soil systems

Review

Rhizosheath: Roles, Formation Processes and Investigation Methods

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Abstract: Climate change negatively affects crop productivity, threatening the survival of entire populations from many vulnerable hotspot regions of the world with the risk of exacerbating hunger, malnutrition and international inequality. Selecting plant species manifesting abiotic stress-tolerant adaptive traits represents a challenge towards ensuring that crops are more resistant and resilient to environmental perturbations. The rhizosheath, defined as the complex of root hair, exudates and soil that strongly adheres to plant roots, is a promising root adaptive trait in facing conditions of water and nutrient deficits, as well as acidic soil. Several beneficial ecological functions are attributed to the rhizosheath, such as enhancing water and nutrient uptake; protecting from dehydration, heat and acid stresses; and stimulating microbial activities. It has been described in several Angiosperm species, including crops grown in severe habitats. The aim of this review was to collect the relevant literature produced to date regarding rhizosheaths, focusing on (i) the various processes involved in its formation, including both physicochemical and biological ones; (ii) the evolutionary and ecological role of rhizosheaths; and (iii) the most frequently used methodologies for its investigation and characterization. The present work provides a comprehensive overview of this revolutionary root's great agronomic importance in order to address future research aiming to fill the existing knowledge gaps and define a common and shared methodology.

Keywords: rhizosheath; sustainable agriculture; climate change; root adaptive trait; rhizosheath formation; rhizosheath benefits; rhizosheath investigation methods

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1. Introduction

The climate crisis is now a subject urgency for humanity, given its negative consequences for agricultural productivity that jeopardize global food provisioning [1–5]. According to the latest reports by the Intergovernmental Panel on Climate Change (IPCC), in the coming decades, the planet will confront an intensification of extreme climatic events (e.g., drought, heatwaves, heavy rainfall) which will alter the water cycle and its properties, leading to alarming and unprecedented repercussions on hydrological systems and aquifer recharge [6,7]. Furthermore, increasing temperatures and atmospheric levels of carbon dioxide may entail negative cascade effects influencing the physical, chemical and biological properties of all natural ecosystems of the biosphere, first and foremost the soil, thus limiting the essential ecological functions on which fertility and productivity strongly depend [8–11]. Heavy precipitation can promote soil hypoxia due to water stagnation, as well as nutrient leaching, especially for water-soluble nutrients (e.g., nitrates, sulfates, calcium, magnesium, silicon); on the other hand, drought conditions can lead to soil salinization because of increased water evaporation processes, as well as to a loss of particle cohesion that, in turn, promotes wind erosion [12]. All of this affects microbial communities' compositions and activities due to the impairment of the soil biogeochemical cycles, compromising plant development through changes in growth and functioning [13–16].

Therefore, urgent and accelerated adaptation actions aimed at climate risk mitigation and at increasing the ecosystem's resilience, are needed, considering the global demand for food by a growing population and in view of alternative sustainable practices to conventional intensive agriculture [5,17,18]. A rhizosheath is defined as a complex of root hair, exudates and strongly adhering soil. It ranks among the most promising adaptive traits to focus on for the improvement of agricultural sustainability [19]. Despite a recent increase in scientific literature on the rhizosheath, knowledge about the factors involved in its genesis and its ecological functions is still limited; moreover, most of the studies were conducted in controlled laboratory conditions, without validation in the field [20–22]. Firstly described in several grass species from arid habitats, and, recently, in plants essential for human and animal consumption (e.g., cereals and legumes), the development of such a particular "cylindrical muff" surrounding the root can be associated with various abiotic and biotic factors. Among them are the soil texture and moisture; the genetic determinants controlling root traits, such as root hairs and their architecture; as well as mucilage secretion and relevant microbial (fungal and bacterial) activities [22–26]. The rhizosheath plays a crucial role in coping with environmental stresses, protecting the root system against dry and acid soil conditions and improving the uptake of water and nutrients, which is probably related to better contact at the interface between soil and root surfaces [27–30]. Therefore, the adaptation strategy of these particular plants is considered as a trait of great agronomic importance and a potential feature for breeding and management. It is promising for efforts to enhance the sustainability of the crop production and to shift towards the second green revolution [20,31,32].

Rhizosheath research can rely on advanced techniques spanning from soil imaging to spatially resolved chemistry. Methods for discriminating, sampling and quantifying the rhizosheath are still not standardized. The present review summarizes research findings on rhizosheath formation processes, factors and ecological functions. We also specifically focus on methods applied for rhizosheath characterization, providing a comprehensive picture of the current knowledge and indicating future research needs and developments.

2. Rhizosheath

Described for the first time in the 19th century and identified as rhizosheath in the late 1970s, this particular coating of root-enveloping soil has been indicated as an extraordinary drought-adaptive feature of plants [21,33,34]. In detail, the rhizosheath can be described as the root surface and soil clinging to the roots thanks to the physicochemical and biological action of root hairs and the binding organic compounds secreted by microbes and roots, such as mucilages and other exopolymers [29,35–38] (Figure 1). According to other definitions, the rhizosheath, when combined with the root surface (root epidermis), forms the rhizoplane. The rhizosphere extends far beyond the rhizosheath's limits, representing the whole soil volume influenced by plant roots [32,33,39] (Figure 1). York et al. [33] encouraged researchers to use the correct semantics and to adopt a holistic vision of the rhizosphere, the structure and functioning of which depend on its components and their interactions.

The rhizosheath is often operatively defined as the weight of soil that is strongly adhered to the roots after separation from the surrounding soil. Separation techniques include different methods, ranging from shaking to sonication in water. Several works reported in the literature concern a few spontaneous grass species living in extreme arid habitats under water stress, and highlight some of the processes involved in rhizosheath formation and its crucial role in the ecosystem [40–44]. But recent studies have demonstrated that the rhizosheath is not a specific trait limited to wild species of no agronomic importance; in fact, it is recurrent in several other taxonomic groups among the Angiosperms, both monocotyledons (Poales, Commelinales, etc.) and eudicotyledons (Fabales, Caryophyllales, Brassicales, Solanales, etc.) [22,29,35,45–48]. In view of its beneficial functions on abiotic-stressed plants, rhizosheath have also been investigated in crop species grown in various severe conditions (e.g., drought, low nutrients or acid soil conditions). Among them are cereals, such as wheat [27,28,49–51], rice [21,25,44,52,53], maize [23,26,54], millet [55], barley [24,26,36], sorghum [56] and rye [57]; but also legumes, like lupine [30]; and other eudicotyledon crop plants, such as tomato [37].

