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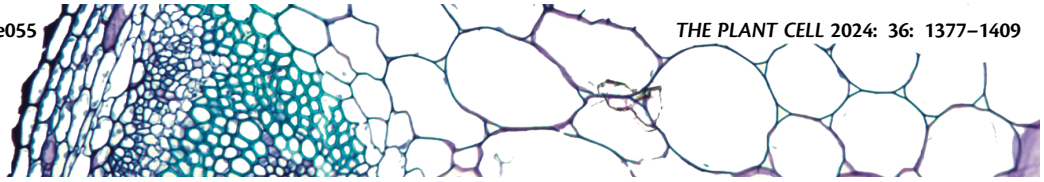

Review

Not so hidden anymore: Advances and challenges in understanding root growth under water deficits

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Abstract

Limited water availability is a major environmental factor constraining plant development and crop yields. One of the prominent adaptations of plants to water deficits is the maintenance of root growth that enables sustained access to soil water. Despite early recognition of the adaptive significance of root growth maintenance under water deficits, progress in understanding has been hampered by the inherent complexity of root systems and their interactions with the soil environment. We highlight selected milestones in the understanding of root growth responses to water deficits, with emphasis on founding studies that have shaped current knowledge and set the stage for further investigation. We revisit the concept of integrated biophysical and metabolic regulation of plant growth and use this framework to review central growth-regulatory processes occurring within root growth zones under water stress at subcellular to organ scales. Key topics include the primary processes of modifications of cell wall–yielding properties and osmotic adjustment, as well as regulatory roles of abscisic acid and its interactions with other hormones. We include consideration of long-recognized responses for which detailed mechanistic understanding has been elusive until recently, for example hydrotropism, and identify gaps in knowledge, ongoing challenges, and opportunities for future research.

Introduction

Limited availability of arable land worldwide creates a pressing need for substantial enhancements of agricultural productivity to satisfy the projected demands for food, feed, fiber, and energy in the near future (Fedoroff et al. 2010). In addition to land limitations, unpredictable changes in climate are creating conditions detrimental to plant growth and crop productivity. Among the stressors, droughts are a major environmental constraint on plant development that adversely affect crop yields and are likely to worsen in many areas of the world (Boyer 1982; Bailey-Serres et al. 2019). To achieve enhanced plant productivity under drought conditions while reducing the environmental footprint of production agriculture (Campbell et al. 2017; Springmann et al. 2018; Pareek et al. 2020), it is critical to elucidate the physiological and molecular mechanisms that regulate plant growth and development under water limitation (Boyer et al. 2013; Tardieu et al. 2018; Bailey-Serres et al. 2019).

It is well known that the growth of different plant organs responds differentially to water deficits. Typically, growth of aerial tissues is reduced or arrested, whereas growth of the root system is relatively maintained or even enhanced under water-limited conditions (Fig. 1; Sharp and Davies 1979; Westgate and Boyer 1985; Sharp et al. 1988). These observations underlie the increased ratio of root to shoot development regarded to be a key adaptive response of plants growing under water-limited conditions (Hsiao 1973; Meyer and Boyer 1981; Sharp and Davies 1989; Hsiao and Xu 2000). The high sensitivities of both vegetative and reproductive shoot growth responses to water deficits (Fig. 1A) are considered to be adaptive rather than injurious effects that

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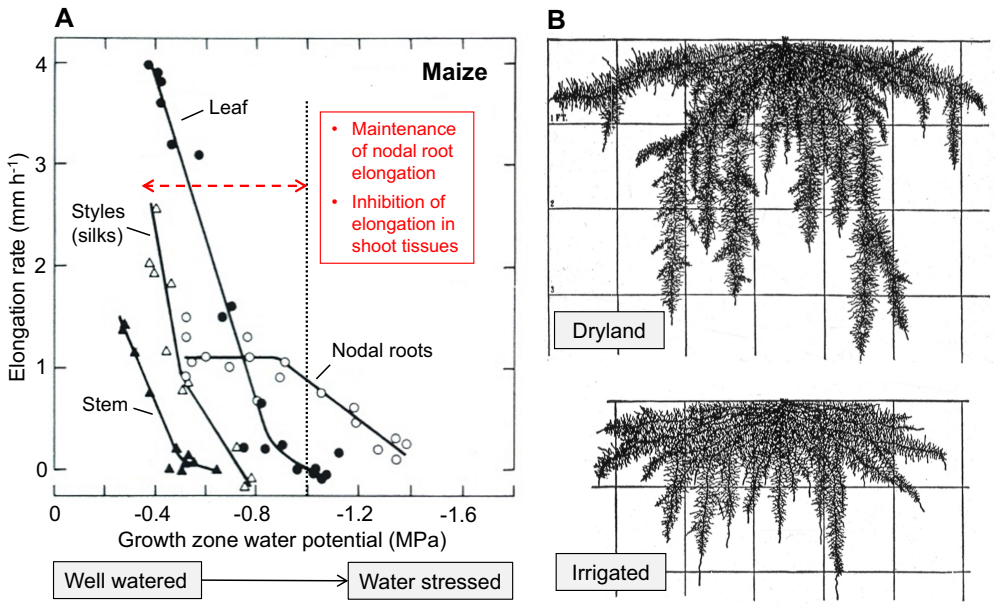

Figure 1. Maintenance of root growth under water deficit conditions. **A)** Comparative responses of elongation rate in different organs of maize to the development of water stress during soil drying. Nodal root elongation continued at growth zone water potentials that caused complete inhibition of elongation in vegetative and reproductive shoot tissues. Because growth responses were determined as a function of the water potentials of the growing tissues, the differential sensitivities reflect inherent differences in how cellular physiology responds to water stress in the different organs. **B)** More extensive root system development in maize plants when grown under soil drying (dryland) compared with irrigated conditions. A modified from Westgate and Boyer (1985), Figure 1, by permission of Springer Nature. B reproduced from Weaver (1926), Figure 87, p 189, by permission of John Wiley and Sons.

are beneficial for plant fitness and survival in an ecological context but tend to reduce yield in an agricultural context (Skirycz and Inzé 2010; Tardieu et al. 2018; Turc and Tardieu 2018). These tradeoffs between survival and growth and the regulatory mechanisms that determine shoot growth responses to water limitation have been studied extensively over the past 50 years, and interested readers are referred to comprehensive reviews on the topic (Hsiao 1973; Skirycz et al. 2011; Tardieu 2012; Claeys and Inzé 2013; Nelissen et al. 2018; Tardieu et al. 2018; Turc and Tardieu 2018).

Increased root system growth under water limitation in several crop and wild species was documented by Weaver (1926) a century ago in a seminal body of work on root development under field conditions. For example, compared with irrigated conditions, maize plants were observed to develop a root system that grew deeper and was more heavily branched under soil-drying conditions (Fig. 1B). These observations in maize and other crops led Weaver (1926, pp 1, 90) to comment on the importance of studying roots, stating that "Frequently, half—and often much more—of every crop plant is invisible. This portion consists entirely or largely of roots which extend far into the soil.... Since roots absorb water and nutrients, a knowledge of their development, extent, and activities and how these are modified by the changes in the environment are necessary for a scientific understanding of plant production." Development of more extensive rooting under water-limited conditions not only reflects the continued growth of root apices into regions of moist soil; in some circumstances, roots must grow through soil that is already dry to reach soil with available water. The ability of roots to grow into and through dry soil has attracted the attention of plant physiologists for many decades (Hendrickson and Veihmeyer 1931; Hunter and Kelley 1946; Portas and Taylor 1976), and it has been shown that certain types of roots—including the primary root of seedlings (see Figs. 2 and 3) and the shoot-borne nodal roots of grasses (Fig. 1A)—have the ability to continue growing at low tissue water potentials that completely inhibit shoot growth (Sharp and Davies 1979; Westgate and Boyer 1985; Sharp et al. 1988; Yamaguchi and Sharp 2010).

Despite early recognition of the adaptive significance of root developmental responses to water-limited conditions, progress in understanding the underlying physiological and genetic control mechanisms has been hampered by the inherent complexity of root systems and their interaction with the soil environment. Different root types, including the primary, seminal, and nodal root axes and their subtending lateral roots, exhibit varying responses to water deficits and are physiologically and genetically distinct (Hochholdinger et al. 2004, 2018; Ahmed et al. 2016, 2018; Waidmann et al. 2020; Freschet et al. 2021). Together with other factors, including root hair production, root exudation, and microbial interactions, this diversity collectively enables optimal root system development and function but complicates experimental investigation. The growth of the root system is further impacted by the spatial and temporal dynamics of soil water and

nutrient availability as well as variability in other physical, chemical, and biological properties within the soil matrix. With heightened appreciation of the critical importance yet understudied nature of root development and function (Russell 1977; Eshel and Beeckman 2013; Gregory 2021), and with advances in experimental approaches and measurement techniques, the past several decades have seen increasingly intensive research on root growth responses to water deficits (Hsiao 1973; Pritchard 1994; Sharp et al. 2004; Ober and Sharp 2007, 2013; Yamaguchi and Sharp 2010; Gowda et al. 2011; Lynch 2013, 2018; Dinneny 2019; Karlova et al. 2021). The development of thermodynamically based methods to measure soil and plant tissue water status in the 1960s was of particular importance in studies of plant responses to water deficits. These techniques allowed precise quantification of experimental conditions and repeatability of plant responses (Slatyer and Taylor 1960; Boyer and Knipling 1965; Scholander et al. 1965; Boyer 1995; Kramer and Boyer 1995; Juenger and Verslues 2023), enabling characterization of the diverse growth responses of different root types, as well as between roots and shoots, to water deficit conditions (Westgate and Boyer 1985; Sharp et al. 1988; Hsiao and Xu 2000; Dowd et al. 2019).

Selected milestones in the understanding of root growth responses to water-limited conditions are the focus of this ASPB Centennial Review, with emphasis on founding studies that have shaped current knowledge and set the stage for further investigation. We first highlight how characteristics of root system architecture (RSA) benefit plant performance under water limitation. We then address the variety of root growth responses that determine the RSA for exploration of the soil profile. These growth responses occur within a relatively small volume of tissue that constitutes the root growth zone at the individual root apices, and it is the mechanisms that control cell production in the meristem and the rate, duration, and direction of cell expansion within the root growth zones that ultimately establish the growth and dimensions of the entire root system. We revisit the concept of integrated biophysical and metabolic control of plant growth and use this framework to review key growth-regulatory processes occurring within root growth zones under water stress at subcellular, cellular, and tissue scales. Whereas knowledge of the molecular regulation of many aspects of root development is advanced (Motte et al. 2019), we focus on long-recognized physiological responses to water deficits for which, in many cases, detailed mechanistic understanding remains limited. Lastly, we propose future avenues for research to increase understanding of root growth under water limitation and, consequently, for enhanced opportunities to improve crop productivity under drought conditions.

Features of RSA for improved drought tolerance

The root system functions to provide both anchorage and the absorption of water and nutrients necessary for plant growth. The response of deeper rooting in water-limited environments (Fig. 1B) can enable access of water from the subsoil (Klepper et al. 1973; Sharp and Davies 1985; Sponchiado et al. 1989; Lopes and Reynolds 2010), which, by maintaining water availability through to reproductive development, can have a major impact on yield sustainability. For example, in Australian wheat production, an additional 10 cm of rooting depth can result in a 10% to 20% increase in grain yield (Kirkegaard et al. 2007; Lilley and Kirkegaard 2007). Moreover, in elegant reciprocal grafting experiments with common bean lines varying in drought tolerance, White and Castillo (1989, 1992) demonstrated that under soil-drying conditions, the deep-rooting phenotype was genetically determined by the rootstock and, rather than the shoot phenotypes, was of greater importance for maintaining yield. Interestingly, in contrast, grafting experiments with potato cultivars led to opposite conclusions on the relative importance of the scion and rootstock in determining root system development under soil-drying conditions (Jefferies 1993). Accordingly, further studies are warranted to investigate root- vs shoot-sourced regulation of root growth responses to water deficits.

Lynch (2013) proposed that an ideotype of steep-angled roots that explore deeper layers of the soil profile and are anatomically cheaper to build and maintain will enhance drought tolerance and referred to such root system characteristics as a "steep, deep and cheap" ideotype. Several studies have demonstrated that under terminal drought conditions, this ideotype of RSA contributes to drought tolerance in rice (Uga et al. 2011, 2013), maize (Zhu et al. 2010; Chimungu et al. 2014a, 2014b), wheat (Gabay et al. 2021, 2023), chick pea (Kashiwagi et al. 2015), and common bean (Strock et al. 2019). The studies in rice are particularly noteworthy because they show mechanistic understanding of the deep rooting phenotype and demonstrate its impact on increasing grain yield in the field under water deficit conditions (Uga et al. 2011, 2013). The quantitative trait locus *DEEPER ROOTING 1* (*DRO1*) was identified in a rice recombinant inbred line population, which accounted for 67% of variation in the deep-rooting phenotype (Uga et al. 2011). Further analyses of the *DRO1* locus found that it is negatively regulated by auxin and is involved in strong gravitropic response of the roots, leading to steeper growth angle and deeper root phenotypes of *DRO1*-containing lines compared with the shallow-rooting control lines (Uga et al. 2013). Phylogenetic analyses revealed that *DRO1* homologs are present in a wide range of plant species, and they have been demonstrated to modify RSA in *Arabidopsis*, *Medicago*, and *Prunus* species in addition to rice (Ge and Chen 2016; Guseman et al. 2017; Kitomi et al. 2020; Uga 2021). A similar multidisciplinary approach was used to understand variation in RSA and drought tolerance in wheat, and these studies found that RSA was regulated by dosage of the genes involved in jasmonic acid biosynthesis (Gabay et al. 2021, 2023). These studies indicate that the mechanistic understanding of genes and gene products regulating RSA can be effectively used to obtain root phenotypes that improve drought tolerance in plants.

Although the steep, deep, and cheap ideotype was favorable in the terminal drought conditions imposed in these studies, it might not be suitable in dry environments where intermittent rainfall provides water in the upper layers of the soil profile. In a study of root phenotypes of diverse maize genotypes in which stress was imposed by providing 50% of the water required for optimal growth, Klein et al. (2020) found that the steep, deep, and cheap ideotype was not favored. The irrigation provided by the center pivot system used in the study is analogous to intermittent rainfall during the growing season that provides water to the upper layers of the soil profile, and the results demonstrated that maize (and likely other crops) has genetic variability in root growth characteristics that are suited for drought tolerance in these conditions. Favored phenotypes included thicker nodal roots, increased lateral root branching, larger proportion of stele, numerous metaxylem elements, larger cortical cells, and aerenchyma formation; the authors suggested that having multiple phenotypes integrated within an ideotype was necessary for adapting to environments with intermittent rainfall. Therefore, it is important to consider the attributes of RSA and individual root phenotypes in the context of particular drought scenarios and the potential tradeoffs of those features in optimal environmental conditions (Tardieu 2012; Lynch 2018; Tardieu et al. 2018; Verslues et al. 2023). In fact, it has been suggested that an average root system growth phenotype combined with developmental plasticity to environmental changes (rather than constitutive expression of traits) is more productive in a variety of environments and stress conditions (Sandhu et al. 2016; Strock et al. 2019; Schneider and Lynch 2020). Developmental plasticity has many potential ecological and physiological benefits for reducing inputs in production agriculture and is particularly important in low-input systems where water and nutrients are more variable (Weaver 1926; O'Toole and Bland 1987; Sponchiado et al. 1989; Fukai and Cooper 1995; Dardanelli et al. 1997; Sandhu et al. 2016; Strock et al. 2019; Schneider and Lynch 2020; Woods et al. 2022). Therefore, it is vital to discover the genetic and physiological mechanisms that regulate the integrated RSA phenotypes that optimize plant performance under water-limited conditions (Schneider and Lynch 2020; Uga 2021; Lynch 2022; Verslues et al. 2023).

