



Review

Hydrotropism: Understanding the Impact of Water on Plant Movement and Adaptation

Malik Urfa Gul ¹, Anand Paul ^{1,2},*, Manimurugan S ³ and Abdellah Chehri ⁴

- Department of Computer Science & Engineering, Kyungpook National University Daegu, Daegu 41566, Republic of Korea
- Department of Computer Science & Engineering, Karpagam Academy of Higher Education, Coimbatore 641021, India
- ³ Department of Computer Engineering, University of Tabuk, Tabuk P.O. Box 741, Saudi Arabia
- Department of Mathematics and Computer Science, Royal Military College of Canada, Kingston, ON K7K 7B4, Canada
- * Correspondence: paul.editor@gmail.com

Abstract: Hydrotropism is the movement or growth of a plant towards water. It is a type of tropism, or directional growth response, that is triggered by water. Plants are able to detect water through various stimuli, including changes in moisture levels and changes in water potential. The purpose of this study is to provide an overview of how root movement towards water and plant water uptake are stabilized. The impact of hydrotropism on plants can be significant. It can help plants to survive in environments where water is scarce, and it can also help them to grow more efficiently by directing their roots towards the most nutrient-rich soil. To make sure that plant growth and water uptake are stabilized, plants must sense water. Flowing down the roots, being absorbed by roots, and evaporating from the leaves are all processes that are governed by plant physiology and soil science. Soil texture and moisture affect water uptake. Hydraulic resistances can impede plants' water absorption, while loss of water and water movement can change plants' water potential gradients. Growth causes water potential gradients. Plants respond to gradient changes. Stomata and aquaporins govern water flow and loss. When water is scarce, stomatal closure and hydraulic conductance adjustments prevent water loss. Plants adapt to water stream changes by expanding their roots towards water and refining the architecture of their roots. Our study indicates that water availability, or gradients, are impacted by systemic and local changes in water availability. The amount of water available is reflected in plant turgor. There is still a lot of work to be done regarding the study of how the loss and availability of water affect plant cells, as well as how biophysical signals are transformed in a certain way during their transmission into chemical signals so that pathways such as abscisic acid response or organ development can be fed with information.

Keywords: plant–water relations; hydrotropism; water sense in plants; water stress in plants; water potential gradient; Darcy's law; Ohm's law; computational modelling

1. Introduction

It is essential that plants are subjected to a never-ending barrage of sensory inputs from their surroundings through which they receive biotic and abiotic signals continuously in the form of environmental signals. It is important to understand that abiotic signals can come from a variety of sources, such as gravity, light, water, temperature, oxygen, carbon dioxide, and other gases, to name a few. The process by which the plant utilizes these inputs is called tropistic growth (or tropism), which refers to a type of growth that is guided by the plant in response to a stimulus. In general, if the growth of a plant is directed toward a signal it is considered to be positive, while when the growth of a plant is directed away from the signal it is considered negative. For instance, stems are typically characterized by a positive phototropism, in which the stem grows in the direction of the light source [1,2].



Citation: Gul, M.U.; Paul, A.; S, M.; Chehri, A. Hydrotropism: Understanding the Impact of Water on Plant Movement and Adaptation. *Water* 2023, *15*, 567. https:// doi.org/10.3390/w15030567

Academic Editor: Guido D'Urso

Received: 2 January 2023 Revised: 26 January 2023 Accepted: 28 January 2023 Published: 1 February 2023



Copyright: © 2023 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https://creativecommons.org/licenses/by/4.0/).

Water 2023, 15, 567 2 of 16

Hydrotropism is the mechanism by which plants grow toward the presence of water in response to stimuli related to water. In this case, it is a form of positive tropism, which is the response of a plant to a stimulus that leads to growth or movement. The importance of hydrotropism for plants can be attributed to the fact that it allows them to maximize the availability and quality of water, which is essential for their growth and survival. In the presence of a moisture gradient, plants use hydrotropism to bend their roots in order to reach moistened areas of the soil. Due to the fact that roots play a crucial role in the uptake of water by plants, hydrotropism may provide plants with an efficient way to obtain water during droughts. Among the tropisms that are less well known than the others, hydrotropism describes how the development of organisms is influenced by gradients of water or moisture. This tropism might just be the smallest of all. Even though hydrotropism had been studied in plant roots by German botanists in the 19th century, its reality was questioned until more recently [3]. Studies have shown that plants with mutations in the HK1 gene exhibit reduced hydrotropism in their roots, suggesting that this gene is essential for the process. Other genes that have been implicated in hydrotropism include the CBL1 and CBL9 genes, which are also involved in the perception of and response to water stimuli in plants [4]. Understanding the genes and signaling pathways involved in hydrotropism can help researchers to better understand how plants respond to water stimuli and how they optimize their access to water. This knowledge may be useful for developing strategies to improve crop yields and for studying the impacts of drought and other environmental stresses on plant growth and development [5].

In the 1800s, Charles Darwin and Francis Darwin discovered that plants responded to the presence of water. Sir Francis Darwin observed that stomatal closure was triggered by dry weather or water stress [5–8]. There has been a great deal of research conducted since then that has revealed many processes. There are two types of reactions of plants to water: short-term and long-term. By removing shoot leaves, it is possible to diminish root hydraulic conductivity, since aquaporins are membrane-channeling proteins and are thus essential. It does not take more than twenty minutes for stomata to close as a result of a lack of vapor pressure [9–11]. A long-term reaction to environmental water resources is usually associated with developmental adaptation. In *Arabidopsis thaliana*, root architecture can be constructed within days or weeks following gradients of water potential, as shown by root bending induced by gradients of water potential. Rhizosphere and environmental moisture levels can affect plant growth. There are several stages of water movement in the ecosystem, beginning with the soil, followed by the plant, and ending with the environment [9,10,12–14].

Depending on the amount of water present in the rhizosphere, roots adopt a variety of architectural styles [15–17]. Hydropatterning is a recently identified response. Hydropatterned plants respond to changes in the distribution of availability of moisture near their roots by preferentially initiating lateral roots on the root angle which is in contact with a more moist environment [18,19]. When roots penetrate an air gap or a particularly dry portion of the land, a process known as xerobranching occurs, which is similar to hydropatterning in that it suppresses the start of lateral roots. It is possible that xerobranching is a more severe form of hydropatterning. For saving minerals, the root crowns of grasses, including maize plants, produce very few shoot-born roots when the soil dries [20–22].

2. Literature Review

Plants' water flow and their response to water changes have been researched extensively. The bodily characteristics that plants detect water, the organs or tissues that detect water, and the molecular machinery that detects water are all still unknown. This paper presents an in-depth analysis of the variation in the type of water transport through plants depending on the availability of water, in order to illustrate how the availability of water impacts plant water transport [22]. A variety of artificial experiments have been conducted on seedling roots to study root hydrotropism. One study aimed to examine hydrotropism in the primary lateral and pivotal roots of desert plants. Water must be transported across

Water 2023, 15, 567 3 of 16

xylem parenchyma cell membranes during embolism recovery, so any biological model addressing embolism recovery processes in woody plants must understand the expression patterns, localization, and activity of stem-specific aquaporins. This review describes the biology of xylem parenchyma cells, with a particular focus on aquaporins. These distributions and activities are analyzed during drought stress, embolism formation, and subsequent recovery from drought stress [23]. Recent advancements in crop water stress monitoring, irrigation scheduling, constraints encountered, and future research needs are discussed [24].