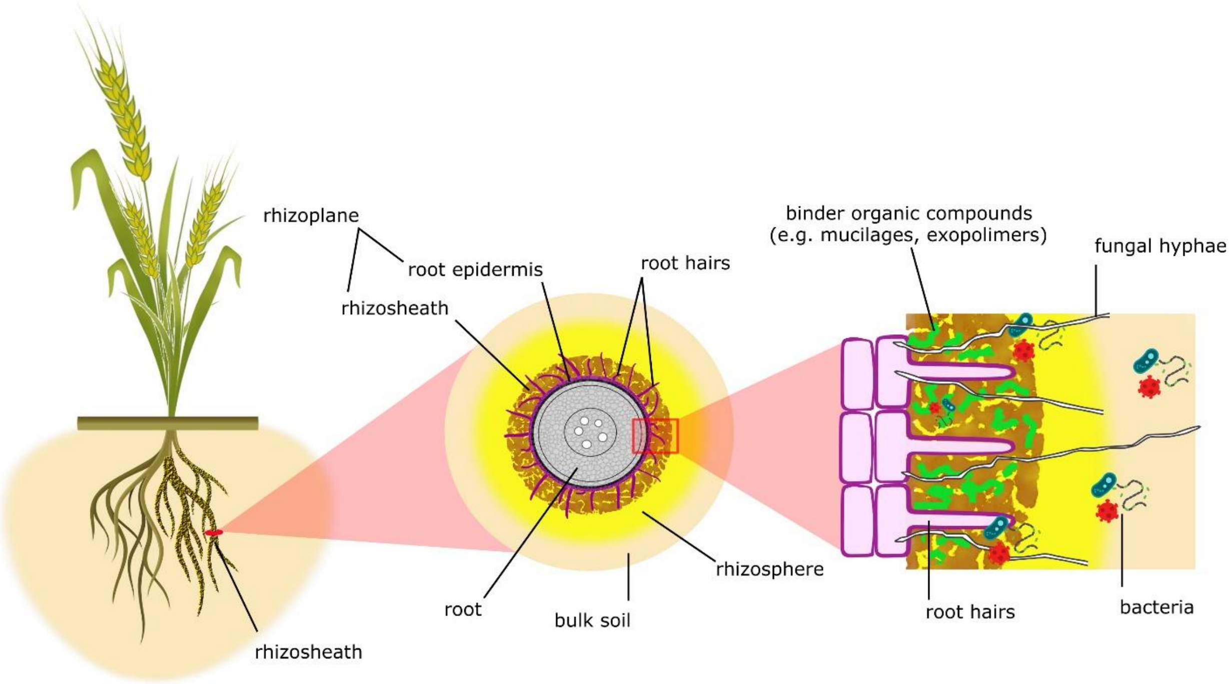

Figure 1. Schematic representation of rhizosheath traits, denoting the several components involved in its formation according to York et al. [33].

3. Factors Involved in Rhizosheath Formation

The processes at the basis of the rhizosheath formation are still under extensive investigation. Several studies have provided clear evidence regarding the multiplicity of factors involved in rhizosheath genesis and evolution, from physicochemical factors linked to root architecture and soil properties to biological, plant genetic and root–microbe interactions [44]. The most important are reported in the following sub-chapters.

3.1. Root Hairs

Root hairs are specialized tubular extensions of root epidermal cells, mainly responsible for nutrient and water acquisition, plant anchoring and microbial interactions. They increase the root surface and the access to soil volume [58,59]. Moreover, they represent the "scaffolding" on which the rhizosheath evolves, providing a physical structure for the stabilization and trapping of soil particles [23,34]. Therefore, they play a crucial role in rhizosheath formation, since root-hairless species do not present this particular feature, or else they exhibit an underdeveloped rhizosheath, where the chemical adhesive action of exudates is dominant [26,29,60].

Liu et al. [61] suggested a highly positive correlation between root hair length and density and the rhizosheath's dimension and weight in induced dry soil conditions for foxtail millet (*Setaria italica* L.). They also defined the soil moisture level (10–14% w/w) below which rhizosheath formation is stimulated. Delhaize et al. [27] highlighted a strong and significant relation between root hair length and rhizosheath's dimensions in wheat (*Triticum aestivum* L.). The same positive relation, but weaker, was reported for barley (*Hordeum vulgare* L.) by George et al. [36] and for pearl millet (*Pennisetum glaucum* L. R.Br) by de la Fuente Cantó et al. [55]. Brown et al. [29] and Adu et al. [54], working on several orders of angiosperms and landraces and varieties of maize, respectively, reported an inconsistent relationship between rhizosheath development and root hair elongation. This suggests that the effect of root hair length on rhizosheaths varies considerably depending on the plant species. However, but other factors dominate its evolution, such as the exudation of mucilage, the density of root hairs and their morphologies (bent or hooked shapes), more or less favoring the enmeshing of soil particles [26,29,54,55]. In turn, the development of root hairs in barley seems to be affected by the physical characteristics of soil, such as strength and particle size, with root hair length decreasing with increasing soil density and increases in soil along with larger particle sizes. This can be associated with the abundance of soil pores, where root hair elongation processes are not limited by mechanical hindrances, but at a different scale, similarly to the roots [24]. The general architecture of root systems affects rhizosheath formation, and there are positive correlations between rhizosheath dimensions and lateral root density, suggesting that greater root ramifications can also promote soil particle agglutination [20].

3.2. Root- and Microbial-Derived Mucilages

Soil mucilages are high-molecular-weight organic compounds which are found in soil as a result of the activity of belowground plant organs and microbial production, with several beneficial ecological functions for plants, such as the promotion of nutrients and water uptake, the attraction of favorable microbes and insects and protection against infections [23,62–64]. Moreover, they promote soil aggregates' stabilization [65] thanks to the adhesion properties related to their nature of viscoelastic gels, which are rich in polysaccharides and glycoproteins, making them the main component in the rhizosheath formation process [23,34,66,67].

Together with the extracellular polymeric substances (EPS) secreted by microorganisms, the compounds found in mucilages can affect soil dispersion/flocculation dynamics through compensation for the negative charges on clay; the absorption of organic acid anions; or by influencing the rhizosphere pH, which causes dissolution or precipitation of the binding compounds [68,69]. Microbial products and root exudates can also influence the mechanical and hydraulic properties of the soil. Mucilages soak the voids between the soil particles, impregnating them; in dry conditions, they increase soil viscosity and strengthen the bond between soil particles and roots, forming a larger and stronger rhizosheath. However, in wet conditions, mucilages can partly dissolve and disperse in the soil, and this results in a weaker rhizosheath. Drying/wetting cycles, also related to the day–night transpiration cycle, can fortify the soil's adhesion to the root surface through new cross-links [23,67,70,71].

Arbuscular mycorrhizal fungi can also promote rhizosheath development, although to a lesser extent. This occurs both directly, by forming mycorrhizal symbioses and indirectly, through the release of glycoproteins (glomalin-related soil proteins, GRSP) able to agglutinate the soil aggregates and contribute to the stabilization of the rhizosheath [19,20,34,52,72].

3.3. Genetics

Plants can respond to environmental abiotic and biotic stresses (e.g., extreme climatic and edaphic conditions, nutrient and water deficiencies, pathogens, etc.) through adaptive molecular strategies controlled by genes and quantitative trait loci (QTLs), allowing them to face hostile conditions. Research in this field is extremely interesting, with a goal of implementing innovative sustainable agricultural practices to allow us to select more tolerant and resilient varieties or to identify relevant and favorable traits for crop breeding. This represents the current challenges of confronting the pressing climate change issue, improving yields and ensuring the healthy growth of crops in vast and various geographical areas [56,73,74].

However, at present, only a few studies have highlighted the genetic determinants modulating rhizosheath formation. In response to abiotic stresses, such as dry conditions, acid or P-deficient soil, the upregulation/downregulation of specific genes has been observed with stimulation of the expression of root characteristics and functions, such as root hair development and root exudation [33,44]. The rhizosheath is a complex, multigenic trait showing a high heritability, with effects differing among species, and the comprehensive understanding of which requires further in-depth analysis [20,33,75]. An overview of the most relevant results of studies on crops is reported in the following section (Methods for rhizosheath investigation—genetic studies).