Integrated biophysical and metabolic regulation of plant cell expansion

In his seminal review on plant responses to water stress, Hsiao (1973, p 536) emphasized that "with the shift of attention to metabolic and molecular aspects of stress physiology in the mid-1960s, the importance of water uptake and the resulting turgor as a physical force needed for cell growth has at times been almost overlooked or ignored." Arguably, the same statement could still be made today, and the role of turgor as well as mechanisms of turgor regulation and turgor sensing remain important areas for further investigation (Ali et al. 2023). The Lockhart model of plant cell expansion (Lockhart 1965) was originally formulated to describe the growth of single cells and, with caution, is also useful to gain an understanding of multicellular organ growth (Boyer 1985; Spollen and Sharp 1991; Pritchard 1994; Dumais 2021). In simplified form, the model describes the interdependence of expansive growth (G) on turgor and cell wall–yielding properties:

$$G = m\,(P\text{-}Y),$$

where m is the cell wall extensibility, P the cellular turgor, and Y the yield threshold turgor (i.e. the minimum turgor required for irreversible cell wall extension). An elaborated equation additionally considers the hydraulic resistance and associated water potential gradient required to drive water flow through tissues and into the growing cells ("growth-induced" or "growth-sustaining" water potential gradients; Molz and Boyer 1978; Silk and Wagner 1980), which, by lowering the cellular water potential, reduces the magnitude of turgor that develops for a given osmotic potential (Lockhart 1965; Boyer 1985; Passioura and Boyer 2003). The Lockhart equation conceptualizes that cell expansion occurs only when the internal pressure exerted on the wall is large enough to exceed the yield threshold, resulting in wall yielding at a rate dependent on the extensibility. More precisely, cell wall metabolism first results in wall relaxation (Cosgrove 2016), which relaxes stress and thus lowers turgor and consequently water potential inside the cell (because turgor is a component of water potential). This generates a water potential gradient that, in water-sufficient situations, drives water flow into the cell, resulting in turgor restoration, cell wall yielding, and cell expansion. The cells also take up or generate metabolites to maintain their osmotic concentration and reinforce the primary cell wall. These processes continue until cells reach their final size as secondary cell wall deposition leads to wall stiffening and growth cessation.

The Lockhart equation indicates that a decrease in turgor under water-limited conditions will result in a decrease in growth rate. However, the equation also illustrates that, theoretically, cell expansion can be regulated under water stress by 2 key mechanisms: first, by modifying cell wall–yielding properties, and second, by manipulating the processes of turgor maintenance. In a pioneering study of the dynamic relationship of plant cell expansion to turgor, Green et al. (1971) provided evidence for metabolic as well as physical control of plant cell expansion. Using the large cells of the alga *Nitella* as an experimentally amenable system, it was shown that a small stepwise decrease in turgor caused essentially immediate cessation of cell elongation. (Turgor was measured in situ using an ingenious inserted capillary method, and decreases in turgor were imposed by lowering the external water potential; Green 1968.) However, the original elongation rate resumed within approximately 30 min while the cell remained at the decreased turgor. Conversely, imposed increases in turgor caused very high but short-lived increases in elongation rate, followed by deceleration to the original rate. These

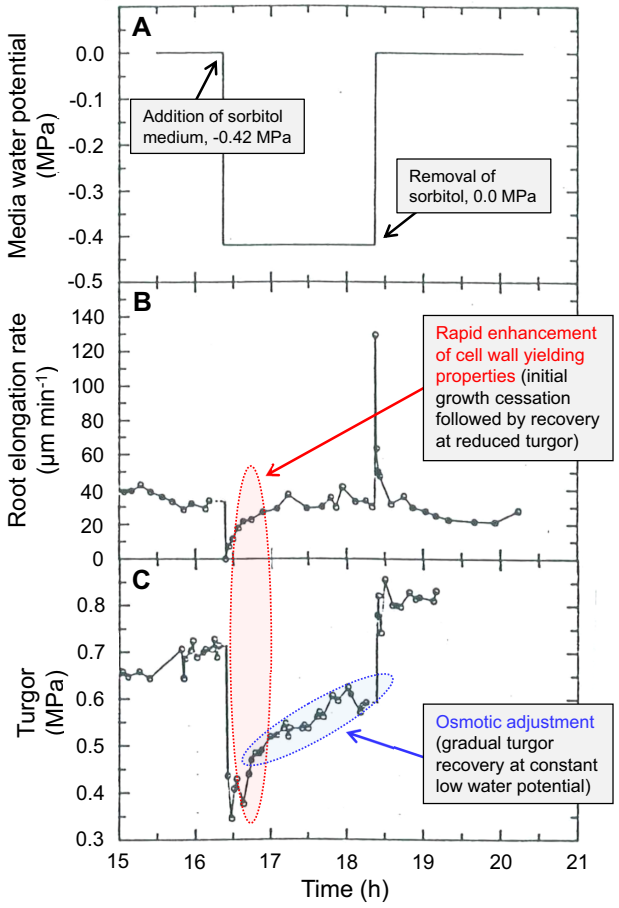

Figure 2. Cell wall–yielding properties are enhanced in maize primary roots after water stress imposition. Maize seedlings were grown in solution at a water potential of approximately 0 MPa (0.1 mM $CaCl_2$). Root elongation rate was monitored with a position transducer, and turgor of surface cells in the central region of the growth zone was measured every few minutes using a pressure microprobe. **A)** A stepwise decrease in media water potential was imposed by addition of −0.42 MPa sorbitol, and after 2 hours the sorbitol was removed. **B)** The abrupt decrease in water potential caused essentially immediate cessation of root elongation, as well as decrease in root turgor **(C)**. Elongation recovered to the well-watered rate within an hour after the onset of stress, whereas turgor recovery as a result of osmotic adjustment was more gradual and turgor did not reach the well-watered level for the duration of the stress treatment. Full recovery of elongation with only partial turgor recovery indicates that cell wall–yielding properties were rapidly enhanced in response to water stress; in terms of the Lockhart model (see text), either the yield threshold decreased or the extensibility increased, or both. Conversely, removal of water stress caused a short-lived spike in root elongation followed by deceleration to the original rate, again pointing to compensatory adjustments of cell wall–yielding properties. Modified from Hsiao and Jing (1987), Figure 7, by permission of ASPB.

observations supported the concept of a yield threshold turgor for cell wall extension that is subject to compensatory and presumably metabolic adjustments (as well as, possibly, changes in wall extensibility) following changes in turgor.

The subsequent development of the pressure microprobe (Husken et al. 1978) allowed similar experiments to be conducted in the much smaller cells within the growth zones of roots and leaves of higher plants. The results indicated that roots exhibit a high capacity for enhanced cell wall yielding and rapid growth resumption in response to turgor decreases (Hsiao and Jing 1987; Frensch and Hsiao 1995; Hsiao and Xu 2000; also see Kuzmanoff and Evans 1981); the original results from Hsiao and Jing (1987) for the maize primary root are shown in Fig. 2. Interestingly, this experiment also showed that turgor began to recover (Fig. 2C) while the low water potential treatment remained constant (Fig. 2A); this observation is indicative of solute accumulation by the process of osmotic adjustment, a process first shown to occur in water-stressed roots by Greacen and Oh (1972). Notably, root elongation remained constant during this phase (Fig. 2B), again pointing to compensatory adjustments of cell wall–yielding properties as turgor increased. Moreover, as a result of the osmotic adjustment, turgor increased to higher levels than in well-watered roots (Fig. 2C) following removal of water stress (Fig. 2A). This resulted in a large spike in root elongation followed by rapid deceleration to the original rate (Fig. 2B), indicating that wall-yielding properties were rapidly moderated. In contrast to the findings with water-stressed roots, studies of leaves indicated that cell wall–yielding properties either did not increase substantially after low water potential imposition or, with longer-term stress exposure, actually decreased, leading to growth inhibition despite turgor maintenance by osmotic adjustment (Matthews et al. 1984; Hsiao and Jing 1987; Serpe and Matthews 1992; Hsiao and Xu 2000).

The Green et al. (1971) study provided the foundation for investigation of the metabolic regulation of plant cell wall expansion, particularly in response to water deficit conditions. The influence of this work was recognized in 2010 by the American Society of Plant Biologists, who included the paper among a "Classics Collection" of 25 papers in *Plant Physiology* that played a key role in shaping modern plant biology research. Modifications of cell wall–yielding properties and osmotic adjustment are now established as primary processes contributing to the ability of roots to maintain growth under water-stressed conditions and are addressed in detail in later sections.

Kinematic approaches to study root growth responses

Among plant organs, roots have a relatively simple growth zone in terms of organization, and root growth zones therefore have been used for many decades as models to study various aspects of plant growth (Sinnott 1939; Erickson and Sax 1956; Goodwin and Avers 1956; Erickson and Silk 1980; Beemster and Baskin 1998; Brady et al. 2005). Cells are first formed in the apical meristem by division of stem cells and then continue to divide for several cycles while cell elongation simultaneously pushes the apex through the soil and

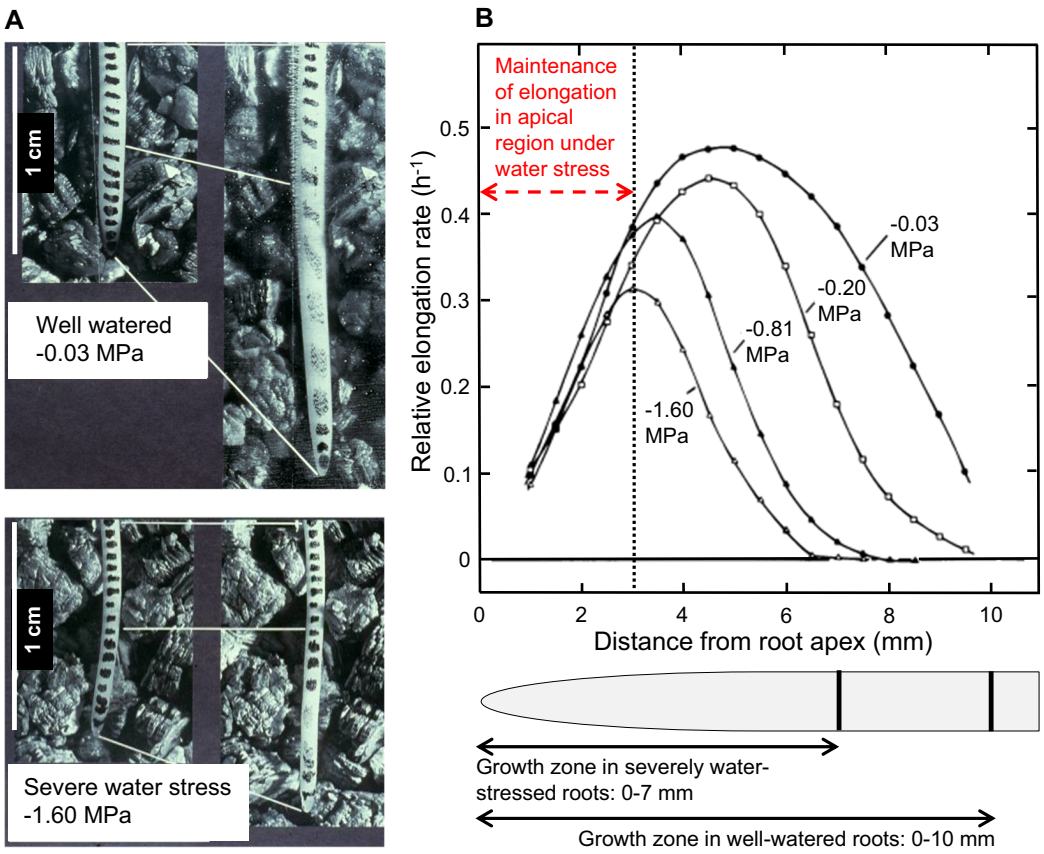

Figure 3. Kinematic analysis reveals spatially differential responses of tissue expansion to water stress within the growth zone of the maize primary root. Maize seedlings were grown under well-watered conditions (water potential of −0.03 MPa) or at mild (−0.20 MPa), moderate (−0.81 MPa), or severe (−1.60 MPa) water stress (obtained by adjusting the vermiculite media water content). When the primary roots were approximately 5 cm long, the apical 10-mm region was marked at approximately 0.6-mm intervals for temporal analysis of mark displacement away from the apex. **A)** Displacement of marks during 3.5 h after marking for representative roots growing under well-watered or severe water stress conditions. White lines indicate vertical displacement of the root apices and of marks originally located at 5 and 10 mm from the apex. In well-watered roots, mark separation, and hence tissue expansion, occurred throughout the apical 10 mm, whereas in severely water-stressed roots, mark separation was confined to the apical 5 mm. Water-stressed roots were also substantially thinner than well-watered controls, indicating inhibition of radial expansion. **B)** Time-lapse analysis of mark displacement during 1 h after marking was used to calculate the distribution of relative elongation rate as a function of distance from the root apex. In all water stress treatments, local elongation rates in the apical 3 mm were maintained at the well-watered rate, whereas elongation was increasingly inhibited with increasing water stress as cells were displaced further from the apex, resulting in progressive shortening of the growth zone. Modified from Sharp et al. (1988), Figures 3 and 5, by permission of ASPB.

displaces older cells away from the apex. The cells continue to expand as they exit the meristem and traverse the growth zone. Hence, as root growth occurs, cells are progressively located at increasing distances from the root apex (Fig. 3A) and experience increasing displacement velocities (Erickson and Silk 1980; Sharp et al. 1988; Baskin et al. 2020). As the cells expand, they typically develop an anisotropic growth pattern due to longitudinal expansion being favored over radial expansion (Liang et al. 1997), resulting in the cylindrical geometry of most roots. The end of the growth zone is marked by cells that have stopped expanding and undergo processes of maturation, including the development of secondary cell wall thickening.