In another study, it was demonstrated that pre-visual water stress detection is possible by using indices such as leaf temperature, leaf water content, and spectral emissivity, which provide a snapshot of leaf water content [25]. The suggested theory combines cohesion and multiphase flow via porous media. Both saturated and unsaturated tree water flow models are presented. Models based on electric circuit analogies are mathematically comparable to saturated porous flow. In this model, pressure, saturation, and interfacial area are explicitly modeled. This unsaturated model illustrates differences between saturated and unsaturated flow characteristics and the necessity of assessing their characteristics at a higher resolution. Using hydrostatic suctions (less than 0.02 MPa), whole-root conductivity (K r) was measured in two angiosperm pioneer trees (Eucalyptus regnans and Toona australis) and two rainforest conifers (Dacrycarpus dacrydioides and Nageia fleurii). Combining K r with stem and leaf hydraulic conductivities calculated whole-plant conductivity and predicted leaf water potential (ΨI) during transpiration [26]. In accordance with the root density and extraction rate described in the literature and in the article, Gardner and Cowan predicted that substantial potential gradients could be observed only in soils with low root density and high extraction rates [27]. A strong relationship was found between the amount of water-temperate tree species redistributed through their root systems towards dry soil for one night and external driving forces such as the PD difference, as well as internal drivers such as the root conduit diameter. HR water, 0.08 ± 0.01 mL/g root dry bulk, seems low. Plants with a mature root mass of 100 kg may require between 4 and 20 L of water each day. According to another study, central European woodlands can transpire up to 30 L per tree per day. Researchers investigated the rate at which roots, stems, leaves, and styles (silks) of maize elongated as soil water was depleted. It was calculated for a region of expansion of cells in each organ [28].

Since the pH of the soil solution is a measure of the activity of hydrogen ions in the soil solution, it is important to know its pH value. Toxicity has a significant adverse effect on roots' growth, which in turn limits the uptake of nutrients and water. A plant's response to the soil is affected by two significant chemical properties, the nutrient content of the soil and the pH value of the soil. A study was conducted combining three pH levels (4, 6, and 8) with four levels of nutrient concentration (NC0, NC1, NC5, and NC10). Various nutrient concentration levels resulted in different responses to pH levels. Magnesium uptake increased with increasing pH and nutrient concentration, whereas calcium uptake decreased. The results indicated that tomato seedlings reduce shoots more than roots under osmotic stress, regardless of nutrient concentration or root zone pH [29]. Soil with a pH of 5.5 or soil with a pH of 8 poses challenges for the plant, including low availability of nutrients and ion toxicities. Alkaline and acidic soils are described. There are two types of alkaline soils: calcareous (pH > 7.5) and sodic (ESP > 15). A pH less than ideal affects the availability of nutrients, particularly calcium, potassium, and phosphorus. The effects of these nutrient elements on plant growth, morphology, and physiological processes were discussed in detail. The recent discovery of complex interactions between salinity, boron toxicity, and pH in plants was discussed [30].

Pioneering groups created a petri dish technique to induce hydrotropic root response. This technique uses split agar plates to establish a water potential gradient. *Arabidopsis* seedlings are placed on the MS agar plate so that their root tips are near the osmolyte-supplemented zone. This causes Arabidopsis root curvature, a hydrotropic reaction [31]. To measure the root xylem water potential of a transpiring soybean plant, an improved Fiscus

Water 2023, 15, 567 4 of 16

root psychrometer was developed. Root xylem water potentials were measured using ground psychrometers. This validated root psychrometer data and allowed the partitioning of root xylem, root cortex (radial resistance), soil rhizosphere, and soil pararhizal resistances. Water intake patterns were influenced by xylem resistance [32].

Some plant species are characterized by differences in xylem elements, leaf tissue, and guttation fluid with respect to water potential between shaded and unshaded leaves. It is important to note that such drops affect plant water transport equations and pressure cell potential measurements [33]. A wide range of research is being conducted in a variety of fields. Table 1 shows a number of studies that we have identified that have been carried out over the years, as well as some that are relatively more recent.

Table 1. An overview of recent research on the effects of hydrotropism stimulation on plants.

Paper Reference	Objective	Experiment	Advantage of Research		
Year		Outcome			
[34] 2017	Under low water potential gradient conditions, the ahr1 mutant is tested for root hydrotropism and growth responses.	As a result of the mutant root cells' ability to proliferate and grow in the presence of progressively negative water potential gradients, the ahr1 phenotype is unique.	Hydrotropism can be understood with the help of this outstanding resource.		
[35] 1988	Xylem embolisms caused by water stress are believed to be caused by the influx of air into functional vessels from embolized adjacent vessels (for example, due to physical damage)	Research suggests that rainforest species are more vulnerable to embolism due to differences in inter vessel pit membrane permeability. A species' habitat influences its pit membrane pore size, making it adaptive.	Xylem embolism can be caused by an air-filled tracheid or vessel. Embolism can be caused by water stress, winter freezing, and dieback. Hydraulic conductivity of the xylem was reduced by 80% by the end of the winter in northern Vermont, even during a wet growing season		
[36] 2013	Study examines how plants communicate water availability information to remote organs. Research on long-distance signaling using hydraulic cues and potential sensors	Hydraulic signals are generated by changes in osmotic potential, water tension, or turgor. Water's cohesion and tension properties spread local changes quickly throughout the plant. In plants, hydraulic signals spread more slowly than in rigid pipes because of cellular resistances.	It is still unclear how sensors relay signals after perception. The solution to this conundrum lies in screening for plant mutants affected in hydraulic signaling.		
[37] 2019	In the soil, roots are branched and follow tortuous paths. Root segments can be considered cylinders to which water flows down a gradient of pressure in soil water despite their complex geometry.	The water status of plants is determined by hydrostatic and osmotic pressures. Plants and soil are driven by hydrostatic pressure gradients. Over microscopic distances they are driven by gradients in water potential.	Water potential is also found in surface water, cells, and xylem vessels. At atmospheric pressure, pure water's water potential is zero, so it is always negative in plants. Adding solutes or imposing suction lowers the water potential in plants.		
[38] 2001	Rice cannot respond to higher transpiration demands when growing in a hydrostatic or osmotic environment. It is concluded that this may account for rice's water shortage in the shoot even in flooded fields.	Two varieties of rice (cv. Azucena and cv. IR64) were grown for 31–40 days at 27 °C daytime and 22 °C nighttime. Transient and steady-state water flow conditions were used to measure root Lpr.	The exodermis and sclerenchyma, as well as the endodermis, have apoplastic barriers. Screening for genotypes with weaker apoplastic barriers or different chemical composition may be worthwhile.		
[39] 2016	Researchers compared vulnerability to loss of hydraulic function, leaf and xylem water potentials, and hydraulic safety margins (compared to water potentials causing a 50% loss of hydraulic conductivity) among four angiosperms and four coniferous tree species.	Measuring one type does not accurately reflect an overall hydraulic strategy.	There is strong support for the HVSH, especially in distal organs. Leaves and roots were more vulnerable to hydraulic dysfunction than branches or trunks.		

Water is vital to all physiological processes in plants. Nonwoody tissues, such as leaves, and roots contain 70–95% water. Water transports metabolites from the cell to the outside. Because of its highly polar structure, water readily dissolves ions, sugars, amino acids, and proteins that are essential for metabolism. A plant's phytohormones,

Water 2023, 15, 567 5 of 16

carbohydrates, and nutrients are transported through water, the medium that carries them. For their overall structure and support, plants rely largely on water, unlike animals with developed skeletal systems. There are a few papers mentioned in Table 1 which show how relative ideas work together.

3. Hydraulic Sensing System

Hydrotropism is the process by which plants respond to stimuli related to water. It is a form of tropism, which is a type of plant growth or movement in response to a stimulus. Hydrotropism is a positive tropism, meaning that the plant grows or moves towards the stimulus (in this case water). Hydrotropism occurs when plant cells on one side of a stem or root grow more rapidly than cells on the other side, causing the plant to bend or curve toward the source of water. This response allows plants to optimize their access to water, which is essential for their survival and growth.

