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Achieving sustainable cultivation of vegetables

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Introduction

Sustainability involves meeting current needs without compromising the ability to meet future requirements. Like other crops, vegetable cultivation faces a number of challenges in ensuring sustainability. These challenges include the need to improve yields and quality to meet rising demand and higher consumer expectations, the need to reduce the ongoing threats from biotic and abiotic stresses linked, in part, to climate change, and the need to use resources more efficiently to minimise environmental impact. Focusing on temperate cultivation, this collection seeks to summarise the wealth of research addressing these challenges, from breeding improved varieties to better techniques for cultivation and crop protection. The book concludes with case studies of developments in breeding and cultivation techniques for selected vegetable crops.

Part 1 Physiology and breeding

Chapter 1 reviews recent advances in understanding vegetable root physiology. Root systems are responsible for the uptake of water and nutrients needed to support crop growth and development, ameliorate the effects of other stressors, and increase vegetable production. Roots are crucial for maintaining plant water status and meeting shoot transpirational demands as the leaves assimilate carbon. This chapter focuses on the potential of root traits to support increases in yield, maximize the effective use of resources and provide abiotic stress tolerance in vegetable crops. The chapter discusses root traits and molecular indicators regarding water and nutrient uptake, root-microbe interactions, reaction to abiotic stress and ways root function can be optimised.

Plants can either suffer from biotic or from abiotic stress arising from a deficit in the physical or chemical environment of the plant. The damage imposed by abiotic stress may limit crop production by more than 70%. Building on themes in Chapter 1, Chapter 2 outlines the different types of abiotic stress, including flood, drought, heat, cold, nutrient deficiency, excess of salt, metalloids or toxic metals, and excess or insufficient light. The chapter then focuses on how water deficit, temperature, and salinity interfere with all kinds of physiological aspects of plant life. The chapter describes advances in horticultural practices to cope with abiotic stress. These techniques include vegetable grafting, mulching, and the application of biostimulants and chemical or physical eustressors.

Objectives in breeding for quality and yield in vegetable crops are determined primarily by consumer preferences and expectations. Measures of quality are complex and include taste and flavor, nutritional value, appearance, and shelf life. Chapter 3 explores new techniques in vegetable breeding, offering an overview of the breeding process and examining the process of streamlining breeding with gene discovery. The chapter looks at expediting selections to shorten breeding cycles and circumventing introgression with genome editing and engineering, offering two detailed case studies based on tomatoes and *Brassica oleracea* vegetables.

Part 2 Cultivation

Water for agricultural use accounts for a very high percentage of worldwide water consumption. In order to maximize productivity and profitability, while reducing the environmental impact of vegetable farming, growers must choose the correct irrigation system for their crop as well as determine the best methods for managing and scheduling irrigation. Chapter 4 considers recent advances in irrigation techniques used in vegetable cultivation. It is divided into three main sections: irrigation systems, irrigation system performance, and irrigation scheduling. The coverage of irrigation systems includes: sprinkler irrigation, drip irrigation, surface flood/furrow irrigation, and subirrigation (including seepage irrigation, irrigation drain tiles and subsurface drip irrigation). Irrigation system performance is then discussed in relation to efficiency, uniformity, and water use efficiency. The section on irrigation scheduling includes techniques such as: the irrigate anytime system, 'Feel and Appearance' irrigation, systematic irrigation, the crop water demand method, the soil water status method, and ways these methods can be combined to minimize waste of water resources.

Sustainability of our food systems depends on the maintenance of healthy soils. The links between soil quality, long-term soil productivity, and environmental quality are now widely acknowledged, as is the importance of conserving soil as a resource for future generations. Determining and predicting key management practices associated with enhanced soil and plant health remains an important goal of sustainable agriculture. Chapter 5 reviews the range of indicators, metrics, and assessment tools that are utilized to define and measure soil health. It also reviews the literature on the links between soil and plant health in the context of vegetable crop production. Sections are included on the importance of soil quality and health in vegetable cropping systems, and the attributes, indicators, and assessments of healthy soil. The chapter also includes a case study on conservation tillage in bell pepper (*Capsicum annuum*) production systems.