4. Benefits and Ecological Functions of Rhizosheaths

The role of rhizosheaths in plant survival and productive behavior is still controversial and not entirely proven, given that there are many genetic and physiological factors involved in this process that are not easy to discern [34,50].

Being described for the first time in species from desert habitats, the rhizosheath was intuitively considered an adaptive trait making plants more tolerant of and resilient to dry conditions. They were thought to protect roots from drought and heat stress, increasing water uptake and decreasing dehydration [50,76]. Over time, various studies highlighted that rhizosheath size was negatively correlated with soil water content and positively correlated to root hair length [27,36,55,61]. The greater rhizosheaths that formed in cactus species in dry conditions showed water potential similar to that of root surfaces and higher than that of bulk soil; this proves a reduced level of water loss from the sheathed root epidermis. On the other hand, in wet conditions, the rhizosheath has been shown to improve soil–root contact, favoring root water uptake [77]. Moreover, considering the transpiration rate as a proxy of the water extraction capacity by plants, wheat cultivars with overdeveloped rhizosheaths can support higher transpiration rates in dry soil compared to those with smaller rhizosheaths [50].

The rhizosheath helps plants to tolerate soil acidity. Delhaize et al. [27] showed a positive correlation between rhizosheath size and root hair length in wheat grown in acidic soil. Root hair elongation in acidic soil has been associated with improved water and nutrient absorption and a greater tolerance to Al^{3+} toxicity. This is due to mechanisms regulated by several genes independently of the well-known TaALMT1 gene encoding for the Al^{3+} tolerance of root hairs.

Moreover, the rhizosheath mucilage increases water retention and contributes to creating a microenvironment with stable water content compared to the surrounding soil due to the hydrophilic/hydrophobic behaviors of mucilage [49,69,78]. As reported by Marasco et al. [79], the quantity and quality of root exudates and microbial metabolites can be modulated by seasonally changing abiotic factors, favoring and ensuring a stable niche for microbial communities from which the plants obtain essential nutrients that would otherwise be limited in soil. Rhizosheaths represent an active compartment of the rhizosphere, enriched by plants in carbon compounds that represent an energy source for microbial growth. They act as inhibitors or stimulators, regulating their abundance, diversity and metabolic activity. Moreover, root exudation, as well as the biogeochemical cycles regulated by microbes, can improve the plant uptake of nutrients such as phosphorous and nitrogen, promoting their solubilization, mobilization and bioavailability [22,25,35,49,67].

In a recent, accurate study, Mo et al. [48] compared several physical, chemical and microbial features of rhizosheath soils from bulk, loose rhizosphere and outer rhizosphere soils, collecting and statistically elaborating upon data from numerous works in the literature. Significant differences were noted between the typologies of the considered soils: in particular, rhizosheath soils presented higher values of gravimetric water content (+66%); porosity (+11%); organic carbon and total nitrogen content (+34 and +78%, respectively); water-extractable organic carbon and total nitrogen content (+56 and +40%, respectively); available nitrogen, phosphorus and potassium content (+30, 12 and 27%, respectively); microbial biomass carbon and nitrogen content (+71 and +38%, respectively); respiration rate (+67%); and higher polyphenol oxidase and peroxidase activity (+20 and +26%). These differences in such properties highlighted in rhizosheath soils are basic in terms of the essential processes of water retention and nutrient uptake, as well as the enzymatic activities by soil microbes which affect organic matter decomposition and the consequent availability of nutrients for plants [47,48]. Finally, the rhizosheath also contributes to the stabilization of soil aggregates, making the soil physically resistant to disruptive forces and conditions [20,80].

5. Methods for Rhizosheath Investigation

The development of standardized methods for rhizosheath characterization (e.g., rhizosheath presence/absence, typology, shape, dimension, weight, strength), as well as the appropriate use of "rhizosemantics" for its description, represents the need to prevent the recurring ambiguities reported in the current literature, which lead to confusion and information loss and make the data incomparable [29,33,34].

5.1. Rhizosheath Sampling

The first cause of misunderstandings may arise from rhizosheath collection methodology, which often affects the results of empirical tests, with a consequent possible underestimation of the rhizosheath's features. In fact, the lack of a definition of a universal sampling technique may be associated with considerable errors for its basic identification: for instance, erroneous sampling can break the roots, with a consequent loss of the rhizosheath. A major source of ambiguity is the incorrect definition of the soil domain to be sampled around the roots: some works in the literature refer to the rhizosphere, but they are actually conducted on the rhizosheath [29,34].

Brown et al. [29] developed an efficient method to define the presence/absence and strength scores of rhizosheaths based on different degrees of soil cohesion to roots. These scores range from (0), indicating no attached soil particles; (1), indicating a few that are eliminating after its agitation; (2), indicating attached soil that is detached from the roots by shaking; (3), indicating root-adhering soil that remains after shaking and is partially removed after 5 min in a sonic bath (75 W; 35–45 kHz); and (4), removed the soil remains attached both after shaking and a sonic bath (Figure 2).

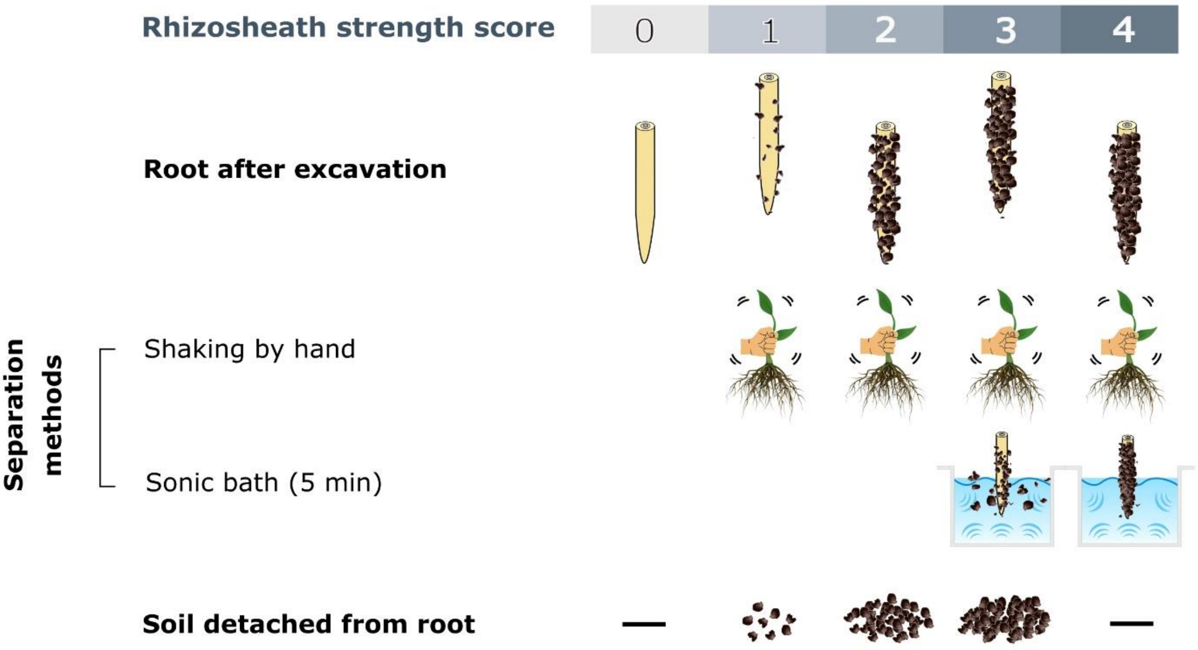

Figure 2. Rhizosheath strength score scheme based on the different degrees of soil cohesion to the roots and separation methods, according to Brown et al. [29]. (—) indicates an undetected feature.