There are several factors that can impact the strength and direction of hydrotropism in plants. These include the concentration of water in the soil, the presence of other stimuli (such as light or gravity), and the genetic makeup of the plant. Different plant species may exhibit different levels of hydrotropism in response to the same stimuli, and the strength and direction of the response can also vary within a single plant species depending on the conditions. Understanding the role of hydrotropism in plant growth and development can help researchers and practitioners to optimize the growing conditions for plants and to develop strategies for improving crop yields.

Various external and internal stimuli can lead to rapid changes in hydrostatic pressure in plant tissues. For instance, shoots may produce a hydrostatic signal because of mechanical perturbations [40]. It is possible that this hydromechanical interaction is the cause of the hydraulic pulses of signals that are transmitted between various far-flung portions of the plant. Variations in the water state of the soil can be swiftly relayed through hydraulic signals, which is another possibility. Aside from phloem transport, which is influenced by water potential differences, hydrostatic pressure differences have been found to control a variety of plant functions, including cellular expansion (for cell growth and development) and cell burst in pollen tubes at the apex. This means that decoding hydraulic signals is necessary for the plant to be able to sense water [41]. A water shortage generates a hydraulic signal that causes turgor to decrease and solute concentration to increase in response to the withdrawal of water from cells. Consequently, both direct and indirect hydraulic signals may be picked up by osmosensors [42–45].

There have been many research studies on the water-dependent movement of roots, also known as hydrotropism. These studies have sought to understand the mechanisms behind this phenomenon and how it impacts plant growth and development. One study that examined the role of the HK1 gene in hydrotropism used *Arabidopsis* thaliana, a small flowering plant that is commonly used as a model organism in plant biology research. The researchers found that plants with mutations in the HK1 gene exhibited reduced hydrotropism in their roots, suggesting that this gene is essential for the process. Other studies have focused on understanding the signaling pathways that underlie hydrotropism in plants. For example, research has shown that the phytohormone auxin plays a key role in the process by causing differential growth in cells on opposite sides of the root. This differential growth leads to curvature in the root towards the source of water [46–49].

Other research has examined the impacts of hydrotropism on plant growth and development, including how it affects root architecture and the distribution of roots in soil. Some studies have also looked at the role of hydrotropism in the response of plants to drought and other environmental stresses. Overall, research on the water-dependent movement of roots has contributed to our understanding of how plants respond to water stimuli and optimize their access to water, which is essential for their survival and growth.

Plants seek out water daily, just like any other living thing. Plant roots utilize moisture gradients to guide their roots through soil after finding a water source. The roots of plants can grow spontaneously toward moist and nutrient-dense areas when growing in arid soils,

Water 2023, 15, 567 6 of 16

which is caused by hydrotropism and chemotropism (the response of plant components to a chemical stimulation and subsequent growth). It is still unknown how plants perceive water in the wild, and different species may detect water in different ways. It is unknown which plant sensors detect water in this context. Roots bend toward water supplies as a response to these elusive water sensors. It is unknown what chemical components and cell signals are involved in this critical plant activity. MIZ1protien inhibits ECA1, an endoplasmic reticulum Ca²⁺-pump, to facilitate long-distance Ca²⁺-signaling in hydrotropism. Much of this mechanism is perplexing, notably with water sensors and intercellular signaling and root bending. Indirect and direct osmosensors also respond to ABA signaling, indicating that hydrotropism is controlled by the same water sensors as other water and osmotic responses [50,51].

According to a study on pea (*Pisum sativum*) hydrotropism, roots can detect vibrations in pipes that indicate a source of water [52]. There was no difference in root preference between moisture and acoustic vibrations when both cues were present, indicating that acoustic gradients enable roots to locate a water source from a distance (as shown in Figure 1), whereas moisture gradients help them reach their targets more precisely. Other plant responses to sound vibration have been confirmed by these studies. A membrane transporter or a cell wall-associated protein may be able to detect these sound vibrations, as these proteins are related to the proteins of the plasma membrane. A cytosolic signal (perhaps Ca²⁺) can trigger a secondary signaling cascade when it detects a water signal (e.g., a change in water potential or hydrostatic signal). The secondary signaling cascade alters downstream effector activity, which controls intracellular, intercellular, and wholeorganism responses. Signals transmitted through vibration can also be transmitted through systemic hydraulics. It has been demonstrated by several studies that electric fields around the root affect tropic responses, which is known as electrotropism [41-43]. The net charge of water droplets according to Ramthun is zero. As soon as an electric field is applied to water droplets, they become dipoles. An electrostatic bond will be formed between three-dimensional droplets of polarized liquid. In a humid atmosphere, push-pull forces are transferred within the cloud by electrostatic connections. Humidity may be polarized due to the earth's electric field. By using electrostatic force, polarized water droplets could attract roots to moist soil patches. It is necessary to conduct further experiments to validate these recommendations, but electric fields cannot be ruled out altogether [53–55].

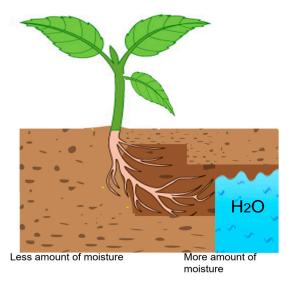


Figure 1. Movement of roots toward a high amount of water (hydrotropism).

Figure 2 depicts the movement of roots toward water under dry and wet soil conditions. The graph also indicates that roots move more toward wet areas than to dry.

Water 2023, 15, 567 7 of 16

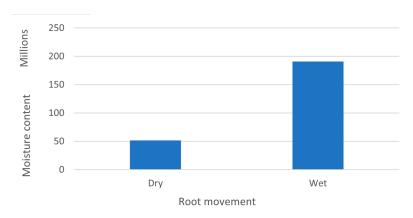


Figure 2. Water-dependent movement of roots (hydrotropism).

Table 2 shows that cucumber roots, like those of many other plant species, can exhibit hydrotropism. In general, cucumber roots are likely to grow toward sources of water when they are exposed to conditions that are relatively dry or drought-like. This response allows the plant to optimize its access to water, which is essential for its survival and growth.

Table 2. Readings obtained from cucumber roots exposed to various water conditions.

Time (h) of Hydrosimulation	Gravitational Condition during Hydrosimulation	Moisture Condition	Side of Roots	Root Bending
	-		Wet	7.9
0			Dry	3
	1G	K ₂ CO ₃ –	Wet	7.8
			Dry	2
		H ₂ O —	Wet	6.2
			Dry	4
4	3D	K ₂ CO ₃ –	Wet	8
			Dry	3
		H ₂ O _	Wet	7.6
			Dry	3.4
			Wet	7.3
		_	Dry	4.0

Note: Data source: https://figshare.com (accessed on 3 December 2022).

On the other hand, cucumber roots may exhibit less hydrotropism when they are exposed to conditions that are very wet or waterlogged, as the plant may not need to expend energy searching for additional water in these conditions. In some cases, roots may even grow away from sources of water if the soil is too wet, as this may help to prevent the plant from becoming waterlogged and stressed [56,57].

It is worth noting that the response of cucumber roots to different water conditions is likely to be influenced by a range of factors, including the genetics of the plant, the presence of other stimuli (such as light or gravity), and the overall growing conditions. As such, the readings obtained from cucumber roots exposed to different water conditions may vary depending on the specific circumstances [57].

The results of readings obtained from cucumber roots exposed to various water conditions were presented in Figure 3. It shows root growth in dry and moist soil. The graph shows that roots prefer wet to dry locations.

Water 2023, 15, 567 8 of 16

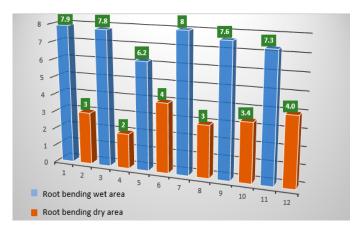


Figure 3. Root growth toward moisture in both dry and wet soil.