Research conducted during recent years (e.g. structure design, covering, climate control, energy use efficiency, water and nutrient management, supplemental lighting, new cultivars) has revolutionized greenhouse vegetable production. Chapter 6 reviews the current status of and recent advances in protected vegetable production around the world. Types of greenhouses and protected structures currently in use are discussed, and the effect of greenhouse location, and selection of the greenhouse covering material and how this impacts plant productivity are also reviewed. Both heating/cooling requirements and climate management (light, carbon dioxide, humidity, etc.) are also covered. The use of both soil and soilless growing systems are assessed as are the impacts of cultivar and rootstock selection on protected vegetable production. The chapter concludes with sections on the use of fertilizers, water management and plant protection within protected systems. A review of the environmental impact of greenhouse and protected vegetable production is also included.

Chapter 6 is complemented by Chapter 7 soilless/hydroponic cultivation of vegetables. In hydroponics, the plants are grown outside the natural soil, either on porous growing media (substrates) or in pure nutrient solution (water culture). The most commonly used growing media, which are characterized by a balanced availability of water and oxygen, are rockwool, perlite, pumice, and coir dust. Furthermore, water culture systems without any solid media, such as floating, NFT, and aeroponics are mainly used for leafy vegetables. This chapter describes the advantages and disadvantages of hydroponics, along with the equipment and substrates used. The chapter examines soilless/hydroponic growing systems for vegetables, including crop nutrition and nutrient solutions, product quality in hydroponics, and the specifics of soilless cultivation of greenhouse vegetable crops. The chapter offers guidance on irrigation and plant protection practices in soilless cultivation. Finally, the chapter looks ahead to future trends in this area.

Organic farming is considered an agroecological system focused on promoting biological cycles, soil biological activity, and biodiversity towards enhancing resource conservation and environmental quality. The global growth of the organic market and production drives the research to improve organic cropping systems. Chapter 8 discusses practices and challenges in organic vegetable production with a focus on nutrient and soilborne pest management. The chapter reviews research on organic amendments (manure and compost), cover crops, crop rotation, soil solarization, biosolarization, organic fertilizers, and plant biostimulants. Specific sections are provided on soilborne pest management and application of anaerobic soil disinfestation, and the use of grafted plants in organic vegetable production. The chapter concludes with a section on no-tillage vegetable production. An interdisciplinary, holistic approach is stressed by the authors in developing and advancing organic systems to enhance nutrient availability and use efficiency as well as plant and soil health in vegetable production.

Part 3 Pests and pathogens

In-depth background knowledge on detecting and identifying plant diseases is essential for helping to raise healthy crops. Chapter 9 provides an overview of developments in understanding and monitoring plant diseases, including the use of electronic microscopes, Koch's postulates on proof of pathogenicity, the development of enzyme-linked immunosorbent assay (ELISA), and the use of nucleic acid-based tools for detection of plant pathogens. The chapter then considers advances in understanding the epidemiology of plant diseases and disease diagnosis in plants. Finally, the chapter looks ahead to future research trends in this area.

Vegetable crops are threatened by a range of insect pests. Chapter 10 provides a fascinating case study of how an understanding of pest biology can be used to develop more effective integrated pest management (IPM) techniques. Sweetpotato is one of the world's most important vegetables, and has added value as an organic, health food and as a biofuel alternative source of energy. The sweetpotato weevil (SPW) *Cylas formicarius* (Coleoptera: Brentidae, Gyladinae), which originated in South Asia, has now become the major pest of this crop and has proved very difficult to control. The chapter summarises what we know about the biology of SPW and how this has led to tactics for monitoring, controlling and managing this pest, using a mix of cultural, biological and chemical methods of control.

Chapter 10 is complemented by Chapter 11 which reviews examples of the successful deployment of IPM techniques in vegetable cultivation, with a focus on treatment of diseases in tomato such as tomato spotted wilt. The chapter reviews innovative techniques such as the use of reflective films to disrupt pest behavior, the use of acibenzolar-S-methyl (ASM) to induce systemic acquired resistance (SAR) to manage diseases in tomato, as well as the use of the use of soil fumigants such as methyl bromide. The chapter includes a detailed case study of IPM in fresh-market tomatoes.