Only those with force levels ≥2 are considered actual rhizosheaths. Moreover, the strength, extent, type and form vary among and within species. Bailey and Scholes [45] identified five categories corresponding to the rhizosheath diameter (from 0 to >3.5 mm) and the cohesion of the soil particles composing it (from well-consolidated soil particles adhering to the sheath to no evidence of them) (Figure 3). A greater or lesser consolidation of the sheath, depending on several known factors (root hairs, binding materials, soil type), leads to different morphologies, from clear cylindrical coatings encasing the roots to less cohesive, almost "bunch-shaped" structures where root hairs are clearly visible.

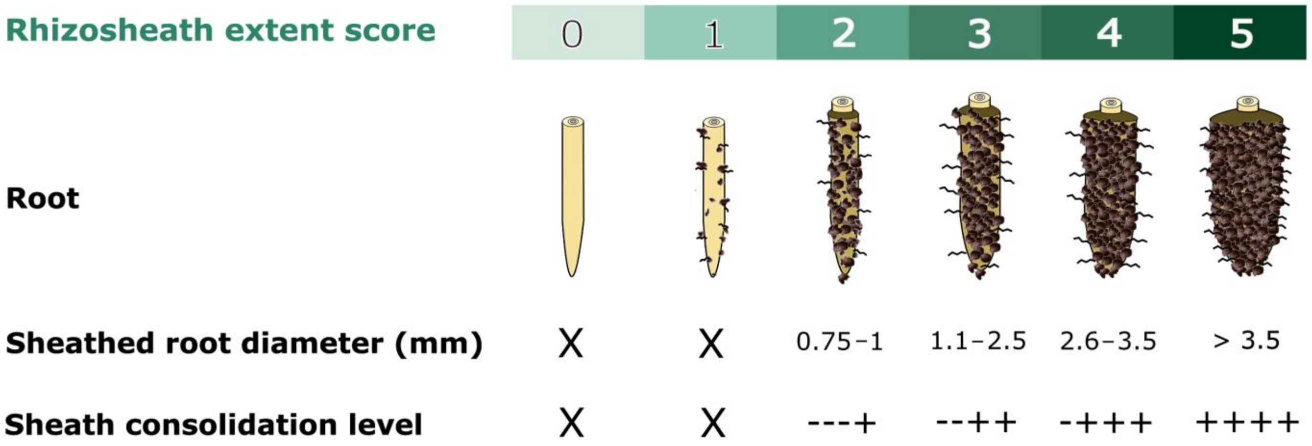

Figure 3. Scheme of rhizosheath extent scores based on the diameter (from 0 to >3.5 mm) and the cohesion of soil particles composing it (from well-consolidated soil particles adhering to the sheath (+) to no evidence of them (−), according to Bailey and Scholes [45]. (X) indicates an undetected feature.

Regarding the sampling phase, after a careful plant harvesting process which includes undamaged root systems, the bulk and rhizospheric soil may be mechanically separated from the rhizosheath by shaking the plants manually or in an electric shaker [32,55,81]. Further separation may be conducted: for example, Bochicchio et al. [51] delicately removed the soil that was not solidly adhered using a soft brush. The soil particles strongly adhering to the roots represent the rhizosheath. Successively, for the purpose of totally detaching the rhizosheath, a widely used method consists of washing the roots with double-distilled or demineralized water and recovering the soil in a container [24–26,29,37,49,51,52,55,61]. Hallama et al. [18] gently separated the rhizosheath, removing the soil around the roots using a toothbrush, whereas Marasco at al. [79] manually divided the rhizosheath compartment from the root epidermis using a stereomicroscope and a sterile scalpel. Zhu et al. [32] applied a phosphate buffer on the roots with adhering soil as a stabilizer of the microbial activity; the rhizosheath was obtained following vortex stirring and centrifugation of the samples.

Sonication was used to measure the rhizosheath bond strength [23,29]; however, this represents a potential functional method by which to collect root-adhered soil.

5.2. Rhizosheath Quantification

For an initial quantitative characterization of rhizosheath, it should be weighed and oven dried at 105 °C to obtaine the absolute rhizosheath dry weight [24,26,37,44,52], which can be also calculated as the difference between the root–rhizosheath complex weight and the root weight after being cleaned of the adhering soil in fresh or dry mass conditions [36,51,54,61].

The specific rhizosheath weight is given by the ratio between the rhizosheath's dry mass (root-adhering soil, RAS) and root tissue (RT, RAS/RT, $g\ g^{-1}$) after being dried at 65 °C [51,55,82]. However, it can be also calculated as the ratio between the RAS and the total length of the root (RL, RAS/RL, $mg\ cm^{-1}$) for each plant. The specific rhizosheath weight allows us to estimate its size [20].

Tahir et al. [49] measured the rhizosheath, in damp condition, in terms of soil water content (%), by the ratio $[(W1 - W2)/W2] \times 100$, where W1 is the fresh rhizosheath weight and W2 is the dry one.

In these quantitative surveys, morpho-metric roots trait characterization (e.g., root type, number, length, diameter, area), as well as root hairs obtained through specific integrated techniques (e.g., scanner, optical microscopy, digital camera, image-processing software), can be useful in defining the root architecture influencing the structure and formation processes of rhizosheaths [24,26,36,37,44,51,52,55,61].

5.3. Genetic Studies

Key genetic determinant studies associated with the expression of rhizosheath characteristics, focused on QTL mapping and gene identification, were conducted on several crop species, among which were cereals (e.g., wheat, pearl barley, millet, rice); others, such as lupine and tomato; and wild relatives [29,44].

Delhaize et al. [83] used multiparent whole-genome analysis (MPWGAIM) in wheat (*Triticum aestivum* L.) populations grown on non-acid soils, and identified six QTLs located on chromosomes 2B, 4D, 5A, 5B, 6A and 7A. Some of them were probably linked to the basic helix–loop–helix (bHLHs) transcription factor family, influencing the root hair elongation in *Arabidopsis* and rice and determining the rhizosheath extent. Others were located close to *Rht* genes influencing the plant structure, such as the height or the root length. On the other hand, five QTLs located on different chromosomes (i.e., 1D, 3A, 3B, 6A2, 7B) contributed to rhizosheath size in wheat (*Triticum aestivum* L.) grown in acid soil, with a notable improvement in phosphorus acquisition [28]. George et al. [36] found genomic regions in barley (*Hordeum vulgare* L.) that were significantly associated with rhizosheath weight on the chromosome 2H. They contained a glutamate receptor and several putative candidate genes which modulate the root system development in rice and *Arabidopsis* in abiotic stress conditions, such as cold and drought, or during the early and delicate plant growth stages. Drought treatment on foxtail millet (*Setaria italica*) increased the expression of five root-hair-elongation-associated genes (Seita.3G196500, Seita.2G057800, Seita.9G333500, Seita. 8G104600, Seita.7G190800). This was revealed by qRT-PCR analysis demostrating the development of a larger root hairs as appendage to which soil particles bond [42]. de la Fuente Cantó et al. [55] suggested the role of root exudation in the formation pearl millet rhizosheaths through genome-wide association studies (GWAS) combined with bulk segregant analysis (BSA). They identified twelve potential QTLs, five of which were validated on chromosomes 5 and 6; many of them regulated the production of several molecules composing the root exudates, and controlled the root-adhering soil aggregation. Moreover, Karanja et al. [37] revealed, by RNA sequencing for transcriptome analysis on wild-type tomatoes in drought conditions, the upregulation of several genes related to the abscisic acid (ABA) signaling pathways (e.g., ABA $8'$-hydroxylase and protein phosphatase 2C), whose accumulation seems to stimulate rhizosheath development. Aslam et al. [30] observed an overexpression of sucrose and phosphorous-related genes (LaSUC1, LaSUC5, LaSUC9 and LaSPX3, LaPHO1, LaPHT1, respectively) in phosphorus-deficient soil drying conditions in white lupine mature cluster roots. A sucrose accumulation and a consequent improvement of the P absorption were observed, and these were mainly related to the vigorous rhizosheaths of these root compartments. Moreover, LaPAP12 gene overexpression was observed in white lupine and rice, together with the increase in rhizosheath development in dry conditions without P-input. This can be linked to the rise in root exudation of acid phosphatases (APases), leading to increased P availability. This promotes bacterial proliferation, in particular, the phosphate-solubilizing and auxin-producing *Bacillus megaterium*, which synergically contributes to increases in the roots length and the consequent greater rhizosheath formation [84].