Root growth towards moisture in both dry and wet soil can be influenced by a number of factors, including the plant's genetics, the presence of other stimuli (such as light or gravity), and the overall growing conditions. In general, roots tend to grow towards sources of moisture when they are exposed to conditions that are relatively dry or drought-like, as this helps the plant to optimize its access to water, which is essential for its survival and growth.

In wet soil, root growth towards moisture may be less pronounced, as the plant may not need to expend energy searching for additional water in these conditions. In some cases, roots may even grow away from sources of moisture if the soil is too wet, as this may help to prevent the plant from becoming waterlogged and stressed.

It is worth noting that the response of roots to different soil moisture levels is likely to vary depending on the specific plant species and the specific conditions. Some plant species may be more tolerant of wet soil conditions than others, and the response of roots to wet soil may also be influenced by factors such as the presence of other nutrients or minerals in the soil. Therefore, understanding the factors that influence root growth towards moisture in both dry and wet soil can help researchers and practitioners to optimize the growing conditions for plants and to develop strategies for improving crop yields [58].

4. Water Physiology in Soil, Plants, and the Atmosphere

The importance of soil water in the management of nutrients cannot be overstated. In addition to supporting all life on earth, soil water contains dissolved nutrients that are readily available to plants for absorption. Therefore, it is essential that soil moisture levels remain at a proper level. The cohesion of water surfaces causes them to behave in a peculiar manner. In contrast to air particles, water molecules are more attracted to each other. A certain insect can walk along water surfaces because of this phenomenon.

Water is drawn up from the roots by evaporation from the leaves, which creates negative pressure. When plants are dehydrated, small gas bubbles (embolisms) grow in the xylem, obstructing the flow of water and decreasing photosynthesis and survival. 70% of woody plants use serious water consumption techniques with low tolerances, according to Dr. Choat and colleagues. A plant's safety margin indicates its tolerance to xylem failure related to drought stress. Weak safety margins are unsafe. There is a tight safety margin in 70% of facilities worldwide. There is stress in forests that were not previously considered drought-prone. There is a point at which liquid water becomes unstable, namely when its pressure goes below its saturation vapour pressure. At 20 °C, there is a pressure of 2.3 kPa absolute and there is a low atmospheric pressure of 99 kPa at sea level. Under negative pressure, liquid water is subject to cavitates, the sudden phase shift to vapour. The homogeneous nucleation of vapor bubbles in pure meta-stable water (spontaneous initiation) does not seem to produce cavitation in plant xylem since it occurs at pressures significantly lower (30–140 MPa) than physiological xylem pressures (0.1–10 MPa, with

Water 2023, 15, 567 9 of 16

exceptions >20 MPa). Xylem cavitation is likely heterogeneous, induced by tiny bubbles of gas in water-conduit borders with reduced adhesion forces [59,60].

There are two types of water cycles in the soil, plants, and atmosphere: liquids and vapors. There is polarity because oxygen and hydrogen have different electronegativity levels [60]. A hydrophilic organic compound or salt can be dissolved in water because of its polarity. In the plant world, water plays an important role in transporting nutrients and metabolites. There is an increase in capillary force and surface tension when water molecules are polarized and are capable of forming hydrogen bonds [61]. For soil and plants to move water, capillary force is used. During capillary motion within soil, water can move from the wet parts of the soil to the dry parts of the soil. The xylem carries water to the leaves due to capillary action and surface tension. There is significant latent heat in water due to hydrogen bonding. As a result of the fact that water is incompressible, turgor pressure can arise [62]. Photosynthesis and respiration are some of the chemical reactions that are carried out by water in plants. Velocity, gravimetric, static pressure, and osmotic potentials make up water potential. Groundwater resources or humidity can change soil moisture potential gradients. Consequently, plant water potential gradients shift inside the plant. Xylem and transpiration can be affected by hydraulic and stomatal conductance's. This balance of water potentials occurs at the cellular level. The turgor pressure decreases when the water potential of a plant diminishes, causing water to leave cells. By gathering solutes from various locations, this decrease can be averted to some extent. A plant droops when the turgor loss point is reached, indicating that the cells are losing their turgor. In the case of plants, water potentials and turgor pressure are certainly connected. It is likely that physiological and molecular reactions are triggered by the interaction between plant water potential, turgor pressure, and osmotic potential [63,64].

It has been well over a century since Darcy's law has been fundamental to understanding subsurface hydrology [64,65]. Buckingham's principles make it feasible to apply it to flux in unsaturated environments. Water science, agriculture, soil mechanics, ecology, waste disposal, mining, and the transport of contaminants commonly use it, but few thorough tests have been conducted. There are many possible variations of the DB law that may occur. Darcy's law states that flow through a porous medium is directly proportional to the net driving force that drives the flow [65,66]. When a medium is saturated with water, the rate of water flow is:

$$q = -K_{Sat} \nabla \phi \tag{1}$$

where q represents the volume flux vector of the fluid at a particular point in the medium, and ϕ indicates the total hydraulic head of the fluid. K represents the hydraulic conductivity tensor at this point in the medium. Scalar representations of hydraulic conductivity can often be used as approximates to hydraulic conductivity. According to the DB law, a medium that is unsaturated can be classified as:

$$q = -k\nabla\Phi\tag{2}$$

As a reasonable explanation for how water enters the leaves from the soil, the cohesion-tension theory has received the most support. Due to the high cohesive forces that are present in the water, this hypothesis proposes that the water in the capillaries of plants organizes itself into columns because of the high cohesive forces it contains. Water moves within the xylem and towards evaporating sites due to negative water potentials generated by transpiration within leaves [67,68].

Water moves throughout a plant because of a gradient in water potential between the roots and the leaves caused by transpiration. An analogy to Ohm's law is derivable from the flow rate and potential difference of the plant's upper and lower halves:

$$s_v = \frac{\Delta \Psi_{plant}}{R_{plant}} = \frac{\Psi_{soil} - \Psi_{root}}{R_{root}} + \frac{\Psi_{root} - \Psi_{stem}}{R_{stem}} + \frac{\Psi_{stem} - \Psi_{leaf}}{R_{leaf}}$$
(3)

Water 2023, 15, 567 10 of 16

 s_v refers to the flow rate during transpiration, R_{plant} refers to the hydraulic resistance along the entire plant, and plant refers to the potential gradient to drive the flow. The hydraulic resistances between plant elements, as well as the gradients of water potential between plant elements, can also be expressed using Ohm's law. A change in hydraulic resistance in plant parts is responsible for controlling water potential gradients.

Water flow from soil to leaves is best explained by the cohesion–tension theory. According to this theory, high cohesive forces cause water to form columns in the capillary network of plants. In leaves, transpiration causes a negative potential of water and transports water to the evaporation sites through xylem. A pressure chamber and probe can be used to measure the negative sap pressure that promotes plant flow [69].

Apoplasts and cells are responsible for root water uptake. According to Darcy's Law, water flows from the soil to the xylem by bulk flow through the apoplast. There is a direct relationship between the pressure gradient and hydraulic conductivity that drives the flow rate. By the means of diffusion and plasmodesmata, water moves from one cell to another within this channel. During the development of mature roots, the symplastic and intracellular flow of water is important for water intake by roots, as hydrophobic barriers impede the apoplastic flow of water. The following equation is provided by [69] to represent osmotic and pressure-driven water flow in roots:

$$J_v = L_p \times [p_a - p_s + \sigma(\pi_a - \pi_s)] \tag{4}$$

In this equation, J_v is the volume of flow rate, L_p is the hydraulic conductivity, p_a and p_s are the symplast and apoplast pressure potentials and is the reflection coefficient. Pressure as well as osmotic gradients change, and hydraulic conductivity changes as well. An aquaporin acts as a gate for hydraulic conductivity. Radial root water flow hydraulic conductance is affected by aquaporins to a considerable extent [69,70].