Over the last decade, fresh fruit and vegetables have been linked to a number of major outbreaks of foodborne illness in North America and Europe. It is becoming clear that sanitation alone will not alleviate the problem of human pathogens in produce, and a systems approach is needed to design comprehensive strategies for ensuring produce safety farm-to-fork. Chapter 12 focuses on the impact of vegetable production practices on microbiological safety of produce. The chapter surveys potential sources of human pathogens in the vegetable production environment, from wild and domestic animals to soil amendments and irrigation water. The chapter then investigates the impact of soil properties, environmental factors, vegetable production and handling practices on microbiological quality of the product. Lastly, the chapter briefly surveys current approaches for controlling human pathogens on fruits and vegetables, using plant breeding, disinfectants and biological controls.

Part 4 Case studies

Chapters in Part 4 review advances in breeding and cultivation of key vegetable crops. The carrot (*Daucus carota*) is an important temperate root crop. Chapter 13 begins by discussing what we know about the origin of this species, before going on to describe the main types of cultivars. The large number of wild relatives of carrot are also discussed. Sections are included on breeding of carrots for both crop performance (covering factors such as yield, resistance to pests and disease and organic production), and for product quality and diversification (variety in colour, nutritional and sensory traits), the latter becoming of growing importance. The main methods and techniques for carrot breeding are discussed, as are the development of new technologies such as sequencing the carrot genome and transcriptome, genome editing and high-throughput phenotyping. A case study on the impact of hybrid carrots is also included, and the chapter concludes with a look to future trends in breeding research.

Complementing Chapter 13, Chapter 14 reviews developments in carrot cultivation including optimizing root shape, use of strip-till systems, improving fertilizer use (including the use of mycorrhizal fungi), irrigation and harvesting techniques. The chapter also discusses advances in crop protection, including management of weeds, insect pests such as the carrot root fly, carrot weevil and aster leafhopper. The chapter surveys advances in dealing with foliar diseases such as leaf blight and root diseases such as Sclerotinia white rot. The authors conclude by reviewing developments in organic carrot cultivation.

As Chapter 15 points out, lettuce faces many challenges from insect pests and diseases which are key targets in breeding improved varieties. Abiotic stressors, such as low calcium in the soil, also significantly affect the crop. This chapter explores advances in understanding lettuce genetics which has provided insights on several important traits related to both biotic and abiotic stressors. The chapter discusses breeding priorities for biotic stressors in lettuce (foliar, soil-borne and other diseases), and also on important insect pests in lettuce. The abiotic stressors of heat, drought, salinity and tipburn in lettuce are also covered. The chapter concludes with sections on other important traits for the improvement of lettuce, and developments in lettuce breeding techniques.

Building on the previous chapter, Chapter 16 highlights the need for modern lettuce production systems to produce a high-quality product cost-effectively whilst minimizing environmental impact. This chapter looks at recent advances in lettuce cultivation. Sections are provided on crop nutrition, irrigation and crop protection. Pesticide application, host plant resistance and other methods of control are also discussed in relation to the management of weeds, pests and diseases. The chapter concludes with an exploration of novel production systems for lettuce, including hydroponic production systems, precision farming and automation.

As Chapter 17 shows, the breeding of cucumber (*Cucumis sativus*) has evolved from open pollinated populations, to inbred lines, to gynoecious hybrids. Speed breeding, marker assisted selection and more efficient field testing have also led to advances with this crop. Production of inbred lines using doubled haploids has further decreased the time required to develop cultivars. Breeding of watermelon (*Citrullus lanatus*) has likewise become more complex. Early cultivars were open pollinated populations selected for useful traits. Later, cultivars were developed by self-pollination of selections from populations. The chapter looks at advances in the breeding of both cucumber and watermelon. It first considers cucumber and such technologies such as speed breeding. Traditional transformation, tissue regeneration and clustered regularly interspaced short palindromic repeats (CRISPR) systems are discussed for both crops. Parthenocarpy in both cucurbits is also reviewed.