5.4. Microbial Investigations

The advances in genomic sequencing methods developed during the last decades has allowed us to overcome the lack of information related to non-readily culturable microbes from several environments [85]. Through these revolutions, technological applications investigating the composition and the physiology of the rhizobiome can shed light on its key role in the soil ecosystem, unraveling the vital mutualistic interactions among soil, roots and microbes [86]. Recent studies have suggested that rhizosheath-associated microbial communities are pivotal in its building processes, as well as in the plant-growth-promoting services provided by root–bacteria relationships. A rhizosheath was defined as an edaphic "mini-oasis" in arid habitats, where several microbial taxa presenting high functional redundancy are in competition to conquer ecological niches that support the beneficial functions of plant biofertilization, biopromotion and bioprotection [79]. Root-associated microorganisms can implement several strategies aimed at improving essential nutrient availability; producing biostimulants (exopolysaccharides, phytohormones, volatile compounds, etc.) for plant growth; and at mitigating abiotic/biotic stresses affecting plants [81]. The current challenge involves deepening the knowledge of these primary mechanisms to be reinforced for the purpose of improving the crops and reducing the use of agrochemical supplies [18,20,44,53,87].

Zhang et al. [25] demonstrated the crucial role of rhizobacteria in rice (*Oryza sativa*) rhizosheath genesis through the upregulation of genes involved in ethylene pathways induced by moderate soil drying conditions. In particular, a high abundance of *Enterobacter aerogenes* was detected from the rhizosheaths of two different rice varieties (Gaoshan 1, a drought-tolerant species, and Nipponbare, a drought-sensitive species), with a high production of the aminocyclopropane-1-carboxylate deaminase (ACCd) enzyme. This enzyme reduces the ethylene levels in roots, favoring plant growth and root hair elongation, which promotes rhizosheath enhancement. Zhu et al. [32], after fine-tuning the separation method of the rhizosheath, the rhizosphere soil, the root epidermis and the root system in *Stipa grandis*, a drought-tolerant species, highlighted significant differences in bacterial and fungal communities between the analyzed compartments, suggesting their different roles in the interaction processes between plants and the soil matrix. In particular, the root epidermis and endophytes displayed different bacterial compositions, with a dominance of *Cyanobacteria* in the root system (~46%) and *Actinobacteria* in the root epidermis (43%), but similar fungal populations, which were mainly composed by *Basidiomycota* (mean value ~71%). The rhizosheath and the rhizosphere soil showed similar compositions, with the presence of *Proteobacteria* (mean value ~22%), *Acidobacteria* (mean value ~9%), *Planctomycetes* (mean value ~8%) and *Verrucomicrobia* (mean value ~3.4%) bacterial groups, as well as *Basidiomycota* (mean value ~35%) and *Ascomycota* (mean value ~25%), among fungal taxa.

Several studies based on bacterial and fungal strain inoculation techniques have demonstrated their particular role in root system development, as well as in rhizosheath evolution. Chen et al. [67], in the rhizosheath of *Kengyilia hirsute,* individuated the enrichment of *Massilia* and *Arthrobacter* species that are likely related to plant molecular mechanisms for specific taxa selection and accumulation involved in rhizosheath formation. *Trichoderma harzianum* T-22 increased the rhizosheath amount in several ancient and modern wheat varieties, affecting their root systems' architectures differently [51]. The endophytic fungus *Piriformospora indica* is able to modulate auxin production under moderate soil drying, enhancing the growth of rice root hairs for soil exploration by seeking water and providing a more suitable physical structure for the formation of the rhizosheath. This leads to an enrichment of *Bacillus cereus* in both the rhizosphere and the rhizosheath, suggesting a strong bacteria–fungi interaction involved in the exudate compounds use [52].

6. Conclusions and Perspectives

The present work reviewed the existing literature on rhizosheath, providing important guidelines for future investigations with the aim of avoiding redundancies and ambiguities in this field. In particular, we clarified the correct rhizosemantics and the standardized sampling methods essential for a cohesive interpretation of the results. Firstly, according to the definition proposed by Puente et al. [39], where the rhizoplane is given by the combination of the rhizosheath and root epidermis, it is important to perform a correct sampling of the several sections composing the root system (bulk soil, rhizosphere, rhizosheath, root epidermis, etc.) in order to achieve a complete comprehension of the complex structure. In particular, rhizosheaths need to be collected after shaking off the bulk soil, ensuring the sampling of the residual root-adhered soil. Then, rhizosheath sampling can be performed mechanically, by using a soft brush, or manually, by washing the soil from the roots with water in a container or through sonication. For microbiological surveys, the use of sterile tools and DNA/RNA stabilization solution is advised. Rhizosheaths are emerging as favorable root features for sustainable agro-systems, ensuring robust crops in view of the pressing environmental changes caused by the climate crisis and by soil exploitation in intensively managed agriculture. The processes controlling its genesis are still unclear, but several studies have highlighted complex plant–soil–microorganism interactions, where root hairs; root- and microbial-derived binder organic compounds; specific genetic determinants regulating responses to abiotic stresses; and physicochemical soil properties can modulate the rhizosheath development.

This particular root trait seems to play a key role in facing abiotic stresses, which safeguards the plants from water deficiency and high-pH soil conditions and promote water absorption, as well as nutrients availability, representing a stable micro-habitat for microbial communities. The relevant limitations of the most of the current research on rhizosheaths are related to experiments in the laboratory, and it is not always clear how the findings can be translated to the real world. Moreover, in some cases, there are also some contradictory results. Therefore, field experiments can be useful to verify the observations obtained in controlled conditions. Bearing this in mind, future efforts should be devoted to delving into several fronts: (i) to widen the spectrum of the plant species investigated, including trees, from different habitats, in order to deepen the knowledge about this particular feature; (ii) considering the promising existing genetic studies, to further investigate the genes associated with rhizosheath expression (enhancing plant stress responses can be useful for breeding and genetic engineering in order to obtain improved and more resistant cultivars); (iii) to delve into the benefits of rhizosheaths in terms of nutrient uptake, also considering the mobility of pollutants and of stabilization mechanisms, preventing soil erosion processes as well as enhancing the carbon sequestration and storage; and (iv) to study rhizosheaths' microbial and ecological niches and their role in its development processes; in facing environmental stresses; and in symbiotic associations among soil, roots and microbes.