Figure 4 shows significant influence on the distribution of water, which is due to the differences in water potentials between the soil and the evaporating surface, as well as between the soil and the evaporating surface. On the right side, we have the simplest example of Ohm's law based on the series conductances.

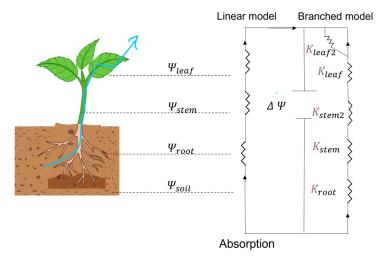


Figure 4. Analogy of Ohm's law as the resultant conductance (K) of the root, stem, and leaf.

An analogy of Ohm's law in the context of the conductance (K) of plant roots, stems, and leaves might involve considering the plant as a "conductor" of water and nutrients from the soil to the rest of the plant. In this analogy, the conductance of the plant could be thought of as equivalent to the current (I) in Ohm's law. The "voltage" across the plant (V) could be thought of as the driving force behind the movement of water and nutrients through the plant, and the "resistance" of the plant (R) could be thought of as the factor that impedes or hinders this movement.

Water 2023, 15, 567 11 of 16

Using this analogy, the conductance of the plant (K) could be thought of as the result of the relationship between the driving force (V), the resistance (R), and the current (I). Factors that influence the conductance of the plant, such as the size and shape of the roots, stem, and leaves, and the presence of other stimuli (such as light or gravity), could be thought of as equivalent to the factors that influence the resistance (R) in Ohm's law.

This analogy is a simplified way of thinking about the conductance of plant roots, stems, and leaves, and it is not intended to be a precise or exact representation of the real-world processes involved. However, it can be a useful way to understand the basic principles of plant conductance and how it is influenced by various factors.

5. Effects of Water Availability on Plants

In response to drought, plants have a variety of responses. The root system can be adapted to enhance the amount of water it takes up or be modified to decrease the amount of stomatal activity to reduce the amount of water lost through evaporation. Regulating tissue hydraulic conductivity, stomatal closure, and osmotic adjustment provides alternative regulatory processes. The roots of plants can continue to grow even if the shoots are affected. It is necessary for the growing tissue to adjust osmotically in order to control its turgor. There was a reduction in tissue turgor when the medium had a low water potential. In response to decreasing turgor pressure, cells may change their characteristics and facilitate growth. Although root growth is affected by root water uptake, growth may also be affected by water supply through the phloem. The xylem is the primary pathway for water movement in a shoot. As a result, the xylem can transport water efficiently despite its huge volume. It was demonstrated that hydraulic conductance and, by extension, water potential gradients can be regulated by hydrogels, whose pits are located in the xylem between intervessel boundaries [71].

As soon as the soils are at their field capacity and water loss is minimal, plants will be able to balance their water uptake and loss easily. It is impossible for plant tissues to develop even the slightest water potential gradients necessary to propel water movement from the soil to the environment in these conditions. The high turgor pressure in low-water-potential plants effectively allows the cells to retain all of the water that they contain. The soil becomes less permeable to water as the soil moisture level drops, due to the increase in hydraulic resistance to water flow and the decrease in matric potential as the soil moisture level drops. This shift increases the plant's water potential gradients, which causes its water potential to become negative. Based on the simulation of root xylem water potentials, lower negative potentials were observed at root tips (0.02 to 0.035 MPa) and higher negative potentials were observed at the shoot (0.1 to 0.2 MPa). Water potentials in maize roots was found to be lower due to growth. Psychrometer readings on the roots of maize indicated water potentials below 0.4 MPa near root tip. Root hydraulics and water uptake have been modeled further [72–74].

There is a movement of water from the soil to the surface in Figure 5. Using this force, water is transported from the xylem through either a symplastic and transmembrane pathway (Sp), an apoplastic pathway (Ap), or a combination of both. As water moves up the xylem, it must be filled with water, not gaseous or "embolized" to function. As water flows from soil to root xylem via root cells (Rc), it passes through pathways Ap and Sp.

Using cell wall viscosities and water uptake as metrics of cell growth, quantified the growth of cells. According to his research, cell wall elements are Bingham substances, and growth is viscous flow, resulting in an equation relating growth rate to turgor pressure (Ψ_p) over a certain threshold.

$$\frac{dV}{Vdt} = E_g \Big(\Psi_p - \Psi_{p,th} \Big) \tag{5}$$

The growth rate is expressed as a percentage of the cell's total volume V, while $\Psi_{p,th}$ is the lowest turgor beyond which the wall will not yield and E_g denotes gross extensibility and time. The data for pea roots and radish cotyledons may all be described by Equation (5).

Water 2023, 15, 567 12 of 16

For example, the equation may be used to justify why growth rate is so sensitive to Ψ_p . The cell turgor may be merely 0.2 MPa or 0.3 MPa above the yield threshold if $\Psi_{p,th}$ is significant.

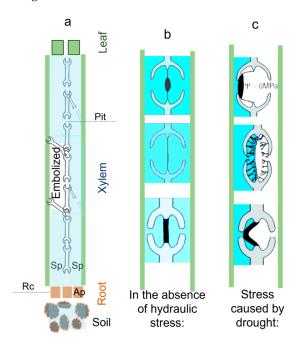


Figure 5. A mechanism for regulating embolisms in the xylem. (a) embolism (b) without hydraulic stress (c) draught-induced stress.

Combining (1) with Lockhart's equation for water uptake clarifies the significance of water intake to plant growth (I965). Adapting Lockhart's combined equation only slightly:

$$\frac{dV}{Vdt} = E_g C \frac{\Delta \Psi + \Psi_p}{E_g + C} \tag{6}$$

 $\Delta\Psi$ represents the variation Ψ between the outside and inside of the cell and C represents the total water conductance of the cell. QT of the external media and cell conductance are shown to have a vital role in determining the growth rate by Equation (6), alongside turgor and the other factors outlined in Equation (5). Parameters E_g and $\Psi_{p,th}$ in Equations (5) and (6) incorporate biological components of the cell wall even if the equations themselves are solely expressed in physical terms. All biological processes that alter the wall's viscoelastic characteristics will be reflected in those two parameters [67,75,76].

Embolisms in the xylem are air bubbles or air spaces that form in the water-conducting cells of plants. They can occur as a result of various factors, including changes in atmospheric pressure, extreme temperature fluctuations, and damage to the plant. Embolisms can disrupt the flow of water through the xylem, which can be detrimental to plant health and survival.

There are several mechanisms that plants use to regulate embolisms in xylem. One mechanism is the formation of negative pressure in the xylem, which helps to pull water upwards through the plant and prevent air from entering the xylem. This negative pressure is generated by the transpiration of water from the leaves of the plant, which creates a suction effect that helps to keep the xylem open and functioning properly.

Another mechanism that plants use to regulate embolisms in xylem is the presence of specific structural features in the xylem cells that help to prevent air from entering the cells. These features include the shape and size of the cells, as well as the presence of special cells called pits that help to maintain a continuous column of water in the xylem [70].

Plants can also regulate embolisms in the xylem by adjusting the rate of transpiration and water uptake in response to changes in atmospheric conditions or other factors. For

Water 2023, 15, 567 13 of 16

example, plants may reduce their transpiration rate or close their stomata (small openings on the surface of leaves) in response to drought or extreme temperatures, which can help to prevent embolisms from forming. These mechanisms help to ensure that plants are able to maintain a continuous supply of water to their leaves, stems, and roots, which is essential for their survival and growth.