Cultural production practices for cucurbit crops have changed over time to become more sustainable with less detrimental impacts on the soil and surrounding environment. Conservation tillage is one of these practices that is gaining acceptance since it conserves soil and water by reducing their loss relative to conventional tillage practices. Chapter 18 reviews advances in conservation tillage practices for cucurbits and cover crop use in cucurbits. The chapter assesses the use of cover crop residues as mulches in conservation tillage systems and fertility management in cucurbit conservation tillage systems. The chapter then moves on to examine cucurbit disease reduction in conservation tillage and cucurbit crops for conservation tillage production systems.

Plasticulture with microirrigation enhances vegetable crop competitiveness in two ways: through sustainable production practices for water and nutrient management and increased production system resiliency to climate variability. Chapter 19 introduces sustainable cultivation of cabbage on plasticulture. The chapter examines plant population studies, the importance of planting dates and irrigation scheduling strategies for cabbage grown using plastic mulch. The chapter addresses nitrogen management, explores the economic benefits of plasticulture, and outlines best management practices.

The final chapter in the book, Chapter 20, reviews advances in pea breeding. Cultivated forms of pea can be classified as dry or field pea (dry seeds for food or feed), vegetable or green pea (young seeds, pods or shoots for food), and forage pea (for silage or grazing). Quality requirements differ for each pea type. Chapter 20 reviews advances in pea breeding, including the importance of genetic resources and diversity to pea breeding. The chapter examines the purposes of breeding, including improved/stable yield, improved quality, and resistance to biotic and abiotic stresses. Finally, the chapter looks ahead to future research trends in this area.

Chapter 1

Advances in understanding vegetable physiology: root systems as the next frontier in improving sustainable vegetable production

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1 Introduction

> 'A complete, scientific understanding of the soils-crops relations cannot be attained until the mechanism by which the soil and plant are brought into favorable relationships, i.e., the root system, is also understood.' (Weaver and Bruner, 1927)

Root systems are responsible for meeting the plant water and nutrient demands, and access to those resources positively correlates with increases in agricultural productivity. Roots are also crucial for decreasing plant abiotic stress, for instance by maintaining plant water status as the leaves assimilate carbon (C) and improving crop performance and yields. Yet, roots receive little attention compared to aboveground crop improvement and management such as canopy size, flowering time and fruit set. Our understanding of root systems has changed relatively little for almost a century since Weaver and

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Bruner (1927) stated its importance. To support higher yields, increased fertilizer inputs and application rates have allowed roots to increase their access to and uptake of nutrients. This strategy has shifted around the world as different agricultural regions aim to maximize their productivity (Lu and Tian, 2017). Since the 1960s, nitrogen (N) and phosphorus (P) application rates have increased by eight- and threefold worldwide, respectively (Lu and Tian, 2017), and yields have more than doubled for several crops in the same time frame (e.g. wheat and processing tomatoes) (Tilman et al., 2002; USDA, 2018). Water consumption follows a similar trend, and usually vegetable crops that receive larger irrigation amounts have higher yields and quality (de Pascale et al., 2011; Leskovar et al., 2014). Vegetable crop production can be a high-input system, partly stimulated by premium prices and the higher revenue the industry receives per unit of crop area (de Pascale et al., 2011; Potopová et al., 2017). The increasing demand for vegetables and current pressure to increase total crop production based on the estimated global population growth can result in a further increase of agronomic inputs to maximize yields (Bishopp and Lynch, 2015; Leskovar et al., 2014; Tilman et al., 2002). In addition, continuous use of degraded soils or incorporation of less productive areas to agriculture may also result in higher input rates in systems where plant resource use efficiency is expected to be lower. It has been well documented that excess nutrients and water not taken up by crops are reasons for environmental degradation (Tilman et al., 2002). The environmental costs, loss of ecosystem services and the occurrence of more extreme and unpredictable weather are driving the scientific and agricultural communities to improve, in addition to productivity, the effective use of resources and reliance on novel techniques to achieve a more sustainable vegetable production system (Bishopp and Lynch, 2015). Since root systems are responsible for capturing nutrients and water, it is imperative to further our understanding, breeding, selection and management of root traits to increase productivity whilst minimizing the impact on the environment.

