecture to preferentially concentrate root biomass in soil strata containing the maximum amount of a limiting nutrient (Rubio et al., 2003). These plant attributes may be directed or modified by the associated rhizosphere microbiome. For instance, application of certain nitric-oxide-producing *Streptomyces* spp. recovered from orchard soils induced apple seedling lateral root development (Mazzola, unpublished data). Differential abundance in the microbiota functional in

nitrogen transformations will yield varied levels of availability; in this regard, it is of interest to note that abundance of the denitrifying bacterium *Steroidobacter denitrificans* was significantly higher in the rhizosphere of apple rootstock M.26 than G.210 (Reed and Mazzola, 2015). Abundance of 16S rDNA sequences of the N-fixing free-living bacterium *Azospirillum brasilense* was 54% higher in the rhizosphere of M.9 than G.11 (Mazzola et al., 2015). Thus, it is plausible that N acquisition efficiency may involve complex interactions between soil/rhizosphere microorganisms and apple rootstock genotype.

The community of mycorrhiza that colonize a plant has been studied for decades, but the diversity of fungi that form the relationship with a given plant species has only been recognized more recently (Vandenkoornhuysen et al., 2002). Of great importance is knowledge that the capacity of tree fruit roots to form functional mycorrhizal relationships differs with the fungal species or isolate. Infection of apple and effective transport of phosphorous from soil to plant was shown to diverge widely among *Glomus* spp., with some species exhibiting a complete inability to do so (Covey et al., 1981). Similarly, Forge et al. (2001) demonstrated that enhanced apple seedling or rootstock biomass in response to colonization by *Glomus* spp. occurred in a species-specific manner. In addition, apple genotype appears to influence the extent of mycorrhizal colonization. When the microbiome of two apple rootstocks cultivated in a single orchard soil was assessed, notable differences in fungal attributes were observed, including the fact that the glomeromycota comprised less than 1% of the fungal ITS sequences detected in the M.26 rhizosphere, but represented as great as 2–8% of the sequences detected in the G.210 rhizosphere (Reed and Mazzola, 2015).

Modification of the rhizosphere microbiome through targeted introduction of microbial inoculants has long been examined as a means to enhance crop productivity, including tree fruits. Response of tree growth and yield of apple by selected plant-growth-promoting rhizobacteria (PGPR) applied as root inoculants was assessed using two rootstocks (M.9 and MM.106) and two scion cultivars (Granny Smith and Stark Spur Golden) (Aslantas et al., 2007). The PGPR strains utilized exhibited indoleacetic acid (IAA) and cytokinin production as well as phosphate solubilization ability. Among those studied, the isolate BA-8 (*Pseudomonas* sp.) demonstrated the greatest capacity to enhance shoot proliferation. However, all PGPR strains examined in the study increased fruit yield in a manner dependent on rootstock, scion cultivar and PGPR strain. In a field trial, all four bacterial strains independently increased tree fruit yields; however, trees treated with *Pseudomonas* BA-8 produced yields significantly greater than all other treatments. The higher fruit yields in response to BA-8 were associated with significantly higher quantities of IAA and cytokinin produced *in vitro* by this strain (Aslantas et al., 2007), suggesting the possible contribution of exogenous hormone production to the observed growth response.

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