6. Conclusions

In conclusion, hydrotropism is a phenomenon in which plants respond to stimuli related to water by moving or growing towards the source of the stimulus. It is a form of positive tropism, which is a type of plant growth or movement in response to a stimulus. Hydrotropism is important for plants because it helps them to optimize their access to water, which is essential for their survival and growth. To improve crop yields and to optimize the growing conditions for plants, researchers and practitioners need to understand how hydrotropism affects plant growth and development. This knowledge can help them to develop strategies that can improve plant growth and development.

There are several factors that can impact the strength and direction of hydrotropism in plants, including the concentration of water in the soil, the presence of other stimuli (such as light or gravity), and the genetic makeup of the plant. Different plant species may exhibit different levels of hydrotropism in response to the same stimuli, and the strength and direction of the response can also vary within a single plant species depending on the conditions.

Our study of the literature demonstrates that systemic and local changes in water availability can cause fluctuations in turgor pressure and water potential gradients in plants. Changes in plant turgor or water potential gradients reflect water availability. How biophysical cues are translated into chemical messages is unknown. Knowing where these changes occur helps link them to sensory systems. At the cellular level and deep within tissues, it is difficult to alter osmotic potentials. Computational modeling fills these gaps. To examine systemic or local water deficiency effects in plants, it is important to know how environmental changes affect plant water relations. Future investigations should use physiologically appropriate circumstances and assess how lab observations translate to soil- or field-grown plants. Plant hydraulics is better understood. Despite the limitations of studying metastable liquid water, we have the information, tools, and procedures to detect artifacts. Increasing methods enables the cross-checking of experiments and the evaluation of whole plants. All embolism detection methods have advantages and limits. Importantly, there are many areas of general agreement, including the validity of the cohesion-tension mechanism, cavitation by air seeding, and the role of pit membranes. Many plant functions depend on a functional transpiration stream; hence, xylem function is crucial. Large-vessel angiosperms' susceptibility is an unsolved problem. Ring-porous trees, lianas, and root systems have very large vessels, and their functional features must be established as clearly as for smaller-conduit species. Refilling against xylem pressure hasn't been shown after much research. Membranes and end walls control cavitation and hydraulic efficiency. Their development, chemistry, and biomechanics are unknown. We cannot yet predict vascular cambium (VC) from xylem structure alone. The relationship between plant hydraulics and stomatal control may be a useful modeling tool, although maximizing gas exchange under hydraulic restrictions is poorly understood. The genetics and molecular biology underpinning the VC phenotype are ripe for groundbreaking investigation.

Author Contributions: Conceptualization, A.P.; methodology, M.U.G.; validation: M.U.G.; investigation, A.C.; resources, M.S.; data curation: A.C.; writing—original draft preparation, M.U.G.; writing—review and editing, A.P. and A.C.; visualization, M.U.G.; supervision, A.P.; project administration, M.S.; funding acquisition, A.P. All authors have read and agreed to the published version of the manuscript.

Water 2023, 15, 567 14 of 16

Funding: This work is funded by BK21 Four Project, AI-Driven Convergence Software Education Research Program 41999902143942. And also supported by National Research Foundation of Korea 2020R1A2C1012196.

Data Availability Statement: Data supporting reported results can be found on: https://figshare.com (accessed on 3 December 2022).

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Izzo, L.G.; Aronne, G. Root Tropisms: New Insights Leading the Growth Direction of the Hidden Half. *Plants* **2021**, *10*, 220. [CrossRef] [PubMed]

- 2. Muthert, L.W.F.; Izzo, L.G.; van Zanten, M.; Aronne, G. Root Tropisms: Investigations on Earth and in Space to Unravel Plant Growth Direction. *Front. Plant Sci.* **2020**, *10*, 1807. [CrossRef] [PubMed]
- 3. Kiss, J.Z. Where's the water? Hydrotropism in plants. Proc. Natl. Acad. Sci. USA 2007, 104, 4247. [CrossRef] [PubMed]
- 4. Falik, O.; Reides, P.; Gersani, M.; Novoplansky, A. Root navigation by self inhibition. *Plant. Cell Environ.* **2005**, *28*, 562–569. [CrossRef]
- 5. Baluška, F.; Mancuso, S.; Volkmann, D.; Barlow, P.W. The 'root-brain' hypothesis of Charles and Francis Darwin: Revival after more than 125 years. *Plant Signal. Behav.* **2009**, *4*, 1121. [CrossRef]
- 6. Marder, M. Plant intentionality and the phenomenological framework of plant intelligence. *Plant Signal. Behav.* **2012**, *7*, 1365–1372. [CrossRef] [PubMed]
- 7. Kutschera, U.; Briggs, W.R. From Charles Darwin's botanical country-house studies to modern plant biology. *Plant Biol.* **2009**, *11*, 785–795. [CrossRef] [PubMed]
- 8. Gambetta, G.A.; Knipfer, T.; Fricke, W.; McElrone, A.J. Aquaporins and Root Water Uptake. In *Plant Aquaporins*; Springer Science and Business Media LLC: Berlin, Germany, 2017; pp. 133–153. [CrossRef]
- 9. Kaldenhoff, R.; Ribas-Carbo, M.; Sans, J.F.; Lovisolo, C.; Heckwolf, M.; Uehlein, N. Aquaporins and plant water balance. *Plant Cell Environ.* **2008**, *31*, 658–666. [CrossRef]
- 10. Vandeleur, R.K.; Sullivan, W.; Athman, A.; Jordans, C.; Gilliham, M.; Kaiser, B.; Tyerman, S.D. Rapid shoot-to-root signalling regulates root hydraulic conductance via aquaporins. *Plant Cell Environ.* **2014**, *37*, 520–538. [CrossRef]
- 11. Johansson, I.; Karlsson, M.; Johanson, U.; Larsson, C.; Kjellbom, P. The role of aquaporins in cellular and whole plant water balance. *Biochim. Biophys. Acta Biomembr.* **2000**, 1465, 324–342. [CrossRef]
- 12. Schulze, E.-D.; Beck, E.; Buchmann, N.; Clemens, S.; Müller-Hohenstein, K.; Scherer-Lorenzen, M. Water Deficiency (Drought). *Plant Ecol.* **2019**, 165–202. [CrossRef]
- 13. Miyamoto, N.; Ookawa, T.; Takahashi, H.; Hirasawa, T. Water Uptake and Hydraulic Properties of Elongating Cells in Hydrotropically Bending Roots of *Pisum sativum L. Plant Cell Physiol.* **2002**, *43*, 393–401. [CrossRef] [PubMed]
- 14. Carminati, A.; Zarebanadkouki, M.; Kroener, E.; Ahmed, M.A.; Holz, M. Biophysical rhizosphere processes affecting root water uptake. *Ann. Bot.* **2016**, *118*, 561–571. [CrossRef] [PubMed]
- 15. Carminati, A.; Schneider, C.L.; Moradi, A.B.; Zarebanadkouki, M.; Vetterlein, D.; Vogel, H.-J.; Hildebrandt, A.; Weller, U.; Schüler, L.; Oswald, S.E. How the Rhizosphere May Favor Water Availability to Roots. *Vadose Zone J.* **2011**, *10*, 988–998. [CrossRef]
- 16. Carminati, A.; Moradi, A.B.; Vetterlein, D.; Vontobel, P.; Lehmann, E.; Weller, U.; Vogel, H.-J.; Oswald, S.E. Dynamics of soil water content in the rhizosphere. *Plant Soil* **2010**, *332*, 163–176. [CrossRef]
- 17. Giehl, R.F.H.; von Wirén, N. Hydropatterning—How roots test the waters. Science 2018, 362, 1358–1359. [CrossRef]
- 18. Robbins, N.E.; Dinneny, J.R. The divining root: Moisture-driven responses of roots at the micro- and macro-scale. *J. Exp. Bot.* **2015**, *66*, 2145–2154. [CrossRef]
- 19. Orman-Ligeza, B.; Morris, E.C.; Parizot, B.; Lavigne, T.; Babé, A.; Ligeza, A.; Klein, S.; Sturrock, C.; Xuan, W.; Novák, O.; et al. The Xerobranching Response Represses Lateral Root Formation When Roots Are Not in Contact with Water. *Curr. Biol.* **2018**, *28*, 3165–3173.e5. [CrossRef]
- 20. Scharwies, J.D.; Dinneny, J.R. Water transport, perception, and response in plants. J. Plant Res. 2019, 132, 311–324. [CrossRef]
- 21. Maurel, C.; Nacry, P. Root architecture and hydraulics converge for acclimation to changing water availability. *Nat. Plants* **2020**, *6*, 744–749. [CrossRef]
- 22. Takano, M.; Takahashil, H.; Hirasawa, T.; Suge, H. Rapid communication Hydrotropism in roots: Sensing of a gradient in water potential by the root cap. *Planta* **1995**, *197*, 410–413. [CrossRef]
- 23. Secchi, F.; Pagliarani, C.; Zwieniecki, M.A. The functional role of xylem parenchyma cells and aquaporins during recovery from severe water stress. *Plant Cell Environ.* **2017**, 40, 858–871. [CrossRef] [PubMed]
- 24. Ihuoma, S.O.; Madramootoo, C.A. Recent advances in crop water stress detection. *Comput. Electron. Agric.* **2017**, 141, 267–275. [CrossRef]
- 25. Gerhards, M.; Rock, G.; Schlerf, M.; Udelhoven, T. Water stress detection in potato plants using leaf temperature, emissivity, and reflectance. *Int. J. Appl. Earth Obs. Geoinf.* **2016**, *53*, 27–39. [CrossRef]
- 26. Brodribb, T.J.; Hill, R.S. Increases in Water Potential Gradient Reduce Xylem Conductivity in Whole Plants. Evidence from a Low-Pressure Conductivity Method. *Plant Physiol.* **2000**, 123, 1021–1028. [CrossRef] [PubMed]