2 Roots and the effective use of resources

The term resource use efficiency has been embraced by many scientists and producers because it aims to maximize yields per unit of resource applied (e.g. water and nutrients); yet, the caveat with a 'more crop per drop' (or per N) motto is that two contrasting plant strategies can maximize resource use efficiency. One strategy aims for plant survival with a very conservative resource use and low biomass production, and the second one maximizes biomass production by an effective resource capture and ultimately the utilization by the plant. Among researchers, there is no clear separation between both strategies when working towards crop improvement and sustainable management, but in general terms, we should identify traits or technologies that favour water and nutrient uptake and biomass accumulation, even under stress conditions. For instance, Blum (2009) argued that instead of targeting increases in the commonly (mis)used water-use efficiency (WUE; yield per total evapotranspiration) indicator, efforts should be placed on the effective use of water (EUW). The argument is that C assimilation and growth are positively correlated with plant transpiration, and instead of selecting a genotype with low stomatal conductance and conservative consumption of water, the selected genotype should be able to meet the transpirational demands under limited water supply. This implies a root system capable of taking up water from deeper places in the soil profile or a better capacity for uptake at lower soil water potentials. This seems to have happened inadvertently in California processing tomatoes from decades of breeding for higher yields. Modern tomato cultivars tend to have higher stomatal conductance (g_s) and lower intrinsic WUE (WUE_i: P_n/g_s), although crop total evapotranspiration remains about the same (Barrios-Masias et al., 2014; Hanson and May, 2005). The newer processing tomato cultivars have a suite of interrelated traits that contribute to higher crop WUE, partly through a higher transpiration capacity per unit leaf area, which is compensated, among several traits, by smaller canopies and shorter growing periods than older cultivars (Barrios-Masias and Jackson, 2014). Although the trade-off for C assimilation is loss of water through the stomata, there is also room for improving the effective use of water by implementing management practices based on plant physiological responses to stress that result in reductions in total amount of water used. For instance, partial root-zone drying applied as alternate furrow irrigation can maintain high yields in processing tomatoes with at least 25% reduction in applied irrigation water (Barrios-Masias and Jackson, 2016). As in the latter study, most of the research conducted to understand the use of resources and yield increases has focused on aboveground responses to management strategies, but root traits are rarely considered (Barrios-Masias et al., 2014; de Pascale et al., 2011; Koevoets et al., 2016; Pinto and Reynolds, 2015; Riedelsberger and Blatt, 2017; Weaver and Bruner, 1927).

In this chapter, we focus on the potential of root traits to support increases in yield, maximize resource capture and provide abiotic stress tolerance in vegetable crops. Resistance to biotic stress in roots (e.g. nematodes and diseases) has contributed to yield increases in almost all vegetable crops as well but is not discussed here. It is possible that breeding for plant tolerance to diseases can result in the inadvertent selection of advantageous root traits under different environments, and warrants the study and identification of desirable root characteristics among a wide range of genetic material (e.g. commercial rootstocks, cultivars and wild relatives). Currently, no clear information or consensus exists with regard to the desirable root traits for sustainable vegetable production. Moreover, vegetable production is practised in very diverse soil environments and requires root systems well suited to different environmental constraints (Comas et al., 2013; Koevoets et al., 2016; Leskovar et al., 2014; Weaver and Bruner, 1927). Factors such as soil nutrient and water availability, osmotic potential, pH, texture, density and temperature affect the growth and development of roots (Epstein and Bloom, 2005; Jin et al., 2017), yet how roots acclimate to a heterogeneous soil environment and how this affects their capacity for resource capture is not clearly understood. Because of this complexity and the challenges for measuring root traits under field conditions, the study of roots has mainly focused on architectural and morphological traits (e.g. rooting depth and root length density) (Bishopp and Lynch, 2015; Comas et al., 2013; Johnson et al., 2000; Koevoets et al., 2016; Weaver and Bruner, 1927). Yet, a wide range of constitutive or induced changes in root anatomy, morphology, physiology and molecular biology could also enhance the effective capture of resources.