The overall rate of root elongation is determined by the rate of cell production from the meristem and the rate and duration of cell elongation. However, the apparent simplicity of this relationship belies the realization that within the growth zone there is massive spatial and temporal heterogeneity of cellular growth rates and, thus, of underlying growth-regulatory processes. This heterogeneity occurs in the course of normal development (Erickson and Sax 1956; Beemster and Baskin 1998) and in response to various environmental conditions, including, for example, water limitation (Sharp et al. 1988) and soil mechanical resistance (Croser et al. 1999). To obtain detailed analyses of spatio-temporal growth patterns within plant growth zones, powerful kinematic approaches that apply concepts of fluid dynamics to tissue expansion were pioneered by Ralph Erickson and Wendy Silk (Erickson and Sax 1956; Erickson 1976; Silk and Erickson 1979; Silk 1984;

Walter et al. 2009). These analyses revealed that in a typical root growth zone, the local elongation rate dramatically accelerates as cells move out of the meristem, reaches a peak in the central region, and then decelerates before growth cessation (Fig. 3B; Erickson and Sax 1956; Goodwin and Avers 1956). Moreover, this large range of tissue expansion rates occurs within a brief frame of space and time. For example, in the maize primary root growing under well-watered conditions, around 8 hours is required for a cell exiting the meristem to be displaced to the end of the growth zone, located at approximately 10 mm from the apex, during which time the relative elongation rate (longitudinal strain rate) accelerates to a remarkably high peak value of almost 50% h^{-1} (i.e. a tissue element at this location would double in length in an hour; Fig. 3B) and then abruptly decreases (Sharp et al. 1988).

Knowledge of cell expansion patterns within plant growth zones allows comparison of local effects to putative local causes and, thereby, facilitates investigation of underlying regulatory processes (Hsiao et al. 1985; Walter et al. 2009). In the maize primary root, kinematic analyses revealed that cell elongation is differentially responsive to water stress in different regions of the growth zone (Fig. 3). Remarkably, in the apical region that encompasses the meristem, longitudinal expansion is maintained even under severe water stress (at tissue water potentials as low as −1.6 MPa). In contrast, elongation is progressively inhibited compared with well-watered roots as cells are displaced further from the apex, resulting in decreased final cell lengths and a shortened growth zone (Sharp et al. 1988; Saab et al. 1992; Fan and Neumann 2004; Voothuluru et al. 2020). Similar findings were reported in primary roots of several other species, including wheat (Pritchard et al. 1991), pine (Triboulot et al. 1995), soybean (Yamaguchi et al. 2010), and cotton (Kang et al. 2022), and have also been observed in water-stressed leaves (Durand et al. 1995; Skirycz et al. 2011; Avramova et al. 2015). On the other hand, cell production decreased substantially in roots growing under moderate to severe water stress conditions (Fraser et al. 1990; Voothuluru et al. 2020; Kang et al. 2022; Verslues and Longkumer 2022). The possible adaptive advantage of inhibited cell production in water-stressed roots is discussed in a later section.

Interestingly, the degree of growth anisotropy was also shown to be altered in water-stressed maize primary roots (Sharp et al. 1988; Liang et al. 1997). In contrast to the maintenance of longitudinal expansion in the apical region of the growth zone (Fig. 3B), radial expansion was inhibited, resulting in substantially thinner roots compared with well-watered controls (Fig. 3A). These results indicate that effects of water stress on root expansion in length and width are regulated independently, although the control mechanisms underlying this differential response are not understood (Baskin et al. 1999). Thinner roots in water-stressed compared with well-watered plants have been reported in several species (Taylor and Ratliff 1969; van der Weele et al. 2000). It should be noted, however, that whether roots become thinner under water stress depends on soil properties. Many soils increase in mechanical resistance as they dry, and a common response to physical impedance is root swelling (Moss et al. 1988; Pandey et al. 2021; Huang et al. 2022).

Preferential maintenance of cell elongation in the apical region of the growth zone under water deficit conditions, together with root thinning, likely represents a coordinated adaptive response that enables the root to concentrate its use of limited resources to sustain adequate water and solute transport to the vital apical region that includes the meristem and thereby to continue exploration of the soil for water at minimum cost (Sharp et al. 1990; Voetberg and Sharp 1991; Verslues and Sharp 1999; Wiegers et al. 2009; Voothuluru et al. 2020). As described in the following sections, these findings provided a powerful underpinning to investigate the complex network of physiological and molecular processes involved in the regulation of root elongation under water stress conditions (Sharp et al. 2004; Yamaguchi and Sharp 2010, Ober and Sharp 2013).

Historically, kinematic analyses have been an important tool to link cellular growth heterogeneity in root growth zones with spatial variation in, for example, hormones (auxin [IAA]: Hejnovicz 1961; Goodwin 1972; abscisic acid [ABA]: Saab et al. 1992; Ober and Sharp 2003; gibberellin: Band et al. 2012), cell wall proteins (Wu et al. 1994, 1996; Zhu et al. 2007), apoplastic pH (Peters and Felle 1999; Winch and Pritchard 1999; Fan and Neumann 2004) and reactive oxygen species (ROS) (Voothuluru et al. 2020), and other growth-regulatory factors. Further, the application of growth kinematics provides a powerful approach to ascertain rates of associated developmental processes (Silk et al. 1984, 1986; Sharp et al. 1990; Voetberg and Sharp 1991; Silk and Bogeat-Triboulot 2014), as detailed below with regard to osmotic adjustment. However, despite early recognition of the importance of characterizing how growth patterns are altered by environmental variation (Goodwin and Avers 1956), relatively few studies of root stress biology have taken advantage of these approaches. Whereas original tissue marking and time-lapse photographic techniques were laborious (Fig. 3A), modern tools such as computational video image analysis combined with microscopy techniques have enabled kinematic growth analyses to be obtained with relative ease (Silk et al. 1989; van der Weele et al. 2003; Basu et al. 2007).

Cell wall changes impacting root growth under water deficits

The original indications of enhanced cell wall yielding in water-stressed roots, as described above, were based on the temporal responses of turgor and root growth to low water potential imposition (Fig. 2), and similar inferences were made from comparisons of relative elongation rate and turgor profiles within the growth zone of roots growing under steady water stress conditions (Spollen and Sharp 1991;

Triboulot et al. 1995). However, those studies did not provide direct assessments of cell wall–yielding properties or the biochemical basis for stress-induced changes. Taking advantage of the kinematic growth analysis in water-stressed maize primary roots (Fig. 3), Wu et al. (1996) demonstrated that the maintenance of elongation in the apical region and the premature deceleration and cessation of elongation in the basal region of the growth zone were associated with differential responses of wall-yielding properties. Although substantial osmotic adjustment occurred (see following section), this was insufficient to maintain turgor, which was decreased by over 50% throughout the growth zone (Fig. 4A, inset). Accordingly, the maintenance of elongation in the apical region indicated that longitudinal cell wall yielding was enhanced, which was confirmed by demonstration of substantially increased acid-induced extension in water-stressed compared with well-watered roots (Fig. 4A). Acid-induced growth of plant cell walls has long been recognized (Rayle and Cleland 1992; Peters and Felle 1999) and is mediated at least partly by wall-loosening expansin proteins (McQueen-Mason et al. 1992; Cosgrove 2000, 2022). Consistently, expansin activity (Fig. 4B; Wu et al. 1996) and transcript levels of several expansin genes (Wu et al. 2001; Kang et al. 2023) were markedly increased in the apical region of water-stressed roots, as was activity of the "wall remodeling" enzyme (Cosgrove 2022) xyloglucan endotransglycosylase/hydrolase (XTH) (Fig. 4D; Wu et al. 1994). Interestingly, susceptibility to exogenous expansins also increased in the apical region (Fig. 4C), suggesting that stress-induced modifications of cell wall structure or composition facilitated expansin accessibility (Wu et al. 1996). In contrast, acid-induced extension was greatly decreased in the basal region of growth inhibition (Fig. 4A). Although extractable expansin activity also increased in this region (probably reflecting maintained activity as cells were displaced from the apical region), the minimal extensibility was likely attributable to compositional changes resulting in wall stiffening (Wu et al. 1996; Fan et al. 2006; Yamaguchi and Sharp 2010). Water stress–induced cell wall compositional changes are discussed further below.

Correlations between profiles of apoplastic pH and longitudinal expansion have been demonstrated in root growth zones, with more acidic regions coinciding with peak expansion rates (Peters and Felle 1999). Much evidence indicates that the pH profile is metabolically regulated and causally related to the growth rate distribution (e.g. Staal et al. 2011; Xu et al. 2013). In a study of cell wall pH regulation in water-stressed maize primary roots, Fan and Neumann (2004) found that spatial profiles of root surface acidification (proton efflux) and epidermal cell wall pH correlated with the region-specific growth responses. While the apical region of growth maintenance exhibited profiles similar to the well-watered control, the basal region of growth inhibition showed decreased acidification and a higher pH. Importantly, addition of acidic buffer partially restored growth in the basal region, indicating that the stress-induced increase in wall pH was functionally related to the inhibition of growth in this region. Because apoplastic acidification is important for activation of cell wall loosening proteins (Cosgrove 2000; Hager 2003), the pH profile is likely involved in differentially regulating wall loosening and, thereby, contributing to the spatial growth pattern in water-stressed roots.

To gain a more comprehensive understanding of how cell wall protein composition changes in response to water stress in different regions of the maize primary root growth zone, a proteomics analysis of water-soluble and lightly ionically bound cell wall proteins was conducted by Zhu et al. (2007). The results showed predominantly region-specific changes in several functional categories, suggesting the involvement of multiple processes in the growth responses. Notably, an increase in apoplastic ROS was predicted particularly in the apical region of growth maintenance, which was confirmed by imaging techniques (Zhu et al. 2007; Voothuluru and Sharp 2013). As discussed by Voothuluru et al. (2020), apoplastic ROS may have wall loosening or tightening effects and could also be involved in signaling processes that effect cell production. To investigate these possibilities, root growth characteristics of transgenic maize lines (constitutively expressing a wheat *oxalate oxidase*) with altered apoplastic ROS levels were evaluated. The results revealed a complex picture with apoplastic ROS modulating elongation differentially in well-watered (promoted) or water-stressed (inhibited) roots, in both cases via effects on both cell production and spatial profiles of cell elongation, as discussed in a later section.

Root growth depends on the coordinated and integrated expansion of all cells within the organ, but the biomechanical and biochemical properties of individual tissues may be predominant in regulating and/or limiting the overall rate of elongation. As described above, extensibility assays (Fig. 4A) indicated there are differential changes in wall composition in the apical and basal regions of the growth zone of water-stressed maize primary roots that contribute to the growth pattern, and evidence suggests that these changes occur in a tissue-specific manner. Fan et al. (2006) tested the hypothesis that water stress-induced alterations in wall-linked phenolic compounds are linked with the inhibition of elongation in the basal region of the growth zone. Results from Fourier transform infrared spectroscopy indicated region-specific changes in phenolic composition (Fig. 4F), and progressive accumulation of lignin with increasing distance from the apex was observed primarily in stelar tissues in correlation with inhibition of mechanical extensibility of root segments. A similar spatial pattern of water stress–induced lignification was observed in the soybean primary root (Yamaguchi et al. 2010). When the growth zone of well-watered or water-stressed maize roots was bisected, the roots curved inward as they grew, suggesting that the inner tissues were limiting root elongation (as reported over a century ago in *Vicia faba* L. roots by Darwin and Acton 1909). However, Pritchard and Tomos (1993) found in well-watered roots that extensibility of the separated stele was higher than that of the cortical sleeve and therefore suggested that

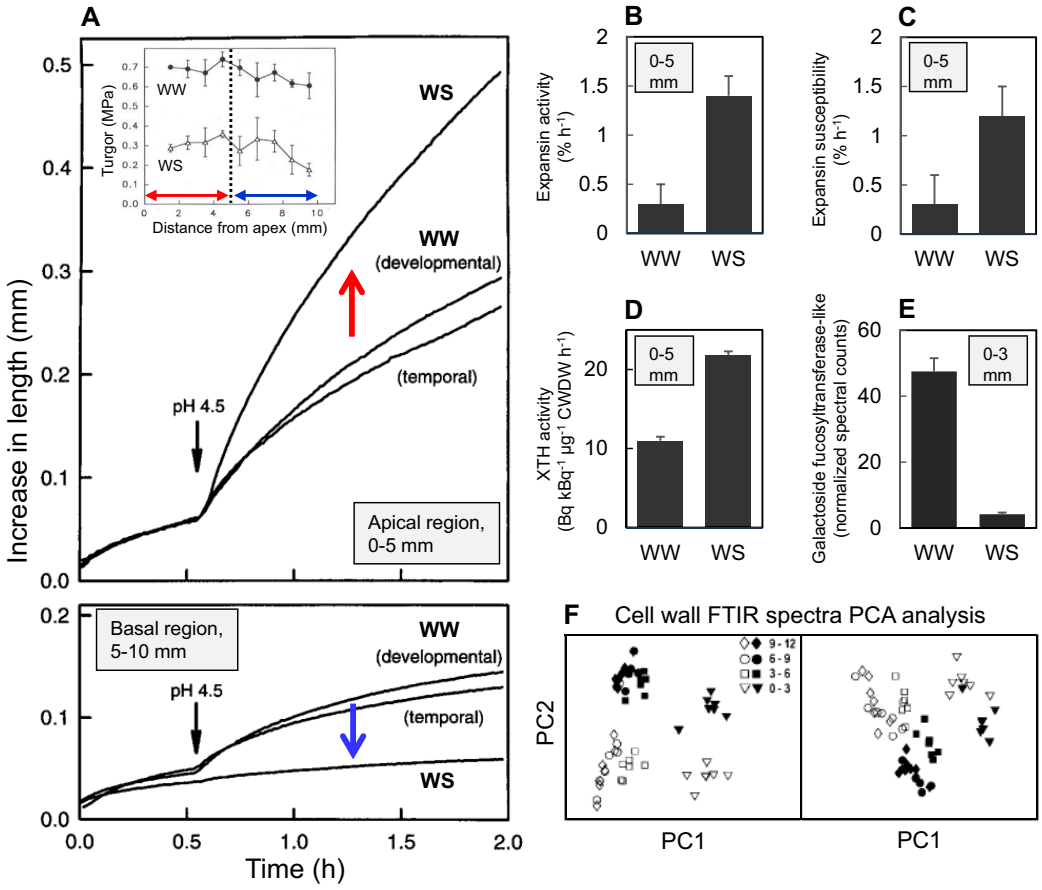

Figure 4. Changes in cell wall–yielding properties and composition in the growth zone of water-stressed maize primary roots. **A)** Acid-induced extension was enhanced in the apical region (0 to 5 mm from the apex) and almost completely inhibited in the basal region (5–10 mm) of the growth zone in water-stressed roots (WS; vermiculite water potential of −1.6 MPa) compared with well-watered (WW) developmental (roots of the same length) and temporal (roots of the same age) controls. The increased acid-induced extension in the apical region is thought to play an important role in maintaining elongation in this region (Fig. 3) despite substantially decreased turgor (inset) due to incomplete osmotic adjustment (see Fig. 6). Conversely, inhibition of acid-induced extension in the basal region, together with decreased turgor, likely contributes to premature slowing and cessation of elongation as cells are displaced through this region (Fig. 3). The apical region of water-stressed compared with well-watered roots also showed large increases in **(B)** expansin activity (change in slope of acid-induced extension of heat-killed cucumber hypocotyl wall preparations following addition of maize root tip expansin extract), **(C)** expansin susceptibility (change in slope of acid-induced extension of heat-killed maize root tip wall preparations following addition of cucumber expansin extract), and **(D)** XTH activity per unit of cell wall dry weight (CWDW), as well as **(E)** decreased abundance of galactoside 2-α-1-fucosyltransferase-like protein. **F)** Principal component analysis (PCA) of cell wall Fourier transform infrared (FTIR) spectra showed that different regions of the growth zone (delineated as mm from the apex) of water-stressed roots (black symbols, water potential of −0.5 MPa imposed with PEG 6000 in solution culture) are compositionally different compared with respective regions of well-watered controls (open symbols). Left and right panels show different wavenumber ranges. **A**, **B**, and **C** modified from Wu et al. (1996), Figures 1, 3B, 6A; **A** inset modified from Spollen and Sharp (1991), Figure 2B; **D** modified from Wu et al. (1994), Figure 3C; **E** modified from Voothuluru et al. (2016), Figure 6; **F** reproduced from Fan et al. (2006), Figure 3; **A–D** and **F** by permission of ASPB, **E** by permission of John Wiley and Sons.

properties of the endodermis and/or the inner layers of the cortex, rather than stelar tissues, are rate limiting for root elongation. Consistently, there is evidence that the endodermis may play a key role in hormone-mediated control of root growth (Dinneny 2014). For example, the endodermis was shown to be the primary GA/DELLA-responsive tissue regulating root growth in *Arabidopsis* (Úbeda-Tomás et al. 2008). On the other hand, evidence suggests that the properties of the epidermis and/or cortex are also important in determining *Arabidopsis* root elongation (Dyson et al. 2014; Vaseva et al. 2018; Verslues and Longkumer 2022), similarly to the more well-characterized regulation of shoot growth (Kutschera and Briggs 1988; Wakabayashi et al. 1989; Peters and Tomos 2000; Passioura and Boyer 2003; Kutschera and Niklas 2007; Savaldi-Goldstein et al. 2007).