Water 2023, 15, 567 15 of 16

- 27. Williams, J. Root Density and Water Potential Gradients near the Plant Root. J. Exp. Bot. 1974, 25, 669–674. [CrossRef]
- 28. Hafner, B.D.; Hesse, B.D.; Bauerle, T.L.; Grams, T.E.E. Water potential gradient, root conduit size and root xylem hydraulic conductivity determine the extent of hydraulic redistribution in temperate trees. *Funct. Ecol.* **2020**, *34*, 561–574. [CrossRef]
- 29. Kang, Y.-I.; Park, J.-M.; Kim, S.-H.; Kang, N.-J.; Park, K.-S.; Lee, S.-Y.; Jeong, B.R. Effects of Root Zone pH and Nutrient Concentration on the Growth and Nutrient Uptake of Tomato Seedlings. *J. Plant Nutr.* **2011**, *34*, 640–652. [CrossRef]
- 30. Läuchli, A.; Grattan, S.R. Soil pH extremes. In Plant Stress Physiology; CABI Publishing: Wallingford, UK, 2012; pp. 194–209.
- 31. Antoni, R.; Dietrich, D.; Bennett, M.J.; Rodriguez, P.L. Hydrotropism: Analysis of the Root Response to a Moisture Gradient. In *Methods in Molecular Biology*; Humana Press Inc.: Totowa, NJ, USA, 2016; Volume 1398, pp. 3–9.
- 32. So, H.B. Water potential gradients and resistances of a soil-root system measured with the root and soil psychrometer. In *The Soil—Root Interface*; Academic Press: Cambridge, MA, USA, 1979; pp. 99–113. [CrossRef]
- 33. Cary, J.W.; Fisher, H.D. Plant Water Potential Gradients Measured in the Field by Freezing Point. *Physiol. Plant.* **1971**, 24, 397–402. [CrossRef]
- 34. Salazar-Blas, A.; Noriega-Calixto, L.; Campos, M.E.; Eapen, D.; Cruz-Vázquez, T.; Castillo-Olamendi, L.; Sepulveda-Jiménez, G.; Porta, H.; Dubrovsky, J.G.; Cassab, G.I. Robust root growth in altered hydrotropic response1 (ahr1) mutant of Arabidopsis is maintained by high rate of cell production at low water potential gradient. *J. Plant Physiol.* **2017**, 208, 102–114. [CrossRef]
- 35. Sperry, J.S.; Tyree, M.T. Mechanism of Water Stress-Induced Xylem Embolism. *Plant Physiol.* **1988**, *88*, 581–587. [CrossRef] [PubMed]
- 36. Christmann, A.; Grill, E.; Huang, J. Hydraulic signals in long-distance signaling. *Curr. Opin. Plant Biol.* **2013**, *16*, 293–300. [CrossRef] [PubMed]
- 37. Lambers, H.; Oliveira, R.S. Plant Water Relations. Plant Physiol. Ecol. 2019, 187–263. [CrossRef]
- 38. Miyamoto, N.; Steudle, E.; Hirasawa, T.; Lafitte, R. Hydraulic conductivity of rice roots. J. Exp. Bot. 2001, 52, 1835–1846. [CrossRef]
- 39. Johnson, D.M.; Wortemann, R.; McCulloh, K.A.; Jordan-Meille, L.; Ward, E.; Warren, J.M.; Palmroth, S.; Domec, J.-C. A test of the hydraulic vulnerability segmentation hypothesis in angiosperm and conifer tree species. *Tree Physiol.* **2016**, *36*, 983–993. [CrossRef] [PubMed]
- 40. Prendergast, P.; Huiskes, R.; Søballe, K. Biophysical stimuli on cells during tissue differentiation at implant interfaces. *J. Biomech.* **1997**, *30*, 539–548. [CrossRef] [PubMed]
- 41. Shabala, S.; White, R.G.; Djordjevic, M.A.; Ruan, Y.-L.; Mathesius, U. Root-to-shoot signalling: Integration of diverse molecules, pathways and functions. *Funct. Plant Biol.* **2015**, *43*, 87–104. [CrossRef] [PubMed]
- 42. Christmann, A.; Weiler, E.W.; Steudle, E.; Grill, E. A hydraulic signal in root-to-shoot signalling of water shortage. *Plant J.* **2007**, 52, 167–174. [CrossRef] [PubMed]
- 43. Tyerman, S.D.; Niemietz, C.M.; Bramley, H. Plant aquaporins: Multifunctional water and solute channels with expanding roles. *Plant Cell Environ.* **2002**, 25, 173–194. [CrossRef] [PubMed]
- 44. Bourque, C.W. Central mechanisms of osmosensation and systemic osmoregulation. *Nat. Rev. Neurosci.* **2008**, *9*, 519–531. [CrossRef]
- 45. Vives-Peris, V.; López-Climent, M.F.; Pérez-Clemente, R.M.; Gómez-Cadenas, A. Root Involvement in Plant Responses to Adverse Environmental Conditions. *Agronomy* **2020**, *10*, 942. [CrossRef]
- 46. Dautel, R. Molecular Characterization of the Arabidopsis Thaliana Histidine Kinase 1 and Transitions from the Multistep Phosphorelay System to Ser/Thr/Tyr Phosphorylation; Eberhard Karls Universität Tübingen: Tübingen, Germany, 2016.
- 47. Han, H.; Adamowski, M.; Qi, L.; Alotaibi, S.S.; Friml, J. PIN-mediated polar auxin transport regulations in plant tropic responses. *New Phytol.* **2021**, 232, 510–522. [CrossRef]
- 48. Péret, B.; De Rybel, B.; Casimiro, I.; Benková, E.; Swarup, R.; Laplaze, L.; Beeckman, T.; Bennett, M.J. Arabidopsis lateral root development: An emerging story. *Trends Plant Sci.* **2009**, *14*, 399–408. [CrossRef] [PubMed]
- 49. Miyazawa, Y.; Takahashi, H. Molecular mechanisms mediating root hydrotropism: What we have observed since the rediscovery of hydrotropism. *J. Plant Res.* **2020**, *133*, 3–14. [CrossRef] [PubMed]
- 50. Shkolnik, D.; Nuriel, R.; Bonza, M.C.; Costa, A.; Fromm, H. MIZ1 regulates ECA1 to generate a slow, long-distance phloem-transmitted Ca²⁺ signal essential for root water tracking in *Arabidopsis*. *Proc. Natl. Acad. Sci. USA* **2018**, *115*, 8031–8036. [CrossRef] [PubMed]
- 51. Gagliano, M.; Grimonprez, M.; Depczynski, M.; Renton, M. Tuned in: Plant roots use sound to locate water. *Oecologia* **2017**, *184*, 151–160. [CrossRef]
- 52. Mishra, R.C.; Ghosh, R.; Bae, H. Plant acoustics: In the search of a sound mechanism for sound signaling in plants. *J. Exp. Bot.* **2016**, *67*, 4483–4494. [CrossRef]
- 53. Zilly, F.E.; Halemani, N.D.; Walrafen, D.; Spitta, L.; Schreiber, A.; Jahn, R.; Lang, T. Ca²⁺ induces clustering of membrane proteins in the plasma membrane via electrostatic interactions. *EMBO J.* **2011**, *30*, 1209–1220. [CrossRef]
- 54. Salvalaio, M.; Oliver, N.; Tiknaz, D.; Schwarze, M.; Kral, N.; Kim, S.-J.; Sena, G. Root electrotropism in Arabidopsis does not depend on auxin distribution but requires cytokinin biosynthesis. *Plant Physiol.* **2022**, *188*, 1604–1616. [CrossRef]
- 55. Ishikawa, H.; Evans, M.L. Electrotropism of maize roots: Role of the root cap and relationship to gravitropism. *Plant Physiol.* **1990**, 94, 913–918. [CrossRef]