As complex root systems explore the soil and respond to different soil environments, the morphological and physiological development of each individual root alters their capacity for water and nutrient uptake (Comas et al., 2013; Epstein and Bloom, 2005; Wang et al., 2006). In vegetable crops, roots can be classified as coarse and young, fine roots. The former provide mainly plant anchorage, define root architecture and determine the total soil volume explored and potential access to soil resources (Morris et al., 2017; Weaver and Bruner, 1927). Young, elongating roots are crucial for resource uptake because they offer less resistance for water and nutrient movement towards the vascular system and facilitate faster and larger uptake of resources per root surface area than more mature zones along the root. This is due to higher root hydraulic conductivity (*Lp*) closer to the root tip than more matured root sections where resistance to water movement increases due to barriers formed from suberin and lignin deposition (e.g. Casparian bands) (for review on root *Lp* see Gambetta et al. (2017) and Steudle (2000)). The physiological capacity for resource uptake in young roots is also enhanced by higher activity of the membrane-intrinsic water-channel proteins (aquaporin) as they increase the root *Lp* (Gambetta et al., 2017). In addition to the higher functionality for nutrient and water uptake, young, elongating roots comprise most of the total root length, increase root surface area in contact with soil and contribute to the C economy of the plant (i.e. thin *vs*. thick roots) (Comas et al., 2013; Kramer and Boyer, 1995). Root hairs, which are epidermal cell extensions, further increase root surface area and contact with the soil, and are an active zone for water and nutrient uptake, and interaction with soil microorganisms (e.g. Cui et al., 2017). They also provide anchorage and enable soil penetration and exploration (Bengough et al., 2016). Root hair diameters are at least ten times smaller than fine roots and can further improve the C economy of the root system under stress conditions (Comas et al., 2013; Wang et al., 2006). The pace at which roots are produced and mature is influenced by environmental cues, which can result in different proportions of the young, active roots at any given time in a root system (Gambetta et al., 2017). Because nutrient and water availability influence responses of root traits (e.g. morphological, de la Riva et al., 2018; physiological, Gambetta et al., 2017), the management of inputs in vegetable crops can shape the root system characteristics to increase their resilience and favour the effective use of soil resources.

3 Roots for sustainable water management

A daunting task, due to the highly diverse rooting systems of vegetable crops (Weaver and Bruner, 1927), is to breed and select for root traits that can cope with or be plastic enough to maximize the effective use of water, taking into account particular genotype by environment by management interactions (G × E × M) (Blum, 2011; Comas et al., 2013; Rouphael et al., 2018). Water management for vegetable crops around the world ranges from rainfed to highly technified, localized irrigation systems, with many areas utilizing more than one water input (e.g. rainfall and drip irrigation) (FAO, 2016; Leskovar et al., 2014). Farmers need new cultivars and technologies (e.g. rootstocks) to adapt to lower water quality and quantity available for vegetable production as competing demands from cities and industries increase (Eriksen et al., 2016; Leskovar et al., 2014; Rouphael et al., 2018). Climate change is affecting the timing and amount of precipitation, and droughts occur more often during the vegetable growing season, decreasing yields and quality as documented for the Elbeland Basin in the Czech Republic (Potop et al., 2012; Potopová et al., 2017). Agricultural drought is defined here as the condition where soil moisture limits the potential growth of a crop, and it is not necessarily a drastic event such as permanent wilting or plant death (Blum, 2011). Water management is complex and extremely diverse between and within agricultural zones (e.g. Mediterranean climate, semi-arid or tropical) influenced by precipitation pattern, water source and quality, soil type, potential evapotranspiration, access to technology and crop species. Intricacies on how drought affects crops based on the crop stage, the duration of the drought and its intensity entails specific selection of root traits based on a target environment. Years of research to understand how root systems can impact performance of cereal crops under water-limited environments have identified several traits associated with, for instance, root physiology and anatomy in rice (*Oryza sativa*; Henry et al., 2016; Grondin et al., 2016) and root architecture and proliferation in wheat (Pinto and Reynolds, 2015; Richards, 2006). In vegetable crops, very few studies on root traits relevant to water uptake capacity have been conducted. One of those is the screening of wild relatives of watermelon (e.g. *Citrullus amarus*) which yielded material with drought resistance associated with rooting depth, vigour and growth rate (Levi et al., 2017; Zhang et al., 2011). Yet, a search on Google Scholar for 'vegetable crops' and 'root hydraulics' (on Aug. 16, 2018) provided eight results and only one with high relevance (e.g. aquaporins enhancing drought resistance in tomato; Li et al., 2016).