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References

1. Giorgi, F. Climate Change Hot-Spots. *Geophys. Res. Lett.* **2006**, *33*, L08707. [CrossRef]
2. Hare, W.L.; Cramer, W.; Schaeffer, M.; Battaglini, A.; Jaeger, C.C. Climate Hotspots: Key Vulnerable Regions, Climate Change and Limits to Warming. *Reg. Environ. Chang.* **2011**, *11*, 1–13. [CrossRef]
3. Turco, M.; Palazzi, E.; von Hardenberg, J.; Provenzale, A. Observed Climate Change Hotspots: OBSERVED CLIMATE CHANGE HOTSPOTS. *Geophys. Res. Lett.* **2015**, *42*, 3521–3528. [CrossRef]
4. Islam, S.N.; Winkel, J. *Climate Change and Social Inequality*; DESA Working Paper 152; Department of Economic & Social Affairs, United Nations: New York, NY, USA, 2017.
5. FAO. *Strategy on Climate Change 2022–2031*; Food and Agriculture Organization of the United Nations: Rome, Italy, 2022.

6. IPCC. Climate Change 2021: The physical science basis. In *Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*; Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S.L., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L., Gomis, M.I., et al., Eds.; Cambridge University Press: Cambridge, UK, 2021.
7. IPCC. Summary for policymakers. In *Climate Change 2022: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*; Pörtner, H.-O., Roberts, D.C., Tignor, M., Poloczanska, E.S., Mintenbeck, K., Alegría, A., Craig, M., Langsdorf, S., Löschke, S., Möller, V., et al., Eds.; Cambridge University Press: Cambridge, UK, 2022. Available online: https://report.ipcc.ch/ar6wg2/pdf/IPCC_AR6_WGII_SummaryForPolicymakers.pdf (accessed on 1 April 2022).
8. Reynolds, W.D.; Bowman, B.T.; Drury, C.F.; Tan, C.S.; Lu, X. Indicators of Good Soil Physical Quality: Density and Storage Parameters. *Geoderma* **2002**, *110*, 131–146. [CrossRef]
9. Heyder, U.; Schaphoff, S.; Gerten, D.; Lucht, W. Risk of Severe Climate Change Impact on the Terrestrial Biosphere. *Environ. Res. Lett.* **2011**, *6*, 034036. [CrossRef]
10. Farkas, C.; Gelybó, G.; Bakacsi, Z.; Horel, Á.; Hagyó, A.; Dobor, L.; Kása, I.; Tóth, E. Impact of Expected Climate Change on Soil Water Regime under Different Vegetation Conditions. *Biologia* **2014**, *69*, 1510–1519. [CrossRef]
11. Mills, R.T.E.; Gavazov, K.S.; Spiegelberger, T.; Johnson, D.; Buttler, A. Diminished Soil Functions Occur under Simulated Climate Change in a Sup-Alpine Pasture, but Heterotrophic Temperature Sensitivity Indicates Microbial Resilience. *Sci. Total Environ.* **2014**, *473–474*, 465–472. [CrossRef]
12. Mondal, S. Impact of Climate Change on Soil Fertility. In *Climate Change and the Microbiome*; Choudhary, D.K., Mishra, A., Varma, A., Eds.; Soil Biology; Springer International Publishing: Cham, Switzerland, 2021; Volume 63, pp. 551–569, ISBN 978-3-030-76862-1.
13. Schimel, J.; Balser, T.C.; Wallenstein, M. Microbial stress-response physiology and its implications for ecosystem function. *Ecology* **2007**, *88*, 1386–1394. [CrossRef]
14. Gelybó, G.; Tóth, E.; Farkas, C.; Horel, Á.; Kása, I.; Bakacsi, Z. Potential Impacts of Climate Change on Soil Properties. *Agrokem. És Talaj.* **2018**, *67*, 121–141. [CrossRef]
15. Patil, A.; Lamnganbi, M. Impact of Climate Change on Soil Health: A Review. *Int. J. Chem. Stud.* **2018**, *6*, 2399–2404.
16. Smith, J.L.; Halvorson, J.J.; Bolton, H. Soil Properties and Microbial Activity across a 500m Elevation Gradient in a Semi-Arid Environment. *Soil Biol. Biochem.* **2002**, *34*, 1749–1757. [CrossRef]
17. Altieri, M.A.; Nicholls, C.I.; Henao, A.; Lana, M.A. Agroecology and the Design of Climate Change-Resilient Farming Systems. *Agron. Sustain. Dev.* **2015**, *35*, 869–890. [CrossRef]
18. Hallama, M.; Pekrun, C.; Mayer-Gruner, P.; Uksa, M.; Abdullaeva, Y.; Pilz, S.; Schloter, M.; Lambers, H.; Kandeler, E. The Role of Microbes in the Increase of Organic Phosphorus Availability in the Rhizosheath of Cover Crops. *Plant Soil* **2022**, *476*, 353–373. [CrossRef]
19. Etesami, H. Potential Advantage of Rhizosheath Microbiome, in Contrast to Rhizosphere Microbiome, to Improve Drought Tolerance in Crops. *Rhizosphere* **2021**, *20*, 100439. [CrossRef]
20. Ndour, P.M.S.; Heulin, T.; Achouak, W.; Laplaze, L.; Cournac, L. The Rhizosheath: From Desert Plants Adaptation to Crop Breeding. *Plant Soil* **2020**, *456*, 1–13. [CrossRef]
21. Wang, J.; Ding, Y.; Cao, Y.; Xu, W.; Zhang, Y. Rhizosheath Microbes Induce Root Immune Response under Soil Drying. *Plant Signal. Behav.* **2021**, *16*, 1920752. [CrossRef]
22. Honvault, N.; Houben, D.; Firmin, S.; Meglouli, H.; Laruelle, F.; Fontaine, J.; Lounès-Hadj Sahraoui, A.; Coutu, A.; Lambers, H.; Faucon, M. Interactions between Below-ground Traits and Rhizosheath Fungal and Bacterial Communities for Phosphorus Acquisition. *Funct. Ecol.* **2021**, *35*, 1603–1619. [CrossRef]
23. Watt, M.; McCully, M.E.; Canny, M.J. Formation and Stabilization of Rhizosheaths of *Zea mays*. (Effect of Soil Water Content). *Plant Physiol.* **1994**, *106*, 179–186. [CrossRef]
24. Haling, R.E.; Brown, L.K.; Bengough, A.G.; Valentine, T.A.; White, P.J.; Young, I.M.; George, T.S. Root Hair Length and Rhizosheath Mass Depend on Soil Porosity, Strength and Water Content in Barley Genotypes. *Planta* **2014**, *239*, 643–651. [CrossRef]
25. Zhang, Y.; Du, H.; Xu, F.; Ding, Y.; Gui, Y.; Zhang, J.; Xu, W. Root-Bacteria Associations Boost Rhizosheath Formation in Moderately Dry Soil through Ethylene Responses. *Plant Physiol.* **2020**, *183*, 780–792. [CrossRef]
26. Burak, E.; Quinton, J.N.; Dodd, I.C. Root Hairs Are the Most Important Root Trait for Rhizosheath Formation of Barley (*Hordeum Vulgare*), Maize (*Zea Mays*) and *Lotus Japonicus* (Gifu). *Ann. Bot.* **2021**, *128*, 45–57. [CrossRef]
27. Delhaize, E.; James, R.A.; Ryan, P.R. Aluminium Tolerance of Root Hairs Underlies Genotypic Differences in Rhizosheath Size of Wheat (*Triticum aestivum*) Grown on Acid Soil. *New Phytol.* **2012**, *195*, 609–619. [CrossRef]
28. James, R.A.; Weligama, C.; Verbyla, K.; Ryan, P.R.; Rebetzke, G.J.; Rattey, A.; Richardson, A.E.; Delhaize, E. Rhizosheaths on Wheat Grown in Acid Soils: Phosphorus Acquisition Efficiency and Genetic Control. *J. Exp. Bot.* **2016**, *67*, 3709–3718. [CrossRef]
29. Brown, L.K.; George, T.S.; Neugebauer, K.; White, P.J. The Rhizosheath—A Potential Trait for Future Agricultural Sustainability Occurs in Orders throughout the Angiosperms. *Plant Soil* **2017**, *418*, 115–128. [CrossRef]
30. Aslam, M.M.; Karanja, J.K.; Yuan, W.; Zhang, Q.; Zhang, J.; Xu, W. Phosphorus Uptake Is Associated with the Rhizosheath Formation of Mature Cluster Roots in White Lupin under Soil Drying and Phosphorus Deficiency. *Plant Physiol. Biochem.* **2021**, *166*, 531–539. [CrossRef]
31. Lynch, J.P. Roots of the Second Green Revolution. *Aust. J. Bot.* **2007**, *55*, 493. [CrossRef]