Along with the increases in lignin, there is evidence suggesting that water-stressed maize primary roots have differential accumulation of cell wall–bound ferulates in the apical and basal regions of the growth zone (Fan et al. 2006; Spollen et al. 2008; Yamaguchi and Sharp 2010). Ferulates and other hydroxycinnamates are abundant in the cell walls of monocotyledonous plants and have a role

in cross-linking wall polysaccharides, including hemicellulose, xylans, pectins, and lignin (Vogel 2008; Vermerris et al. 2010; Hatfield et al. 2018). In mature root and shoot tissues, decreased wall extensibility strongly correlates with increases in cell wall–bound ferulates (Tan et al. 1992; MacAdam and Grabber 2002; Azuma et al. 2005). Therefore, increased accumulation of ferulates in the basal region of the growth zone in water-stressed roots could be involved in enhanced cell wall cross-linking, thereby decreasing cell wall extensibility and elongation. Substantial modifications of cell wall composition in the growth zone of water-stressed maize primary roots were also suggested by cell wall and plasma membrane–enriched proteome analyses (Zhu et al. 2007; Yamaguchi and Sharp 2010; Voothuluru et al. 2016) together with transcriptome studies (Spollen et al. 2008; Opitz et al. 2016; Kang et al. 2023). In particular, modification of xyloglucan composition in the apical region was implicated by the spatial patterns of abundance of enzymes involved in xyloglucan biosynthesis (Fig. 4E). Xyloglucan forms load-bearing associations with cellulose microfibrils, and the potential structural modifications in xyloglucan composition likely impact the susceptibility of cell walls to wall-loosening and remodeling proteins. Along with previous reports of high levels of XTH activity in the root and shoot growth zones of several species (Fry et al. 1992; Wu et al. 1994), the evidence collectively indicates that cell wall remodeling from xyloglucan composition may have an important role in growth regulation of water-stressed roots.

The specific examples of lignin, ferulate, and xyloglucan compositional changes as well as the findings of substantial modifications of cell wall extensibility in water-stressed roots indicate that combining kinematic growth analyses with comprehensive cell wall compositional analyses will enable deciphering of the functional role of various cell wall components. Furthermore, it will be important to ascertain whether stress-induced changes occur in a cell type-specific manner and how these changes impact tissue-level and organ-level growth characteristics. The technical challenge of obtaining the requisite amounts of tissues for cell wall compositional analysis has prevented detailed characterization of the relationship with root growth responses to water stress (Wu and Cosgrove 2000; Cosgrove 2016). Recent developments in glycome profiling and immunohistochemistry (Pattathil et al. 2010) as well as nanoimaging and nanomechanical techniques (Kozlova et al. 2019; Coste et al. 2020) provide unprecedented opportunities for studying plant cell walls from subcellular to organ scales (Bou Daher et al. 2018; Sampathkumar et al. 2019; Petrova et al. 2021). This multiscale approach will unveil how components interact within the cell wall matrix and how they impact cell expansion and root growth under normal and water deficit conditions. In the long term, knowledge from these studies will pave the way to selectively alter cell wall components in a tissue-specific manner to promote stress-responsive growth in plants and enhance agricultural productivity under water deficits.

Osmotic adjustment in roots growing under water deficits

As discussed above, roots exhibit a high capacity to enhance cell wall–yielding properties under water deficit conditions, allowing elongation to continue despite substantial decreases in turgor (Figs. 2 and 4A). However, if tissue water potentials continue to decline with further soil drying, turgor may decrease below the lower limit to which the yield threshold can be adjusted, in which case cell expansion can no longer occur. Accordingly, a second key mechanism for growth maintenance in water-stressed tissues is turgor maintenance by osmotic adjustment (Morgan 1984; Blum 2017; Turner 2018). With osmotic adjustment, increases in cellular solute concentrations (by processes other than dehydration, which does not result in turgor maintenance) lower the osmotic potential and thereby maintain the osmotic driving force for water uptake. A number of early studies reported increased concentrations of sugars and other solutes in root and shoot tissues under water stress conditions and recognized that these changes may positively correlate with drought resistance (Martin et al. 1931; Eaton and Ergle 1948; Iljin 1957). Subsequent studies established that roots, especially the growth zone, have a high capacity for turgor maintenance by osmotic adjustment (Fig. 5) and that this response is associated with continued root elongation under water deficit conditions (Greacen and Oh 1972; Sharp and Davies 1979; Westgate and Boyer 1985). Further, it has been shown that roots can exhibit more pronounced osmotic adjustment than leaves under equivalent water stress conditions (Fig. 5; Sharp and Davies 1979; Hsiao and Xu 2000).

To understand the regulation of osmotic adjustment in growing regions, it is important to recognize that increases in solute concentration can occur by 2 distinct overall processes. First, there may be increases in the net rate of solute deposition (encompassing uptake, import, local generation, utilization), which could contribute to growth maintenance. Second, if tissue volume expansion is inhibited, this will reduce rates of water uptake (water represents about 90% of volume increases) and, therefore, of solute dilution. Indeed, this distinction combined with the sensitivity of shoot growth to water stress (Fig. 1A) contributed to early controversy about the potential benefits of osmotic adjustment (Turner and Jones 1980; Steponkus et al. 1982; Munns 1988; Serraj and Sinclair 2002). For example, Wilson and Ludlow (1983, p 536) suggested: "It seems somewhat contradictory to consider osmotic adjustment as a benefit to maintaining growth if the contributing solutes only increase in concentration because growth (and hence solute demand) has slowed down." This view led in turn to the important question of whether selection pressure for enhanced osmotic adjustment might result in reduced growth potential (Quisenberry et al. 1984).

In the case of roots, the observed association of osmotic adjustment with maintenance of elongation under water stress appeared to satisfy this concern (Greacen and Oh

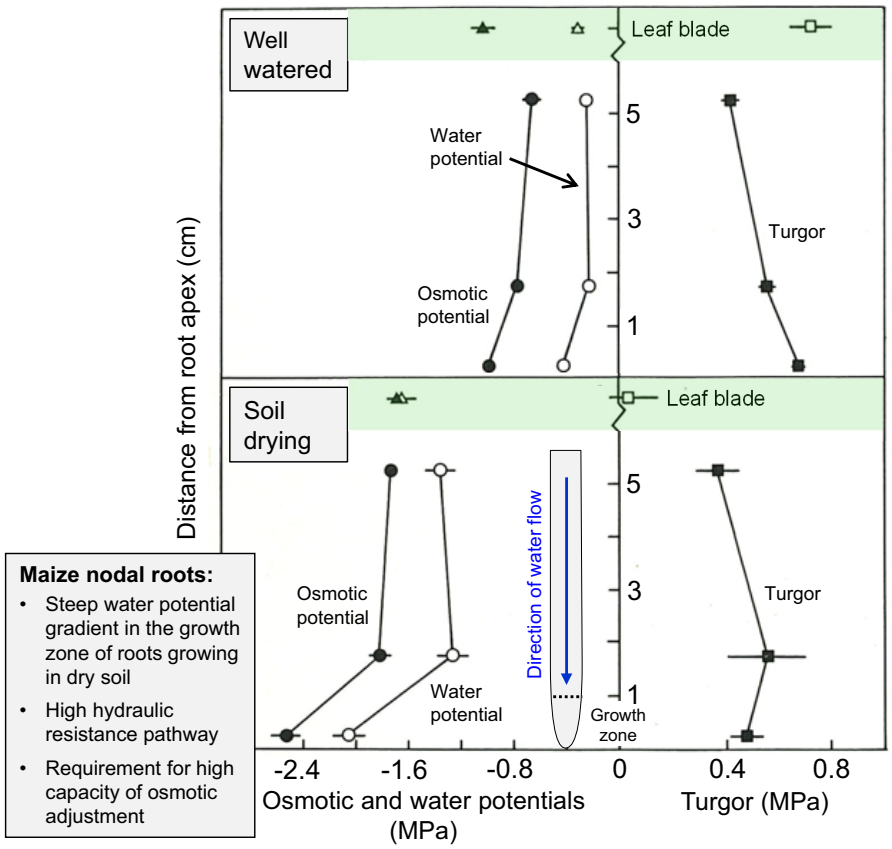

Figure 5. Osmotic adjustment in maize nodal roots under soil-drying conditions. Water potential, osmotic potential, and turgor in the growth zone and mature regions of nodal roots and in mature leaf blade tissues (green shading) of maize plants growing under well-watered or soil-drying conditions. In roots growing through dry soil, a steep "growth-induced" water potential gradient developed between the growth zone and adjacent mature region due to axial delivery of water and the hydraulic resistance of nonvascularized root tip tissues. This necessitates a high capacity for osmotic adjustment to maintain turgor in the root growth zone. The leaf blade was completely wilted in the same plants. Modified from Sharp and Davies (1979), Figure 6, by permission of Springer Nature.

1972; Sharp and Davies 1979; Westgate and Boyer 1985). However, quantitative assessment of this question in the growth zone of the maize primary root revealed a more complex picture, showing that osmotic adjustment involves a multifaceted interplay of morphogenic and metabolic responses (Sharp et al. 1988, 1990; Voetberg and Sharp 1991). While substantial decreases in osmotic potential occurred throughout the growth zone with increasing levels of water stress (Fig. 6A), different solutes were major contributors in the apical region where elongation was maintained vs the basal region of growth inhibition. The apical region showed a dramatic increase in proline concentration that contributed up to 50% of the decrease in osmotic potential (Fig. 6B; Voetberg and Sharp 1991). The particular use of proline for osmotic adjustment in the only slightly vacuolated cells of the apical region is consistent with its function as a cytoplasmic solute that is compatible with metabolism at high concentrations (Yancey 2005; Verslues and Sharma 2010). In contrast, hexoses increased minimally in the apical region but greatly in the basal region, suggesting a primarily vacuolar compartmentation, where they accounted for up to 60% of the adjustment (Fig. 6C; Sharp et al. 1990). The kinematic analysis of tissue expansion rate profiles (Fig. 3) was used to calculate spatial distributions of solute and water deposition rates using the continuity equation from fluid dynamics (Silk 1984), which revealed that the increased concentrations of these 2 solutes occurred by contrasting mechanisms (Sharp et al. 1990; Voetberg and Sharp 1991). In the apical region, the increase in proline resulted primarily from a large stimulation of the rate of proline deposition (by as much as 10-fold; Fig. 6D) in combination with an approximately 50% decrease in water deposition that was due specifically to the root thinning response as described above (Fig. 3A). In the basal region, in contrast, the large increase in hexose concentration occurred despite the fact that the rate of hexose deposition greatly decreased (Fig. 6E); this result is explained because the rate of water deposition decreased to an even greater extent due to the inhibition of both longitudinal and radial expansion in this region (Fig. 3).