A desirable root system should maintain water uptake capacity, shoot water status and C assimilation capacity under decreasing soil water potential and high transpiration demands. This is especially important in vegetable crops because drought severely affects crop growth, yield and quality (de Pascale et al., 2011). Traits associated with root architecture, size and morphology (e.g. rooting depth, root length density, root surface area) are important for water acquisition across herbaceous and woody species as they increase the volume of soil explored and the soil-root contact area (Bishopp and Lynch, 2015; Comas et al., 2013; Johnson et al., 2000; de la Riva et al., 2018). In vegetable crops, water management mainly focuses on the top 30–60 cm of the soil profile, known as the 'effective root zone', especially under irrigated systems where most of the root system proliferates, driven by a higher resource availability (Hartz et al., 2017; Lott and Hammond, 2013; Schmidt and Gaudin, 2017). Root architectural traits have not received much attention in the selection and breeding for new genotypes (Bishopp and Lynch, 2015). Instead, breeding for increases in yield under high-input, irrigated systems (e.g. California Central Valley) has inadvertently resulted in smaller root systems unable to effectively exploit soil moisture deeper in the soil profile (Epstein and Bloom, 2005; Jackson and Koch, 1997; Johnson et al., 2000). Smaller root systems allow higher allocation of C to the harvestable organ, but the trade-off may be a reduction in root plasticity to acclimate to drought events, and higher dependency on frequent water inputs in the top soil to avoid stress (Jackson and Koch, 1997).

In older tomato cultivars, rooting depths were reported to reach down to 1.5 m deep, and it was perceived as an advantage for plants to avoid sharp fluctuations in soil moisture content and minimize drought stress (Weaver and Bruner, 1927). Currently, water and nutrients in processing tomatoes under drip-irrigated systems are managed in close proximity to the buried drip tape (20–30 cm below the surface) and the effective root zone is assumed to be no deeper than ~46 cm (Hartz, 2017). Yet, some modern processing tomatoes seem to have retained deep rooting traits, and were able to consistently extract water from at least 1.2 m deep (Barrios-Masias and Jackson, 2016). In lettuce (*Lactuca sativa* L.), a highly water and nutrient demanding crop, root systems are shallow and proliferate abundant lateral roots, especially in the top 5 cm, which makes them more prone to water deficits from higher soil evaporation (Jackson, 1995). Instead, its nearest wild relative (*Lactuca serriola* L.) is characterized by a deep taproot with access to deeper soil moisture and lateral roots more proportionally distributed across the soil profile (Jackson, 1995).

Recently, in the Central Valley of California the area planted to lettuce crop has drastically decreased because of less water availability, and farmers would benefit from new drought-tolerant cultivars (Eriksen et al., 2016). Johnson et al. (2000) evaluated several individuals from an $F_{2:3}$ population from the cross between *L. sativa* cv. Salinas and *L. serriola* (UC92G489), and identified alleles from *L. serriola* that improved water capture deeper in the soil profile such as increased lateral roots along the taproot and closer to the taproot tip. Several other lettuce population studies on quantitative trait loci (QTL) have confirmed that root architecture and rooting depth in lettuce is associated with tolerance to abiotic stress and vigour (e.g. Uwimana et al., 2012; Wei et al., 2014; but see Hartman et al., 2014). A large screening in California that started with >3500 lettuce cultivars from which 200 cultivars were evaluated in the field under high and low water availability (150% and 50% irrigation of ET_c) showed that fresh weight biomass reductions under the water deficit treatment were less than 25% compared to the over-irrigated treatment for several cultivars (Eriksen et al., 2016). These studies on lettuce and tomato suggest that some modern vegetable cultivars have access to water stored deeper in the soil profile, and if further studied for relevant root traits, farmers and breeding programmes could use them to address the challenge of producing food with less water available.