32. Zhu, A.-M.; Wu, Q.; Liu, H.-L.; Sun, H.-L.; Han, G.-D. Isolation of Rhizosheath and Analysis of Microbial Community Structure around Roots of *Stipa Grandis*. *Sci. Rep.* **2022**, *12*, 2707. [CrossRef]
33. York, L.M.; Carminati, A.; Mooney, S.J.; Ritz, K.; Bennett, M.J. The Holistic Rhizosphere: Integrating Zones, Processes, and Semantics in the Soil Influenced by Roots. *J. Exp. Bot.* **2016**, *67*, 3629–3643. [CrossRef]
34. Pang, J.; Ryan, M.H.; Siddique, K.H.M.; Simpson, R.J. Unwrapping the Rhizosheath. *Plant Soil* **2017**, *418*, 129–139. [CrossRef]
35. Bergmann, D.; Zehfus, M.; Zierer, L.; Smith, B.; Gabel, M. Grass Rhizosheaths: Associated Bacterial Communities and Potential for Nitrogen Fixation. *W. N. Am. Nat.* **2009**, *69*, 105–114. [CrossRef]
36. George, T.S.; Brown, L.K.; Ramsay, L.; White, P.J.; Newton, A.C.; Bengough, A.G.; Russell, J.; Thomas, W.T.B. Understanding the Genetic Control and Physiological Traits Associated with Rhizosheath Production by Barley (H*Ordeum Vulgare*). *New Phytol.* **2014**, *203*, 195–205. [CrossRef]
37. Karanja, J.K.; Aslam, M.M.; Qian, Z.; Yankey, R.; Dodd, I.C.; Weifeng, X. Abscisic Acid Mediates Drought-Enhanced Rhizosheath Formation in Tomato. *Front. Plant Sci.* **2021**, *12*, 658787. [CrossRef]
38. Marasco, R.; Fusi, M.; Mosqueira, M.; Booth, J.M.; Rossi, F.; Cardinale, M.; Michoud, G.; Rolli, E.; Mugnai, G.; Vergani, L.; et al. Rhizosheath–Root System Changes Exopolysaccharide Content but Stabilizes Bacterial Community across Contrasting Seasons in a Desert Environment. *Environ. Microb.* **2022**, *17*, 14. [CrossRef]
39. Puente, M.E.; Bashan, Y.; Li, C.Y.; Lebsky, V.K. Microbial Populations and Activities in the Rhizoplane of Rock-Weathering Desert Plants. I. Root Colonization and Weathering of Igneous Rocks. *Plant Biol.* **2004**, *6*, 629–642. [CrossRef]
40. Haling, R.E.; Richardson, A.E.; Culvenor, R.A.; Lambers, H.; Simpson, R.J. Root Morphology, Root-Hair Development and Rhizosheath Formation on Perennial Grass Seedlings Is Influenced by Soil Acidity. *Plant Soil* **2010**, *335*, 457–468. [CrossRef]
41. Haling, R.E.; Simpson, R.J.; Culvenor, R.A.; Lambers, H.; Richardson, A.E. Effect of Soil Acidity, Soil Strength and Macropores on Root Growth and Morphology of Perennial Grass Species Differing in Acid-soil Resistance. *Plant Cell Environ.* **2011**, *34*, 444–456. [CrossRef]
42. Liu, T.-Y.; Chen, M.-X.; Zhang, Y.; Zhu, F.-Y.; Liu, Y.-G.; Tian, Y.; Fernie, A.R.; Ye, N.; Zhang, J. Comparative Metabolite Profiling of Two Switchgrass Ecotypes Reveals Differences in Drought Stress Responses and Rhizosheath Weight. *Planta* **2019**, *250*, 1355–1369. [CrossRef]
43. Marasco, R.; Mosqueira, M.J.; Fusi, M.; Ramond, J.-B.; Merlino, G.; Booth, J.M.; Maggs-Kölling, G.; Cowan, D.A.; Daffonchio, D. Rhizosheath Microbial Community Assembly of Sympatric Desert Speargrasses Is Independent of the Plant Host. *Microbiome* **2018**, *6*, 215. [CrossRef]
44. Aslam, M.M.; Karanja, J.K.; Dodd, I.C.; Waseem, M.; Weifeng, X. Rhizosheath: An Adaptive Root Trait to Improve Plant Tolerance to Phosphorus and Water Deficits? *Plant Cell Environ.* **2022**, *45*, 2861–2874. [CrossRef]
45. Bailey, C.; Scholes, M. Rhizosheath Occurrence in South African Grasses. *S. Afr. J. Bot.* **1997**, *63*, 484–490. [CrossRef]
46. Smith, R.J.; Hopper, S.D.; Shane, M.W. Sand-Binding Roots in Haemodoraceae: Global Survey and Morphology in a Phylogenetic Context. *Plant Soil* **2011**, *348*, 453–470. [CrossRef]
47. Cheraghi, M.; Mousavi, S.M.; Zarebanadkouki, M. Functions of Rhizosheath on Facilitating the Uptake of Water and Nutrients under Drought Stress: A Review. *Plant Soil* **2023**, *491*, 1–25. [CrossRef]
48. Mo, X.; Wang, M.; Zeng, H.; Wang, J. Rhizosheath: Distinct Features and Environmental Functions. *Geoderma* **2023**, *435*, 116500. [CrossRef]
49. Tahir, M.; Mirza, M.S.; Hameed, S.; Dimitrov, M.R.; Smidt, H. Cultivation-Based and Molecular Assessment of Bacterial Diversity in the Rhizosheath of Wheat under Different Crop Rotations. *PLoS ONE* **2015**, *10*, e0130030. [CrossRef] [PubMed]
50. Basirat, M.; Mousavi, S.M.; Abbaszadeh, S.; Ebrahimi, M.; Zarebanadkouki, M. The Rhizosheath: A Potential Root Trait Helping Plants to Tolerate Drought Stress. *Plant Soil* **2019**, *445*, 565–575. [CrossRef]
51. Bochicchio, R.; Labella, R.; Vitti, A.; Nuzzaci, M.; Logozzo, G.; Amato, M. Root Morphology, Allometric Relations and Rhizosheath of Ancient and Modern Tetraploid Wheats (Triticum Durum Desf.) in Response to Inoculation with Trichoderma Harzianum T-22. *Plants* **2022**, *11*, 159. [CrossRef] [PubMed]
52. Xu, F.; Liao, H.; Zhang, Y.; Yao, M.; Liu, J.; Sun, L.; Zhang, X.; Yang, J.; Wang, K.; Wang, X.; et al. Coordination of Root Auxin with the Fungus Piriformospora Indica and Bacterium Bacillus Cereus Enhances Rice Rhizosheath Formation under Soil Drying. *ISME J.* **2022**, *16*, 801–811. [CrossRef]
53. Lei, Z.; Ding, Y.; Xu, W.; Zhang, Y. Microbial Community Structure in Rice Rhizosheaths under Drought Stress. *J. Plant Ecol.* **2023**, *16*, rtad012. [CrossRef]
54. Adu, M.O.; Asare, P.A.; Yawson, D.O.; Ackah, F.K.; Amoah, K.K.; Nyarko, M.A.; Andoh, D.A. Quantifying Variations in Rhizosheath and Root System Phenotypes of Landraces and Improved Varieties of Juvenile Maize. *Rhizosphere* **2017**, *3*, 29–39. [CrossRef]
55. de la Fuente Cantó, C.; Diouf, M.N.; Ndour, P.M.S.; Debieu, M.; Grondin, A.; Passot, S.; Champion, A.; Barrachina, C.; Pratlong, M.; Gantet, P.; et al. Genetic Control of Rhizosheath Formation in Pearl Millet. *Sci. Rep.* **2022**, *12*, 9205. [CrossRef]
56. Adu, M.O.; Zigah, N.; Yawson, D.O.; Amoah, K.K.; Afutu, E.; Atiah, K.; Darkwa, A.A.; Asare, P.A. Plasticity of Root Hair and Rhizosheath Traits and Their Relationship to Phosphorus Uptake in Sorghum. *Plant Direct* **2023**, *7*, e521. [CrossRef] [PubMed]
57. Duell, R.W.; Peacock, G.R. Rhizosheaths on Mesophytic Grasses. *Crop Sci.* **1985**, *25*, 880–883. [CrossRef]
58. Bibikova, T.; Gilroy, S. Root Hair Development. *J. Plant Growth Regul.* **2002**, *21*, 383–415. [CrossRef]
59. Grierson, C.; Nielsen, E.; Ketelaarc, T.; Schiefelbein, J. Root Hairs. *Arab. Book* **2014**, *12*, e0172. [CrossRef]