The proline results shown in Fig. 6D provided the first demonstration that increased solute deposition rates can make a major contribution to the osmotic adjustment of

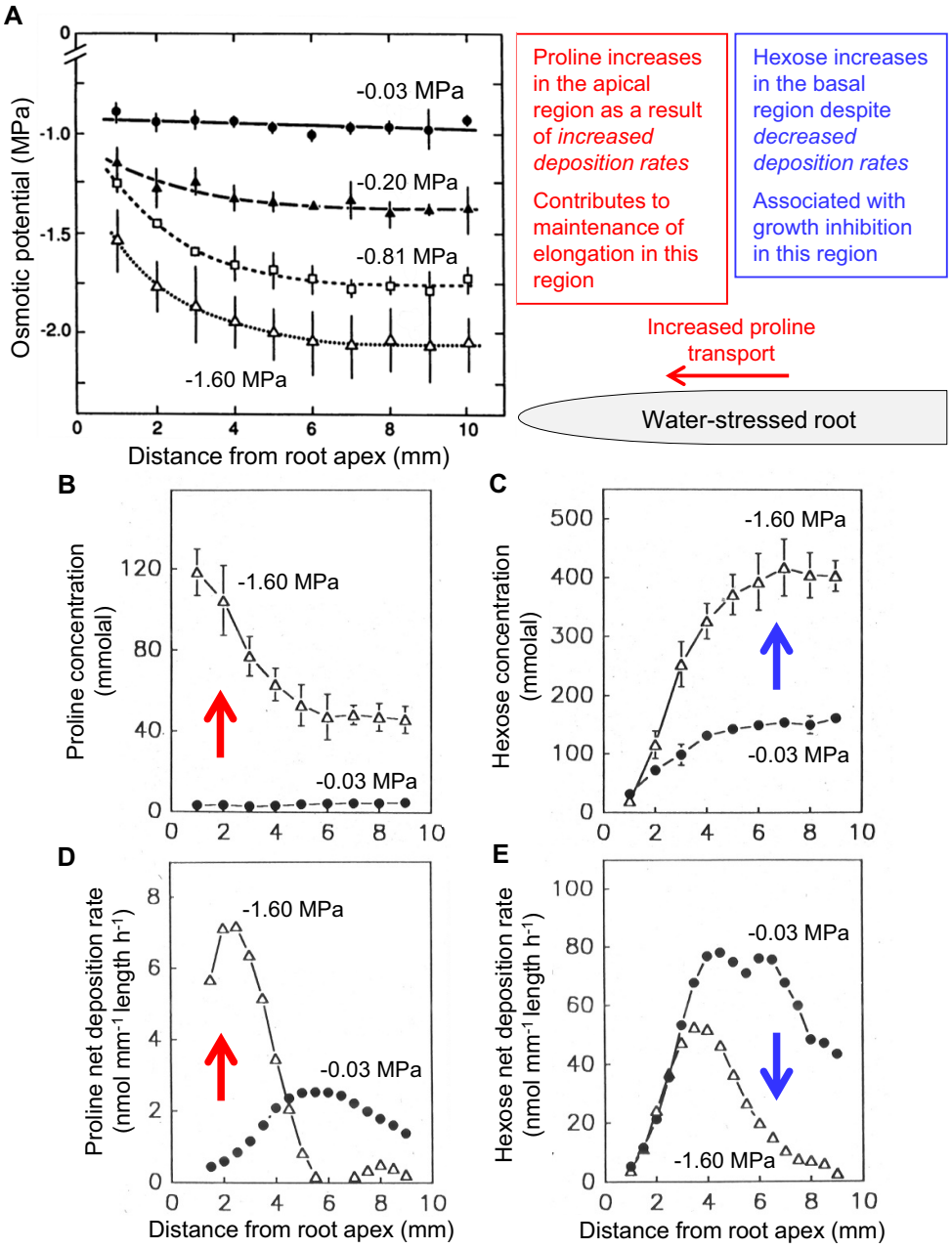

Figure 6. Different solutes contribute to osmotic adjustment in the apical and basal regions of the maize primary root growth zone. **A)** Spatial distribution of osmotic potential in the apical 10 mm of roots growing under well-watered conditions (water potential of −0.03 MPa) or at mild (−0.20 MPa), moderate (−0.81 MPa), or severe (−1.60 MPa) water stress. In the apical region where elongation is maintained in water-stressed roots (Fig. 3), increased proline concentrations **(B)** resulted primarily from increased net rates of proline deposition **(D)**. In the basal region of growth inhibition (Fig. 3), conversely, increased hexose concentrations in water-stressed roots **(C)** occurred despite decreased net rates of hexose deposition **(E)** because tissue expansion, and hence water deposition, decreased to a greater extent. **A**, **C**, and **E** modified from Sharp et al. (1990), Figures 2, 4A, 6C; **B** and **D** modified from Voetberg and Sharp (1991), Figures 1A, 2A; by permission of ASPB.

growing regions and, accordingly, this response is likely to be critical for the maintenance of elongation in the apical region of water-stressed roots (Fig. 3). Subsequent studies indicated that the response is attributable to increased rates of proline import from more basal regions of the root and/or the seed (Verslues and Sharp 1999; Raymond and Smirnoff 2002). In related observations, increased levels of proline in phloem sap (Girousse et al. 1996; Lee et al. 2009) and induction of proline transporter expression (Rentsch et al. 1996; Lehmann et al. 2010) were reported in water-stressed plants. Further analysis of proline metabolism showed that under water limitation, plants can coordinate the metabolism and transport of proline in shoot and root tissues to optimize growth and redox regulation (Verslues et al. 2023). In photosynthesizing shoot tissues, proline is synthesized to regenerate oxidized NADP pools (Sharma et al. 2011). The synthesized proline can then

be used for osmotic adjustment in mature tissues or transported to growing tissues for osmotic adjustment and catabolism (Sharma et al. 2011; Bhaskara et al. 2015; Verslues et al. 2023).

In contrast, because the dramatic increase in hexose concentration in the basal part of the root growth zone (Fig. 6C) was associated with inhibition of elongation in this region, this response is not so obviously adaptive—although it is emphasized that in the absence of the increased solute levels the tissues would have become significantly dehydrated. As discussed by Sharp et al. (1990), increases in solute concentrations are not an inevitable result when root growth is restricted by adverse conditions. Accordingly, it was concluded that the osmotic adjustment throughout the root growth zone likely represents an important and highly regulated process involving selective increases of specific solutes in combination with modulation of the growth pattern. More recently, multiomics analyses have provided additional insights into region-specific osmotic regulation within the growth zone of water-stressed maize and cotton primary roots (Spollen et al. 2008; Voothuluru et al. 2016; Kang et al. 2022, 2023).

An important aspect of osmotic adjustment and continuation of cell expansion in water-stressed plants is the maintenance of sink strength in growing tissues. When the root growth zone cannot obtain water from the surrounding soil, for example, during elongation into dry regions or across air gaps (see later section on lateral roots), water is delivered to the growth zone axially via the xylem and/or phloem from regions with greater water availability (upper layers after rainfall or irrigation, or via hydraulic lift from roots in deeper and wetter layers) (Boyer et al. 2010). However, functional xylem does not develop until some distance beyond the growth zone (McCully 1995), whereas phloem occurs closer to the apex and is understood to supply much of the water, along with sugars and other solutes, to support continued cell expansion under these circumstances (Bret-Harte and Silk 1994; Wiegers et al. 2009; Boyer et al. 2010; Rostamza et al. 2013). Water must then flow radially and apically via symplastic and/or apoplastic routes to the expanding cells. Due to the hydraulic resistance to water flow across the nonvascularized root tip tissues, the required growth-induced water potential gradients can be large in this situation (Fig. 5). In dry soil conditions especially, this necessitates a substantially higher capacity for osmotic adjustment in the growth zone than in adjacent mature tissues (Fig. 5; Sharp and Davies 1979; Westgate and Boyer 1985), which, in turn, requires high concentration gradients to drive growth-sustaining solute fluxes. Accordingly, mechanisms that lessen the magnitude of the water potential gradient are predicted to facilitate continued root elongation under water stress. The shortening of the growth zone and thinning of water-stressed roots (Fig. 3) could play adaptive roles in this regard because of the associated decrease in volume of expanding tissue. Additionally, a modeling study of root tip hydraulics indicated an advantage of more apical phloem differentiation (Wiegers et al. 2009). Modulation of aquaporin-regulated water transport across cell membranes within the growth zone (Chaumont et al. 1998; Hachez et al. 2006; Gambetta et al. 2013) could also play an important role. Notably, increased abundance of a TIP aquaporin was observed in the growth zone of water-stressed maize primary roots specifically in the apical region where elongation was maintained (Voothuluru et al. 2016), and upregulated expression of several aquaporin genes in the growth zone of water-stressed maize roots has also been reported (Poroyko et al. 2007; Opitz et al. 2016).

At the same time, species or genotypes that are able to maintain or enhance source-sink allocation to roots are likely to be better adapted to growing in water-limited conditions (Hsiao and Xu 2000). For example, in a comparison of 2 maize lines with differing abilities for primary root growth maintenance under water stress, the more tolerant line exhibited greater osmotic adjustment and accumulated more sugars and proline in the root growth zone (Velázquez-Márquez et al. 2015). Notably, a plasma membrane–enriched proteomics analysis revealed that 2 sugar transporters increased in abundance in the maize primary root growth zone under water stress conditions (Voothuluru et al. 2016). In related observations in *Arabidopsis*, sugar transporter loss-of-function mutants exhibited impaired primary and lateral root development under control and water stress conditions (Valifard et al. 2021), and conversely, enhanced activity of sucrose transporters was found to increase sucrose levels in the phloem and roots together with increased root growth and enhanced root/shoot ratio under water stress (Chen et al. 2022). These studies indicate that manipulation of source strength can enhance long-distance sugar transport and promote root growth under water stress. However, the authors did not study the accumulation of sugars and osmotic adjustment in developing root tissues, and further studies are needed to assess whether an integrated phenotype of enhanced sugar transport from source tissues and maintenance of osmotic adjustment as well as enhanced sink strength within the root growth zone underlies genetic variability of root development under water-limited conditions.

Studies of several plant species have provided unequivocal evidence that osmotic adjustment is linked to increased yield under water limitation (Blum 2017; Turner 2018). Osmotic adjustment in the roots, by enabling continued root growth and exploration of the soil for water, is recognized as a likely contributing factor (Serraj and Sinclair 2002). Indeed, several early reports showed a greater depth of soil water extraction, indicative of greater rooting depths, in lines selected for high osmotic adjustment in the leaves of wheat (Morgan and Condon 1986; Morgan 1995), sorghum (Wright and Smith 1983; Tangpremsri et al. 1991), and maize (Chimenti et al. 2006). However, it is possible that the enhanced root growth resulted from greater assimilate availability and diversion to the root system due to leaf osmotic adjustment sustaining photosynthesis (Wright et al. 1983; Mervyn and Ludlow 1987) rather than from osmotic adjustment in the roots

themselves. Definitive selection or metabolic engineering studies of the importance of osmotic adjustment in roots are lacking, reflecting the fact that over 50 years after first being reported (Greacen and Oh 1972) osmotic adjustment in roots remains an understudied area of investigation.

Reduced cell production in root meristems under water deficits

Organ growth can be regulated by impacting cell production and/or cell elongation processes. The previous sections focused on cell wall changes and osmotic adjustment as processes that contribute to the ability of roots to continue cell elongation under water-limited conditions. Interestingly, several studies showed that although local elongation rates were maintained in the apical region of the growth zone that encompasses the meristem, cell production was substantially reduced (Fraser et al. 1990; Saab et al. 1992; Sacks et al. 1997; Voothuluru et al. 2020; Kang et al. 2022). Reductions in cell production occurred even under moderate water stress (Longkumer et al. 2022), indicating that the effects were likely not due to insufficient availability of resources or cellular damage but, rather, represent an active restriction of meristem activity under water-limited conditions (Verslues and Longkumer 2022). This response could have an adaptive advantage for roots growing under water stress. Decreased cell production combined with maintenance of local elongation results in longer cells in the apical region of the growth zone (Sacks et al. 1997; Voothuluru et al. 2020). This response likely facilitates symplastic translocation of solutes from the phloem to the expanding cells because of the smaller number of plasmodesmata that have to be traversed, thereby helping to promote osmotic adjustment and the maintenance of cell elongation (Bret-Harte and Silk 1994; Sacks et al. 1997; Wiegers et al. 2009; Voothuluru et al. 2020). In addition, given the tendency for shortening of the growth zone in water-stressed roots (Fig. 3) and because fewer cells require less space for expansion, decreased cell production may be part of a coordinated response to reduce the energy costs of continued root elongation.

Nevertheless, it is possible that in an agricultural setting, the downregulation of cell production may be too sensitive to water stress and that overcoming this restriction could improve root growth under water-limited conditions (Verslues and Longkumer 2022). Indeed, recent studies showed that by increasing cell production using chemical or genetic approaches, it was possible to increase root elongation under water-stressed conditions. As mentioned earlier, water-stressed maize primary roots exhibit an increase in apoplastic ROS specifically in the apical region of the growth zone (Zhu et al. 2007; Voothuluru and Sharp 2013). Voothuluru et al. (2020) showed that decreasing ROS levels using scavenger treatments resulted in increased root elongation compared with control roots via promotion of both cell production and the spatial profile of cell elongation. In *Arabidopsis*, Longkumer et al. (2022) reported that mutant and transgenic lines with modified EGR-MASP1 protein stoichiometry (Clade E Growth-Regulating 2 protein phosphatase and Microtubule-Associated Stress Protein 1) exhibited enhanced meristem size and root elongation under water stress conditions. In both cases, the results showed that cell production was normally downregulated under water stress, with the result that root elongation was more inhibited than would otherwise have been the case. It remains unclear how signals from the apoplast/cytosol impact the cell cycle process in the nucleus (Voothuluru et al. 2020; Longkumer et al. 2022), and further studies are needed to identify the direct regulators of cell production and meristem size under water-limited conditions.

In contrast to the evidence for reduced cell production in moderately to severely water-stressed roots, it was reported that cell production was stimulated in the primary root of *Arabidopsis* under mild stress conditions (van der Weele et al. 2000). Also, a recent report showed that enhancement of maize lateral root length under mild water deficit was associated with sustained rates of cell production compared with well-watered controls (Dowd et al. 2020), as discussed in a later section. A future challenge will be to investigate whether specific manipulations of meristem size, cell production, and elongation in different root types can be achieved to optimize root system development under water-limited conditions that are relevant to production agriculture scenarios.

Hydrotropism and root growth responses to heterogenous soil water availability

In addition to the influence of water deficits on the rate and duration of elongation in different root types, effects of soil drying on root architecture are also determined by modifications of the direction of root elongation. For example, nodal root axes of maize (Nakamoto 1993), sorghum, and millet (Rostamza et al. 2013) exhibit phenotypic plasticity to grow more vertically in dry soil conditions, relating to the steep-angled root system ideotype discussed earlier in this review (Lynch 2013; Uga et al. 2013). Besides the possibility of enhanced gravity sensing and response, another potential contributing process to such responses is the phenomenon of hydrotropism, whereby to varying degrees the tips of plant roots can sense the moisture gradient of their surroundings and grow toward wetter areas. Hydrotropism was first observed over 150 years ago (reviewed in Takahashi 1997; Cassab et al. 2013; Dietrich 2018). Sachs (1872) and Molisch (1883) germinated pea, maize, and other seeds in a wet matrix that was suspended in the air. As soon as young roots grew out of the matrix and into the air (due to gravitropism), the roots curved and grew nearly horizontally along the bottom of the wet matrix. These results showed that the roots defied gravitropism to grow toward a water source. However, despite the potential importance of hydrotropism for water acquisition and drought tolerance, the physiological and molecular mechanisms of control have not been extensively studied.

Owing mainly to the efforts of a small number of research groups, we now have a basic understanding of the hydrotropic response (Cassab et al. 2013; Moriwaki et al. 2013; Dietrich 2018; Wang et al. 2020a). Like other responses to environmental signals, hydrotropic responses can be roughly divided into 3 stages: signal sensing, transduction, and the final response. Where in the root the moisture gradient is sensed remains a topic of active investigation, as detailed below. The signal then triggers complex biochemical and physiological changes in the elongating cells of the growth zone, including differential modifications of cell wall–yielding properties in the drier and wetter sides of the root. Kinematic analysis of the maize primary root revealed that these changes result in slower cell elongation on both the drier and wetter sides of the root compared with control roots but more so on the wetter side, and thus the root curves toward the water source (Wang et al. 2020a). Interestingly, this analysis also showed that relative to control roots, cell production rate was enhanced on the drier side of the root and inhibited on the wetter side during hydrotropic bending.