Decreasing xylem vessel diameter is considered as a strategy to limit hydraulic conductance and manage plants under a more conservative water regime (Comas et al., 2013). This selection strategy was successful for rainfed wheat in Australia and resulted in yield gains under dry environments (Richards and Passioura, 1989). Based on the Poiseuille equation to estimate water flow through a vessel, the vessel conductivity (L_{th}) is strongly driven by its radius (r) as it is raised to the fourth power ($L_{th} = \pi r^4/8\eta$); where η is the viscosity of water (Zwieniecki et al., 2001). Thus, slight decreases in vessel diameter could reduce plant hydraulic conductance as it increases the resistance of water moving through the soil–plant–atmosphere continuum (SPAC).

In the SPAC the xylem hydraulic resistance is small when compared to resistance of the radial movement of water in roots and the diffusion of water vapour from the leaf to the atmosphere (Steudle, 2000; but see Scoffoni et al. (2017) regarding the hydraulic vulnerability segmentation hypothesis). Another possibility is that narrower vessels embolize less, preventing hydraulic failure and maintaining conductance (i.e. capacity to supply water to the shoot) as soil drying increases the water tensions in the SPAC (Knipfer et al., 2015; Scoffoni et al., 2017). Breeding for narrower xylem vessels could still restrict the total conductance of a plant, especially as leaf area increases to a point where transpiration requirements are not met and feedback mechanisms regulate leaf growth and expansion, and reduce stomatal conductance. If the leaf can maintain a high photosynthetic rate with reduced stomatal conductance, the leaf intrinsic water use efficiency (WUE_i) would increase without compromising C assimilation. Yet, the potential trade-offs of vegetable crops bred with narrower xylem vessels could be smaller canopies, reduced C assimilation capacity, lower plant water status at high vapour pressure deficits and yield reductions. An alternative to regulate hydraulic conductance through the SPAC is the implementation of water management techniques that regulate plant water status and water use that result in reductions in xylem vessel diameter without compromising yields. For instance, tomato plants exposed to prolonged, drying cycles between irrigations produced smaller xylem vessel diameter (e.g. Fig. 1), reduced root *Lp* and lowered stomatal conductance even when soil moisture was at field capacity (Barrios-Masias and Hernandez-Espinoza, *under review*). Although reductions in shoot biomass were observed in the previous pot study, field trials have shown that slight reductions in canopy size do not compromise processing tomato yields under alternate furrow irrigation (Barrios-Masias and Jackson, 2016).

As discussed above, the root maturation process results in suberin and lignin deposition that increase hydraulic resistance, and this process can be accelerated closer to the root tip as plants respond to drought stress. As the exo- and endodermis suberize to prevent backflow of water to the soil, the resistance to the radial movement of water increases and limits the capacity for root water uptake (Richards and Caldwell, 1987). Briefly, the radial movement of water from the soil to the root xylem occurs through the apoplastic and cell-to-cell pathways, and their relative contribution to the total water flow depends on the resistances offered by each pathway.

As barriers prevent movement of water through the cell wall (i.e. apoplast), water has to cross cell membranes (i.e. cell-to-cell) through diffusion, which is facilitated by the presence and activity of plasmodesmata and aquaporins (Gambetta et al., 2017). Root hydraulic conductivity decreased in grapevines

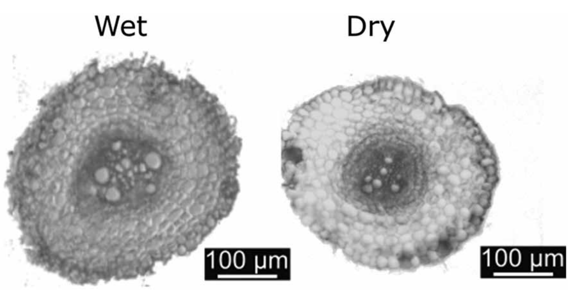

Figure 1 Changes in xylem vessel diameter of young roots of tomato (*Solanum lycopersicum* L.) grown under 'dry' and 'wet' conditions. Xylem vessel diameter was on average 30% larger in the 'wet' compared to the 'dry' treatment. Plants under the 'dry' treatment received water every 3–5 days, and 'wet' plants received water every day. Root sections were taken 2–3 cm from the root tip and stained with Sudan Red7B.

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