Water 2023, 15, 567 16 of 16

56. Morohashi, K.; Okamoto, M.; Yamazaki, C.; Fujii, N.; Miyazawa, Y.; Kamada, M.; Kasahara, H.; Osada, I.; Shimazu, T.; Fusejima, Y.; et al. Gravitropism interferes with hydrotropism via counteracting auxin dynamics in cucumber roots: Clinorotation and spaceflight experiments. *New Phytol.* **2017**, 215, 1476–1489. [CrossRef] [PubMed]

- 57. Fujii, N.; Miyabayashi, S.; Sugita, T.; Kobayashi, A.; Yamazaki, C.; Miyazawa, Y.; Kamada, M.; Kasahara, H.; Osada, I.; Shimazu, T.; et al. Root-tip-mediated inhibition of hydrotropism is accompanied with the suppression of asymmetric expression of auxin-inducible genes in response to moisture gradients in cucumber roots. *PLoS ONE* **2018**, *13*, e0189827. [CrossRef] [PubMed]
- 58. Choat, B.; Jansen, S.; Brodribb, T.J.; Cochard, H.; Delzon, S.; Bhaskar, R.; Bucci, S.J.; Feild, T.S.; Gleason, S.M.; Hacke, U.G.; et al. Global convergence in the vulnerability of forests to drought. *Nature* **2012**, *491*, 752–755. [CrossRef]
- 59. Cowan, I.R. Transport of Water in the Soil-Plant-Atmosphere System. J. Appl. Ecol. 1965, 2, 221. [CrossRef]
- 60. McCarton, L.; O'Hogain, S.; Reid, A. Properties of Water. In *The Worth of Water*; Springer: Berlin/Heidelberg, Germany, 2021; Available online: https://link.springer.com/chapter/10.1007/978-3-030-50605-6_2 (accessed on 1 January 2023).
- 61. Water Dynamics in Plant Production, 2nd Edition—Wilfried Ehlers, Michael Goss—Google Books. Available online: https://books.google.co.kr/books?hl=en&lr=&id=B7EtDAAAQBAJ&oi=fnd&pg=PR3&dq=During+capillary+motion+within+soil,+water+can+move+from+the+wet+parts+of+the+soil+to+the+dry+parts+of+the+soil.+The+xylem+carries+water+to+the+leaves+due+to+capillary+action+and+sur-face+tension.&ots=eY_-nlnZxB&sig=DySRyUPUnyltlXads-T_GQXO8TM&redir_esc=y#v=onepage&q&f=false (accessed on 3 December 2022).
- 62. Water Transport in Plants: Xylem | Organismal Biology. Available online: https://organismalbio.biosci.gatech.edu/nutrition-transport-and-homeostasis/plant-transport-processes-i/ (accessed on 3 December 2022).
- 63. Passioura, J.B. Plant-Water Relations. *Encycl. Life Sci.* **2010**. Available online: https://onlinelibrary.wiley.com/doi/full/10.1002/9780470015902.a0001288.pub2 (accessed on 2 January 2023).
- 64. Atangana, A. Principle of Groundwater Flow. In *Fractional Operators with Constant and Variable Order with Application to Geo-hydrology*; Academic Press: Cambridge, MA, USA, 2018; pp. 15–47. [CrossRef]
- 65. Hubbert, M.K. Darcy's law and the field equations of the flow of underground fluids. Trans. AIME 2009, 2, 23–59. [CrossRef]
- 66. Narasimhan, T.N. Central Ideas of Buckingham (1907): A Century Later. Vadose Zone J. 2007, 6, 687–693. [CrossRef]
- 67. Turturro, A.C.; Caputo, M.C.; Perkins, K.S.; Nimmo, J.R. Does the Darcy–Buckingham Law Apply to Flow through Unsaturated Porous Rock? *Water* **2020**, *12*, 2668. [CrossRef]
- 68. Tyree, M. Review article. The cohesion-tension theory of sap ascent: Current controversies. *J. Exp. Bot.* **1997**, *48*, 1753–1765. [CrossRef]
- 69. Aston, M.J.; Lawlor, D.W. The Relationship between Transpiration, Root Water Uptake, and Leaf Water Potential. *J. Exp. Bot.* **1979**, 30, 169–181. [CrossRef]
- 70. Kramer, P.J.; Boyer, J.S. Water Relations of Plants and Soils—Google Books. Available online: https://www.elsevier.com/books/water-relations-of-plants-and-soils/kramer/978-0-12-425060-4 (accessed on 3 December 2022).
- 71. McCully, M.E. Root Xylem Embolisms and Refilling. Relation to Water Potentials of Soil, Roots, and Leaves, and Osmotic Potentials of Root Xylem Sap1. *Plant Physiol.* **1999**, 119, 1001. [CrossRef]
- 72. Basu, S.; Ramegowda, V.; Kumar, A.; Pereira, A. Plant adaptation to drought stress. F1000Research 2016, 5, 1554. [CrossRef] [PubMed]
- 73. Li, Y.; Li, H.; Li, Y.; Zhang, S. Improving water-use efficiency by decreasing stomatal conductance and transpiration rate to maintain higher ear photosynthetic rate in drought-resistant wheat. *Crop. J.* **2017**, *5*, 231–239. [CrossRef]
- 74. Lavrov, A. Natural Fractures in Rocks. Lost Circ. 2016, 49–80. [CrossRef]
- 75. Andrii, R.; Vladimir, K.; Yevhen, M. Influence of Bingham fluid viscosity on energy performances of a vortex chamber pump. *Energy* **2021**, *218*, 119432. [CrossRef]
- 76. Schopfer, P. Biomechanics of plant growth. Am. J. Bot. 2006, 93, 1415–1425. [CrossRef] [PubMed]

Disclaimer/Publisher's Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.