The location along the root that is able to perceive a moisture gradient is a controversial topic (Dietrich 2018; Wang et al. 2020a). Conflicting results have been obtained depending on the species or different approaches used within the same species. Early studies of several species suggested that the very tip of the root is responsible, particularly the root cap (e.g. Takahashi and Scott 1993; Takano et al. 1995). However, a study of the *Arabidopsis* primary root by Dietrich et al. (2017) showed that removal of the root cap and meristem using a microdissection or laser ablation technique did not prevent the hydrotropic response, and their results indicated that the elongation zone is able to perceive the moisture gradient via a cortex-specific mechanism. In contrast, a recent study of the maize primary root by Wang et al. (2020a) used a nondestructive approach to establish a moisture gradient at specific locations along the root. The results demonstrated that the very tip of the root (apical 1.5 mm, including the cap) was the most sensitive to the moisture gradient, whereas establishing the gradient only in the zone of elongation resulted in a weaker response. This nondestructive approach presents an opportunity to conduct a wider species survey to investigate the extent to which moisture sensing in hydrotropism varies among different species.

The mechanism by which roots sense a moisture gradient remains unknown. It is probable that the response is associated with changes in cellular water status and water transport in the root tissues, and mechanosensitive ion channels (Hamilton et al. 2015) that respond to cell turgor and volume changes have been suggested as potential sensing mechanisms (Dietrich 2018). In a study of pea primary roots exhibiting hydrotropic bending (Hirasawa et al. 1997), independent turgor measurements of the 2 halves of the growth zone that were facing or facing away from the hydrostimulant (achieved by splitting the root along its axis) did not reveal differences. However, turgor was calculated indirectly from water and osmotic potential measurements of the bulk tissues and lacked spatial resolution along or across the root. Direct turgor measurements of individual cells in the outer tissue layers using a pressure microprobe, and with spatial resolution along the root, are needed to definitively address this question. Alternatively, root cells may possess specific receptors capable of directly sensing the presence of water molecules in the surrounding environment.

Many studies have depicted a complex web of signal transduction pathways involved in hydrotropism. Several hormones, including IAA, ABA, cytokinins, and brassinosteroids, have been reported to be involved (Quiroz-Figueroa et al. 2010; Dietrich et al. 2017; Miao et al. 2018, 2021; Chang et al. 2019; Wang et al. 2020a). Additionally, other regulatory factors, including calcium signaling (Takano et al. 1997; Shkolnik et al. 2016), H^+-ATPases (Miao et al. 2021), and ROS (Krieger et al. 2016), have also been found to influence hydrotropic responses. For further information on the molecular and signaling processes involved in hydrotropism, interested readers are referred to a comprehensive review by Dietrich (2018). It is not yet known how these signal transduction pathways ultimately regulate the cell production and cell elongation responses that result in hydrotropic bending.

The growth direction of roots is influenced by other processes that may interact with hydrotropism, for example, the interaction of hydrotropism with gravitropism (Takahashi et al. 2009; Dietrich 2018). Among the different hormones that are involved in hydrotropic bending, it has long been proposed that IAA plays an important role. Whether an asymmetric distribution of IAA is necessary for hydrotropic bending, however, remains an active area of investigation. Shkolnik et al. (2016) reported that asymmetric distribution of IAA, based on the fluorescence intensity of an IAA reporter protein, is not required for hydrotropism in *Arabidopsis* because an asymmetric IAA distribution was not observed before bending. Other studies, using indirect approaches such as IAA transporter inhibitors or expression of IAA responsive genes, showed that the asymmetric distribution of IAA is required but is species dependent (Nakajima et al. 2017; Fujii et al. 2018). In maize primary roots, Wang et al. (2020a) quantified hormones directly in the drier and wetter halves of the root tip during hydrotropic bending and found that IAA content, alongside ABA, was higher on the dry side compared with the wet side and that the asymmetric IAA distribution occurred before bending. The higher IAA concentration on the dry side was surprising because a higher concentration of IAA on the lower side of the root during gravitropism results in the inhibition of root cell elongation (Evans 1991; Swarup and Bennett 2009; Konstantinova et al. 2021). This example suggests that the growth control mechanisms involved in gravitropic and hydrotropic curvature may employ different mechanisms, even though both involve IAA.

Because signal sensing, transduction, and root bending encompass the entire growth zone and involve many cell types on both sides of the root, further studies will need to be conducted with spatial resolution and at the tissue- or cell-specific level. Among the tools currently available, single-cell

transcriptome analysis has become a mature technology (Rodriques et al. 2019; Ryu et al. 2019) that will allow for the construction of transcript response maps along the root in different cell types and at different time points. With the aid of such comprehensive approaches combined with gene function analysis, our understanding of the complex molecular mechanisms underlying root hydrotropism is likely to advance significantly. There is also a need to develop techniques that are more sensitive than those currently available so that the responses of different root types, including lateral roots, can be characterized. These advances will allow assessment of genetically controlled traits and the biological significance of hydrotropism, particularly its potential role in enhanced water acquisition and drought tolerance.

Role of ABA in root growth responses under water deficits

The involvement of plant hormones in the regulation of plant growth responses to water deficits has been investigated for many decades (Vaadia 1976; Davies and Zhang 1991; Wilkinson and Davies 2002; Waadt et al. 2022). Even for the focus of this review on root growth responses, comprehensive coverage of the roles of different hormones, and their many interactions, is beyond the scope of the article. Instead, we provide a brief history of key discoveries of the role of ABA in root growth regulation under water deficit conditions. Among the hormones, ABA has received the most attention in this regard. However, despite the long-standing interest in the involvement of ABA in root (and shoot) growth regulation, its roles have been challenging to decipher (Sharp 2002; Humplik et al. 2017; Li et al. 2017).

Early interest in the involvement of ABA in regulating plant growth responses to water stress was stimulated because first, it often accumulates in water-stressed tissues in correlation with growth inhibition, and second, it commonly inhibits growth when applied to nonstressed plants. Accordingly, ABA was frequently cited as a potential cause of reductions in root and shoot growth under water-stressed conditions (Quarrie and Jones 1977; Creelman et al. 1990; reviewed in Trewavas and Jones 1991). An example is provided by the observation that in well-watered maize seedlings, primary root elongation is progressively inhibited when increasing concentrations of exogenous ABA are applied (Fig. 7A; Sharp et al. 1994). However, interpretation of such findings assumes that effects of applied ABA on growth of nonstressed plants are similar to those of endogenous ABA accumulation in water-stressed plants, which may not be the case. To bypass this concern, mutants, transgenics, or chemical inhibitors can be used to examine the effects of decreasing ABA synthesis or sensitivity on the growth of water-stressed plants. However, despite the availability of ABA-deficient mutants as early as the 1970s (Imber and Tal 1970), this approach was not taken until a study of ABA-deficient maize seedlings by Saab et al. (1990, 1992). Both the *vp5* mutant, which is deficient in carotenoid (and ABA) biosynthesis, and fluridone, an inhibitor of carotenoid (and ABA) biosynthesis, were used to reduce ABA levels under water stress. To ensure that inhibition of carotenoid synthesis, rather than ABA itself, was not a cause of observed growth responses, confirmatory experiments were subsequently conducted (Sharp 2002) using the *vp14* mutant (mutated in a *9-cis-epoxycarotenoid dioxygenase* [*NCED*] gene), which is impaired in the synthesis of xanthoxin that represents the first committed step in ABA biosynthesis and is considered rate-limiting for water stress-induced ABA production (Tan et al. 1997; Qin and Zeevaart 1999). Also, the experiments were performed under conditions of minimal transpiration (darkness and near-saturation humidity) to avoid the typical "wiltiness" of ABA-deficient plants (due to impaired stomatal function) that can confound interpretation of growth responses (Sharp et al. 2000; Sharp 2002). All 3 approaches showed that reduced ABA levels substantially inhibited primary root elongation under water stress, with a common relationship of growth inhibition to ABA deficiency in the root growth zone (Fig. 7A). Notably, the inhibition of root growth involved impairment of the normal ability to maintain cell elongation in the apical region of the growth zone (Fig. 3), resulting in further shortening of the growth zone toward the apex (Saab et al. 1992; Sharp et al. 1994). Root elongation was restored when growth zone ABA content was returned to normal levels by applying exogenous ABA (Fig. 7B; Sharp et al. 1994). These experiments revealed that rather than acting as a growth inhibitor, ABA accumulation is required for the maintenance of primary root elongation in water-stressed maize seedlings. Notably, this conclusion could not be inferred by applying ABA to nonstressed seedlings, which resulted in growth inhibition over the same range of tissue ABA levels (Fig. 7A). Accordingly, the results reveal that the root growth response to ABA accumulation was altered by the water-limited environment.

Subsequent studies have similarly reported that under water stress conditions, primary root elongation was inhibited in an ABA-deficient tomato mutant (*notabilis*, also a *NCED* mutation; Zhang et al. 2022) and in fluridone-treated *Arabidopsis* and rice seedlings (Xu et al. 2013). In addition, several studies have shown that ABA, generally at low concentrations, can promote root growth in well-watered plants, whereas higher concentrations are generally inhibitory (Li et al. 2017; Miao et al. 2021). Based on these observations, Li et al. (2017) speculated that the biphasic response to applied ABA may be causally related to the promotion of root elongation that has occasionally been reported under mild water stress conditions (Triboulot et al. 1995; Maia et al. 2013), whereas root growth eventually becomes inhibited under more severe water stress (Figs. 1A and 3; Westgate and Boyer 1985; Sebastian et al. 2016). However, it is important to note that the necessity for ABA accumulation in water-stressed maize primary roots (Fig. 7, A and B) was demonstrated under severe water stress conditions (water potential of −1.6 MPa), and the highest levels of ABA occurred in the apical region of the growth zone, where local elongation rates were maintained (Fig. 3B; Saab et al. 1992). It

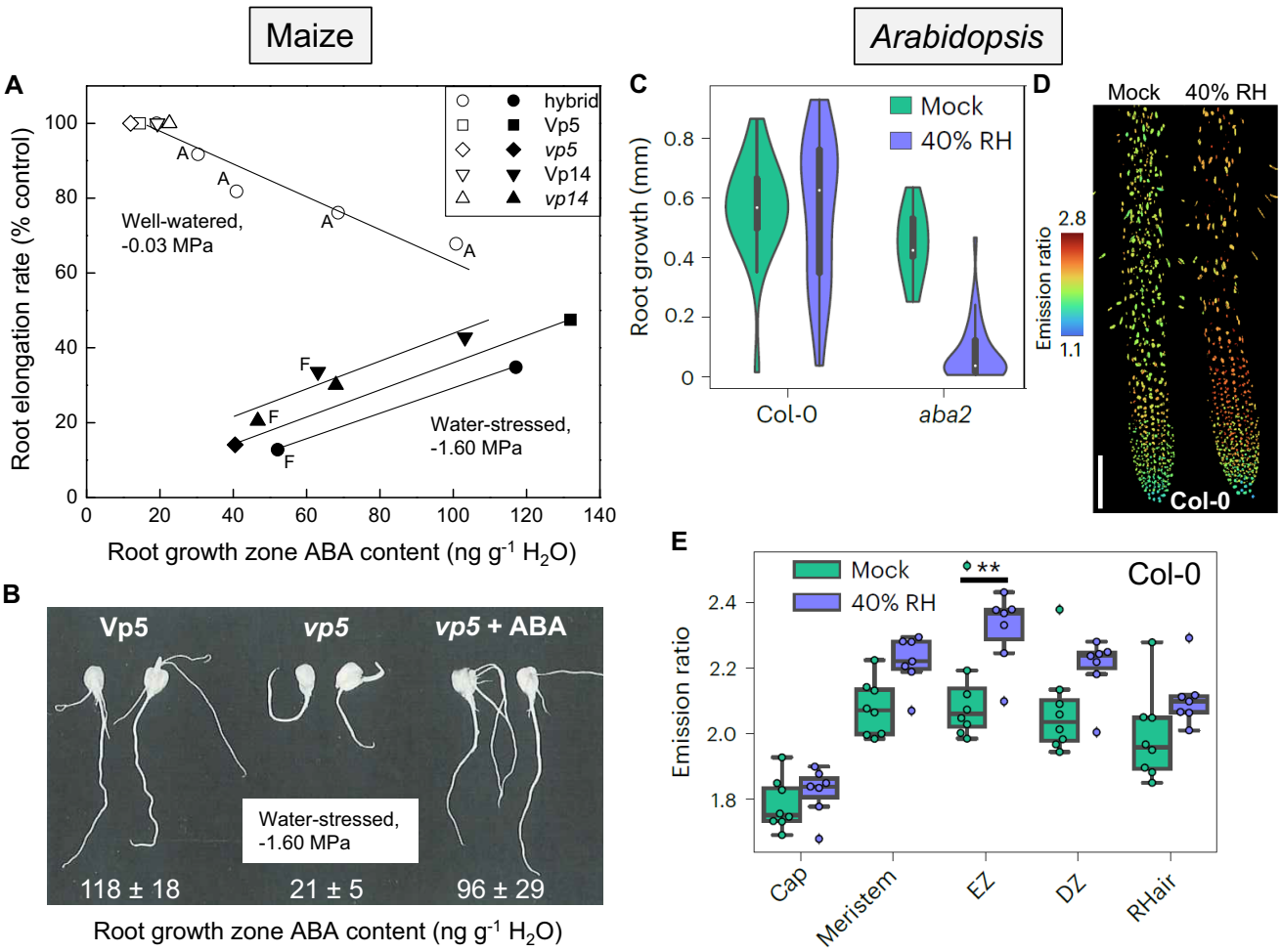

Figure 7. Increased endogenous ABA levels are necessary for maintaining root growth under water deficit conditions. **A)** Maize primary root elongation rate as a function of ABA content in the growth zone (apical 10 mm) for various genotypes growing in vermiculite under well-watered (water potential of −0.03 MPa, open symbols) or water-stressed (water potential of −1.60 MPa, closed symbols) conditions. In well-watered roots, the growth zone ABA content of hybrid (cv. FR27 × FRMo17) seedlings was raised above the normal level by adding various concentrations of ABA (A) to the vermiculite, which caused progressive inhibition of root elongation. Conversely, in water-stressed roots, the growth zone ABA content was decreased below the normal level by treatment with fluridone (F) or by using the *vp5* or *vp14* mutants (ABA deficient), which resulted in inhibition of root elongation with a common relationship of growth inhibition to ABA deficiency. Data are plotted as a percentage of the rate for the same genotype at high water potential. **B)** Recovery of elongation in water-stressed roots of the *vp5* maize mutant when growth zone ABA content was restored by applying exogenous ABA. **C)** *Arabidopsis* primary root growth was greatly reduced in the *aba2* mutant (ABA deficient) but not in the Col-0 wild-type when grown under conditions of low aerial relative humidity (40% RH) compared with a high humidity control (Mock) treatment. The roots were growing in well-watered soil. **D)** ABA accumulation in the growth zone of wild-type roots in the low humidity treatment was visualized using the ABACUS2s ABA biosensor. **E)** Relative quantification of the emission ratio signal in **(D)** in various regions of the root showed that the elongation zone (EZ) accumulates more ABA when grown in the low humidity treatment. DZ, differentiation/maturation zone; RHair, root hair zone. **A** reproduced from Sharp (2002), Figure 2, by permission of John Wiley and Sons; **B** modified from Sharp et al. (1994), Plate 2 and Table 1, by permission of Oxford University Press; **C** to **E**, modified from Rowe et al. (2023), Figure 4, CC BY 4.0.

should also be noted that in the ABA-deficient roots in which elongation under water stress was impaired, ABA levels remained much higher than in well-watered plants (Fig. 7A).

Interestingly, a recent study using the ABA-deficient *aba2* mutant of *Arabidopsis* (impaired in the conversion of xanthoxin to ABA-aldehyde) showed that increased levels of ABA in the primary root growth zone are also required for growth maintenance under conditions of low (40%) aerial relative humidity but where the roots were growing in well-watered soil (Rowe et al. 2023). ABA accumulation in the root growth zone of the wild-type (Col-0) in the low-humidity treatment was visualized using the recently developed ABACUS2s ABA biosensor (Fig. 7, D and E). The water status of the root growth zone was not measured, but effects were likely to have been minimal due to the relative hydraulic isolation of the apical region of roots growing in wet soil from lower water potentials in more shootward locations (Zwieniecki et al. 2003; Wiegers et al. 2009). In this situation,

the accumulated ABA in the root growth zone likely represents delivery of shoot-sourced ABA via the phloem (McAdam et al. 2016). As shown in Fig. 7C, the low–aerial humidity treatment caused severe inhibition of root elongation in the *aba2* mutant, whereas there was no effect in the wild-type control. Thus, the results showed that increased levels of ABA in the root growth zone are required to maintain root growth even under very mild water stress conditions.

These findings raise the question of why increased levels of ABA are required for root growth maintenance under plant water deficit conditions regardless of whether the water status of the root tissues themselves changes minimally or substantially. Continuing the study of ABA deficiency (*vp5*, *vp14*, fluridone treatment) in severely water-stressed maize primary roots described above, it was shown that an important role of ABA accumulation is to prevent excess ethylene production that would otherwise cause root growth inhibition (Spollen et al. 2000; Sharp 2002). In ABA-deficient seedlings under water stress, rates of ethylene evolution increased in correlation with both the degree of ABA deficiency and the inhibition of root elongation, and moreover, root elongation was restored by each of 3 inhibitors of ethylene synthesis or action (Spollen et al. 2000). These findings were consistent with an early observation that ABA-deficient tomato mutants exhibit increased ethylene production (Tal et al. 1979) and supported the idea initially suggested by Wright (1980) that ABA accumulation in water-stressed plants may function to restrict stress-induced ethylene production. This hypothesis was based on observations that pretreatment with exogenous ABA prevented wilting-induced increases in ethylene in wheat leaves. More recently, ABA-ethylene interactions have been shown to be involved in various growth responses of plants to water deficits and other abiotic stress conditions (Yang et al. 2004; Rowe et al. 2016; Valluru et al. 2016; Huang et al. 2022). Interestingly, it was recently reported that ethylene is involved in modulating shoot responses to high aerial humidity in *Arabidopsis* (Jiang et al. 2024). Accordingly, it is tempting to speculate that ABA-ethylene interactions may also be involved in the above-described ABA dependency of root growth under low–aerial humidity conditions (Fig. 7, C–E).

Research over several decades has demonstrated that ABA also plays regulatory roles in several other processes contributing to root growth responses to water deficits that were described in earlier sections of this review (Fig. 8). These processes include proline accumulation for osmotic adjustment (Ober and Sharp 1994; Sharma et al. 2011), shoot-to-root sugar transport and accumulation (Chen et al. 2022; Gong and Yang 2022), cell wall XTH activity (Wu et al. 1994), plasma membrane H^+-ATPase activity and cell wall pH regulation (Ober and Sharp 2003; Xu et al. 2013; Miao et al. 2021), ROS regulation (Zhang et al. (2014), hydraulic conductivity including aquaporin activity (Hose et al. 2000; Shahzad et al. 2024), and hydrotropism (Miao et al. 2021). In addition, ABA is involved in the regulation of suberin deposition in the root exodermis and/or endodermis (Wang et al. 2020b; Shiono et al. 2022) and can thereby impact root/soil hydraulics (Baxter et al. 2009; Kreszies et al. 2019; Cantó-Pastor et al. 2024). In many cases, ABA's function involves interactions with IAA and other hormones as well as ethylene (Xu et al. 2013; Rowe et al. 2016; Zhang et al. 2022). Further work is needed to fully decipher the interplay between ABA and other plant hormones in coordinately regulating the cellular processes involved in root growth and RSA development under water deficits.

Growth of lateral roots and root hairs under water deficits

Although this review has focused on the growth responses of root axes to water deficit conditions, the responses of lateral roots are also essential to understand. Lateral roots comprise the bulk of the root system's length, and their spatial and temporal distribution within the soil matrix has major impacts on the ability of the plant to forage for water and nutrients (Russell 1977; Ahmed et al. 2016). Hence, considerable research has focused on understanding how the production and elongation of lateral roots is affected in plants growing under various adverse environmental conditions (Waidmann et al. 2020). A brief synopsis of key responses of lateral root development to water deficits follows.

Lateral roots develop in the maturation zone of primary, seminal, and nodal root axes and subsequently undergo higher-order branching. In terminal drought conditions, evidence in maize indicates that the development of fewer and longer lateral roots on deeper nodal roots can be more efficient than shorter and numerous lateral roots that are more widely distributed throughout the root system (Zhan et al. 2015). Conversely, analysis of root growth phenotypes in diverse maize lines showed that lateral root branching is a plastic response and that more prolific lateral rooting can be beneficial under intermittent irrigation conditions (Klein et al. 2020). Indeed, increased lateral root proliferation under soil-drying conditions (Fig. 1B) was reported a century ago by Weaver (1926). Several later studies reported that promotion of lateral root elongation and/or number occurs specifically in response to mild water deficits, whereas inhibition of lateral root development generally follows as stress becomes more severe (Read and Bartlett 1972; Ito et al. 2006; Kano et al. 2011; Dowd et al. 2019). A biphasic response of lateral root development to increasing water deficits is rational from the perspective of water uptake; growth promotion under mild water deficits facilitates access to moisture in regions where water is still available, whereas in drier soil continued lateral root development is less effective in obtaining water and, therefore, maintenance of axial growth is prioritized to access deeper and wetter soil layers. It should be noted that although many other studies have concluded that water deficits inhibit lateral root development, imposed stress levels may have been too severe or the rate of dry-down too rapid to characterize the phase of growth promotion, for which high-resolution studies at mild stress levels are necessary (Dowd et al. 2019).

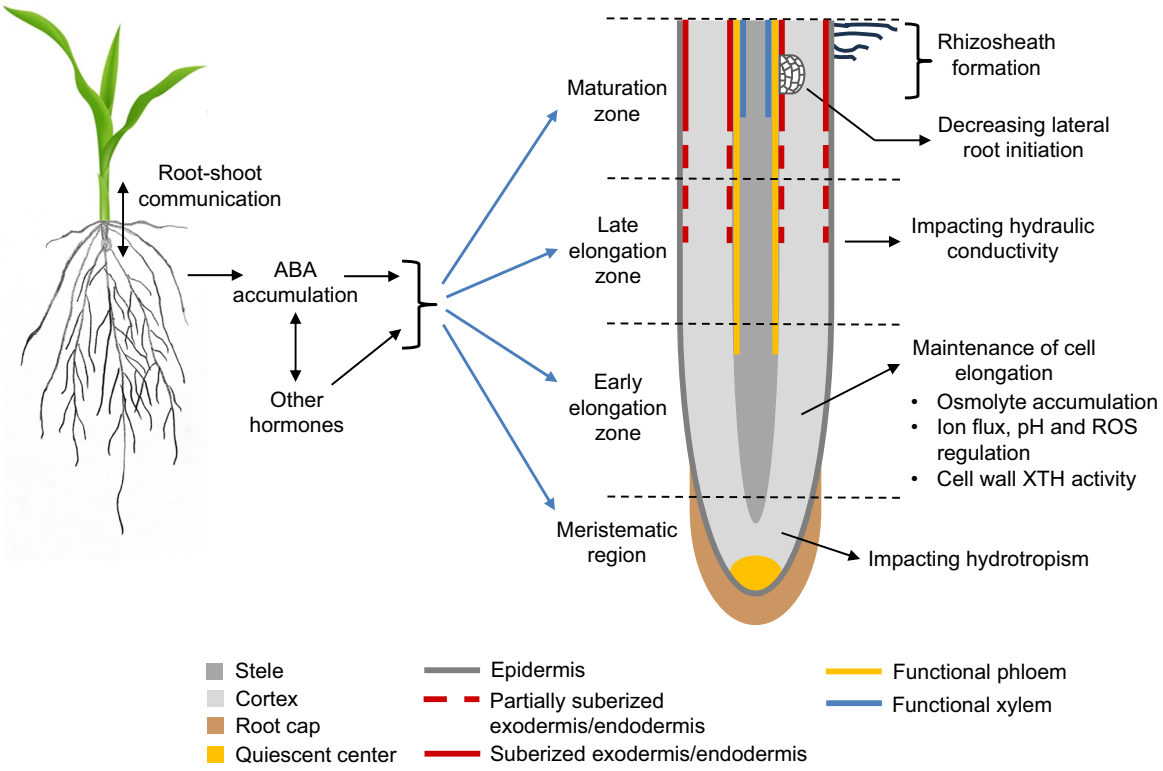

Figure 8. Schematic summarizing the effects of ABA accumulation on diverse cellular processes in different regions of roots growing under water stress conditions.

Although much is known about the regulation of lateral root formation and elongation (Motte et al. 2019; Waidmann et al. 2020), studies of mechanisms underlying increased lateral root growth under water deficits are limited. A significant aspect of lateral root development is their determinate growth pattern, whereby the meristem is genetically programmed to stop cell production at a particular stage of development, resulting in finite growth durations and root lengths (Varney and McCully 1991; Passot et al. 2018, Dowd et al. 2020). As a root approaches determinacy, exhaustion of the apical meristem results in progressive shortening of the growth zone and cell maturation closer to the apex. Dowd et al. (2020) used kinematic growth analyses to demonstrate that enhanced elongation of maize (cv. FR697) first-order lateral roots from the primary root of mildly water-stressed plants (Fig. 9A) was attributable to a delay in the determinate growth program. This was evident from sustained rates of cell flux (approximating the rate of cell production from the meristem; Fig. 9B) and repression of decreases in cell elongation and growth zone length (Fig. 9C) that occurred over time in roots of well-watered plants. Further, large genotypic variation in these responses was evident, because a contrasting genotype (B73) that did not exhibit lateral root growth promotion under water deficits also did not exhibit any changes in the determinate growth program. Interestingly, in FR697 (but not B73), mild water deficits also suppressed lateral root thinning that accompanied the progression of determinacy in well-watered roots (Dowd et al. 2020). This contrasts with water stress–induced thinning of the maize primary root (Fig. 3A). As discussed above, thinning of water-stressed root axes is thought to be adaptive, enabling the root to efficiently maintain elongation and exploration of deeper soil. The contrasting suppression of thinning in lateral roots, along with the maintenance of elongation and thus of volumetric expansion, may help to maintain root-soil contact and thereby facilitate continued water uptake from the surrounding soil.

The cellular and genetic mechanisms underlying the interaction of water deficits with lateral root determinacy are not known. A number of transcription factors, auxin transport and signaling processes, folate metabolism, and other processes are involved in regulating indeterminate-to-determinate root development (Shishkova et al. 2008; Lucas et al 2011; Reyes-Hernández et al. 2014; Rodriguez-Alonso et al. 2018). Future studies of the regulation of delayed determinacy in lateral roots may provide new opportunities to enhance root system developmental plasticity under water deficits. It is also likely that, as in primary roots, mechanisms including changes in cell wall–yielding properties, osmotic adjustment, hormonal regulation, and other processes reviewed above are also important in lateral root growth promotion under water deficits.

Another example of the plasticity of lateral root development with varying water availability is provided by the responses of lateral root formation to transient or local

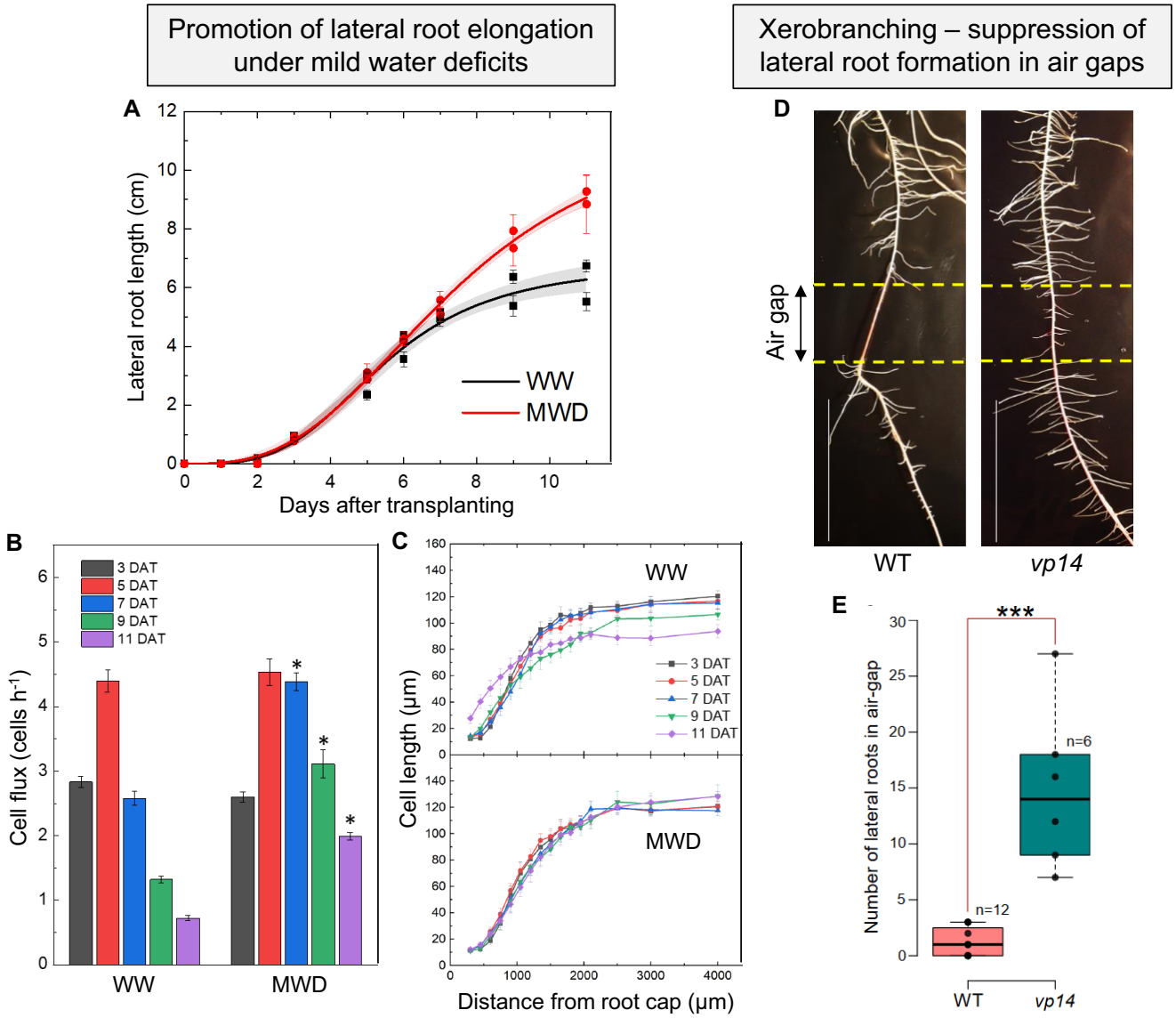

Figure 9. Impact of water availability on lateral root development in the maize primary root system. **A)** Average length, **(B)** cell flux, and **(C)** cortical cell length profiles along the growth zone of the 10 longest first-order lateral roots from the upper 15 cm of the primary root system of maize (cv. FR697) seedlings during 11 days after transplanting (DAT) to well-watered (WW) or mild water deficit (MWD, water potential of −0.28 MPa) conditions. Promotion of lateral root length in the MWD treatment was associated with delayed determinacy compared with WW roots, as evident from sustained rates of cell flux (the rate within a file that cells leave the growth zone, which under steady growth conditions equals the rate of cell production from the meristem) and repression of changes in cortical cell length profile, final cell length, and length of the growth zone that occurred in the WW roots over the course of the experiment. **D)** A xerobranching response is triggered in wild-type (WT) maize when growing root tips lose contact with water, for example, when growing across an air gap, causing repression of lateral root formation until the roots reenter moist conditions. **E)** The ABA-deficient mutant *vp14* produced a significantly higher number of lateral roots in the air gap compared with the wild-type. **A** to **C** modified from Dowd et al. (2020), Figures 3A, 5, 4, by permission of John Wiley and Sons. **D** and **E** reproduced from Mehra et al. (2022), Figure S3, by permission of AAAS.

heterogeneity of soil water. Interestingly, in contrast to the above-described promotion of lateral root development in response to mild soil water deficits, lateral root formation can be completely inhibited under otherwise moist conditions when the root axis temporarily loses contact with moisture, for example, during growth across air gaps (Fig. 9, D and E), in a process known as xerobranching (Orman-Ligeza et al. 2018). It was recently shown that the xerobranching response is regulated by hydraulic flux-responsive redistribution of ABA and IAA within the apical region of the axial root (Mehra et al. 2022). When roots enter an air gap, the phloem rather than the surrounding soil becomes the main source of water to the root growth zone, as described above. This reversal of the direction of water flow also alters the flow of phloem-derived ABA

between the inner and outer tissues, triggering closure of plasmodesmata, which, in turn, decreases the inward symplastic movement of IAA and thereby inhibits lateral root formation. ABA-deficient mutants are disrupted in the xerobranching response, for example, in the *vp14* mutant of maize (Fig. 9, D and E). When the root axis regains contact with moist soil, the changes in ABA and IAA flows are attenuated and normal lateral root branching resumes.

The xerobranching response is phenotypically similar to another response of lateral root formation termed hydropatterning (Bao et al. 2014). Under conditions of heterogeneity in water availability around the circumference of the axial root, lateral root formation occurs preferentially on the root surfaces in contact with moisture and is inhibited on air-exposed surfaces. Interestingly, however, although hydropatterning also involves auxin signaling (Orosa-Puente et al. 2018), the response is independent of ABA signaling, distinguishing it mechanistically from xerobranching as well as from other root growth responses to water stress described above (Fig. 7). Nevertheless, evidence suggests that modification of internal growth-induced water potential gradients that arise from the heterogeneity in water availability around the axial root growth zone are involved in the hydropatterning signaling mechanism (Robbins and Dinneny 2018).

In addition to lateral roots, root hairs, originating from epidermal cells, greatly increase the absorbing surface area and enhance root-soil contact, and there is evidence that longer and denser root hair phenotypes are more beneficial in reducing the water potential gradient across the soil-root interface than shorter and sparer phenotypes (Carminati et al. 2017; Burak et al. 2021; Marin et al. 2021; Cai et al. 2022). Accordingly, root hairs have long been assumed to enhance root water uptake, particularly in drier soils, although experimental evidence has been contradictory (Cai and Ahmed 2022). In addition to differences between species and in soil structural parameters, recent evidence suggests that in dry soil conditions, variable loss of root hair turgidity and shrinkage may explain some of the conflicting results (Duddek et al. 2022, 2023). Although shrinkage diminishes their effectiveness, the results nevertheless indicated that root hairs can facilitate water uptake under a range of low soil water potential conditions. In this regard, it is important to evaluate the capacity for osmotic adjustment and turgor maintenance in root hairs.

Root hairs are also an important determinant of rhizosheath formation, which can also positively influence root water uptake (North and Nobel 1997). Soil water deficits have been reported to increase the length of root hairs and enhance rhizosheath formation, and evidence indicates that these responses involve ABA and IAA signaling (Zhang et al. 2020a, 2021). Root hair density has also been shown to be influenced by heterogenous water availability although, intriguingly, with an opposite response to the above-described xerobranching and hydropatterning responses of lateral root formation. In a field study of wheat, White and Kirkegaard (2010) showed that root hair density was greatest where root-soil contact within pores in the soil matrix was minimal. Similarly, in their hydropatterning studies, Bao et al. (2014) observed that root hair development was much greater on the air-exposed root surface compared with surfaces in contact with water. Perhaps the promotion of root hair density concurrent with inhibition of lateral root formation in both situations facilitates maintenance of root-soil contact with minimal metabolic cost.

Future studies are needed to assess whether there is genetic variability within a species that impacts root hair density and length and whether this variability can improve drought tolerance (Cai et al. 2022). Given that there is considerable knowledge about the genes involved in root hair production and expansion (Li et al. 2016; Salazar-Henao et al. 2016; Zhang et al. 2020b), genetic targets with enhanced root hair phenotypes might improve root water uptake under drought conditions.

Conclusions, challenges, and avenues for future research

This review has highlighted several key advances in the understanding of root growth responses to water deficits that have been made over the past century. As summarized in Fig. 10, in many cases these responses are spatially variable within different regions of the root growth zone. Certainly, as emphasized in the title of the article, roots are not so hidden anymore due to rapid acceleration of interest in root development and function among the international plant biology community (Ephrath et al. 2020). Despite these advances, there are still challenges and gaps in understanding as well as important avenues for future research.

Changes in many processes during water stress occur either sequentially or simultaneously. In many cases, the interrelationships between different responses remain poorly understood, and many of the changes may occur indirectly or secondarily. The importance of gaining greater insight into this question was highlighted by Hsiao et al. (1976, p 497) in their conclusion that "... the causes of growth responses under water stress probably will not be understood until the sequence of physiological events developing as water stress sets in is better known." This knowledge is critical to decipher causal vs consequential components of root growth responses. Further, responses to water stress occur across subcellular, cellular, tissue, and organ scales and can differ depending on the stress severity and stage of development of the plant. It is essential to demonstrate that effects observed at different levels of organization are important for the regulation of root growth responses at the whole-plant level under various water deficit conditions.

In addition to changes in the responses of individual root growth and overall RSA under water deficits per se, it is important to understand how plants respond to other stresses that co-occur with soil drying under field conditions. For example, roots generally experience increased soil strength,

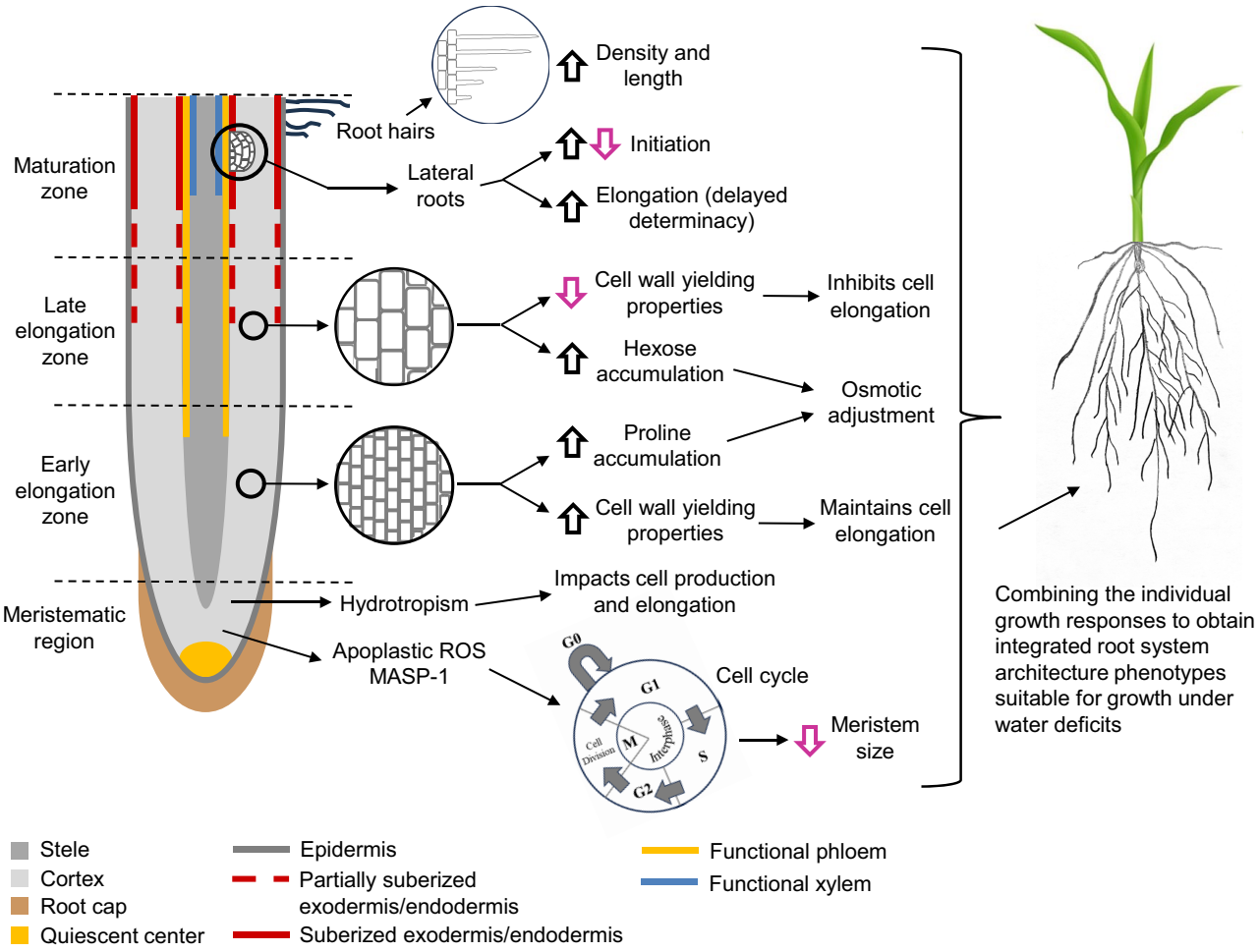

Figure 10. Schematic summarizing the effects of water stress on diverse cellular processes in different regions of roots growing under water stress conditions that eventually determine root system architecture.

which negatively impacts root elongation, simultaneously with decreased water availability (Bengough et al. 2011; Correa et al. 2019). To date, effects of water stress and soil strength on root growth, and the mechanisms underlying the responses, have generally been studied separately, although a few studies have varied soil water content and soil strength to assess the simultaneous impacts of both stresses on root elongation (Greacen and Oh 1972; Mirreh and Ketcheson 1973; Veen and Boone 1990). Importantly, the results suggest that mechanical impedance can be an important limitation to root elongation even in moderately dry soils (Bengough et al. 2011). Accordingly, it is important to examine potential interactions between mechanisms that determine the growth responses to the 2 stresses. Several mechanisms underlying root growth responses to water deficits are also involved in root growth regulation in response to soil strength. Importantly, although some mechanisms are common, for example osmotic adjustment (Greacen and Oh 1972), other processes play contrasting roles. For example, although enhanced cell wall loosening is associated with the maintenance of elongation in the apical region of water-stressed maize primary roots (Fig. 4), Schneider et al. (2021) reported that maize genotypes with thicker and more heavily lignified cortical cell walls (multiseriate cortical sclerenchyma) were better able to penetrate high-strength soils. In another example, it was recently shown that ethylene induces the synthesis of both IAA and ABA to regulate inhibition of elongation and promotion of radial expansion in rice primary roots growing in compacted soil (Huang et al. 2022). This functional pattern contrasts with the role of ABA in preventing excess ethylene production and thereby maintaining elongation in maize primary roots under water stress (Fig. 7, A and B), along with the root thinning response shown in Fig. 3A. Studies are needed to investigate how these and other regulatory processes are impacted when the 2 stresses co-occur.

A second abiotic stress factor that co-occurs with water deficits is high temperature, and future climate change scenarios predict increasing frequencies of combined drought and heat waves that can severely impact plant productivity (Zandalinas et al. 2021; Bheemanahalli et al. 2022). Recent studies with soybean plants subjected to water deficit, heat, and their combination found that leaves, flowers, and pods

respond differentially to the stress combination (Sinha et al. 2023a, 2023b). Although root growth responses were not evaluated, it is likely that root tissues acclimate and respond differentially to the individual and combined stressors.

Another key area for intensified future research is the role of root exudation, root-rhizosphere and root-microbiome interactions in root growth responses to water deficits (McCully 1999; Schnepf et al. 2022). Root exudation and mucilage secretion are considered important processes for root growth, particularly in dry and hardening soil conditions (Watt et al. 1994; Bengough and McKenzie 1997; Iijima et al. 2004), and are thought to impact rhizosphere hydraulic properties (McCully and Boyer 1997; Bais et al. 2006; Kroener et al. 2014; Naylor and Coleman-Derr 2018). There is considerable evidence suggesting that root-rhizosphere interactions, particularly with arbuscular mycorrhizal fungi, enable water and nutrient absorption in normal and water deficit conditions (Augé 2001; Bárzana et al. 2014; Augé et al. 2015). Differential spatial and temporal root exudation is hypothesized to impact the diversity and strength of microbial associations (Marschner et al. 2001; Farrar et al. 2003; Watt et al. 2003; Bais et al. 2006; Voothuluru et al. 2018). However, mechanisms involved in root exudation remain largely unknown (Volkov and Schwenke 2020; Williams and de Vries 2020). A deeper mechanistic understanding of root exudation processes and their modulation by environmental stimuli is important to improve our knowledge of beneficial plant-microbial interactions and to manipulate native microbial communities to enhance root and whole plant growth under water deficit conditions.

The coming decades offer tremendously exciting opportunities to build further on the strong foundation of understanding of the diversity of root growth responses to water deficits that has been summarized in this review. Ultimately, deciphering how plants integrate the effects of combined abiotic stresses and biotic interactions to coordinately regulate the diversity of spatially and temporally variable root growth responses will enable strategies for developing integrated phenotypes with RSA suitable for specific drought scenarios.

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Data availability

This historical review contains no new data.

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