60. McCully, M.E. ROOTS IN SOIL: Unearthing the Complexities of Roots and Their Rhizospheres. *Annu. Rev. Plant. Physiol. Plant. Mol. Biol.* **1999**, *50*, 695–718. [CrossRef]
61. Liu, T.; Ye, N.; Song, T.; Cao, Y.; Gao, B.; Zhang, D.; Zhu, F.; Chen, M.; Zhang, Y.; Xu, W.; et al. Rhizosheath Formation and Involvement in Foxtail Millet (*Setaria italica*) Root Growth under Drought Stress. *J. Integr. Plant Biol.* **2019**, *61*, 449–462. [CrossRef]
62. Morel, J.L.; Habib, L.; Plantureux, S.; Guckert, A. Influence of Maize Root Mucilage on Soil Aggregate Stability. *Plant Soil* **1991**, *136*, 111–119. [CrossRef]
63. Czarnes, S.; Hallett, P.D.; Bengough, A.G.; Young, I.M. Root- and Microbial-Derived Mucilages Affect Soil Structure and Water Transport: Mucilages, Soil Structure and Sorptivity. *Eur. J. Soil Sci.* **2000**, *51*, 435–443. [CrossRef]
64. Galloway, A.F.; Akhtar, J.; Marcus, S.E.; Fletcher, N.; Field, K.; Knox, P. Cereal Root Exudates Contain Highly Structurally Complex Polysaccharides with Soil-binding Properties. *Plant J.* **2020**, *103*, 1666–1678. [CrossRef]
65. Di Marsico, A.; Scrano, L.; Labella, R.; Lanzotti, V.; Rossi, R.; Cox, L.; Perniola, M.; Amato, M. Mucilage from fruits/seeds of chia (*Salvia hispanica* L.) improves soil aggregate stability. *Plant Soil* **2018**, *425*, 57–69. [CrossRef]
66. Ahmed, M.A.; Kroener, E.; Holz, M.; Zarebanadkouki, M.; Carminati, A. Mucilage Exudation Facilitates Root Water Uptake in Dry Soils. *Functional Plant Biol.* **2014**, *41*, 1129. [CrossRef] [PubMed]
67. Chen, Y.; Chen, C.; Zhou, Q.; Hu, J.; Lei, Y.; Liu, W. Specific Rhizobacteria Responsible in the Rhizosheath System of Kengyilia Hirsuta. *Front. Plant Sci.* **2022**, *12*, 785971. [CrossRef] [PubMed]
68. Naveed, M.; Brown, L.K.; Raffan, A.C.; George, T.S.; Bengough, A.G.; Roose, T.; Sinclair, I.; Koebernick, N.; Cooper, L.; Hackett, C.A.; et al. Plant Exudates May Stabilize or Weaken Soil Depending on Species, Origin and Time: Effect of Plant Exudates on Rhizosphere Formation. *Eur. J. Soil Sci.* **2017**, *68*, 806–816. [CrossRef] [PubMed]
69. Kroener, E.; Holz, M.; Zarebanadkouki, M.; Ahmed, M.; Carminati, A. Effects of Mucilage on Rhizosphere Hydraulic Functions Depend on Soil Particle Size. *Vadose Zone J.* **2018**, *17*, 1–11. [CrossRef]
70. McCully, M.E. Water Efflux from the Surface of Field-Grown Grass Roots. Observations by Cryo-Scanning Electron Microscopy. *Physiol. Plant.* **1995**, *95*, 217–224. [CrossRef]
71. Ahmadi, K.; Zarebanadkouki, M.; Ahmed, M.A.; Ferrarini, A.; Kuzyakov, Y.; Kostka, S.J.; Carminati, A. Rhizosphere Engineering: Innovative Improvement of Root Environment. *Rhizosphere* **2017**, *3*, 176–184. [CrossRef]
72. Moreno-Espíndola, I.P.; Rivera-Becerril, F.; de Jesús Ferrara-Guerrero, M.; De León-González, F. Role of Root-Hairs and Hyphae in Adhesion of Sand Particles. *Soil Biol. Biochem.* **2007**, *39*, 2520–2526. [CrossRef]
73. Mickelbart, M.V.; Hasegawa, P.M.; Bailey-Serres, J. Genetic Mechanisms of Abiotic Stress Tolerance That Translate to Crop Yield Stability. *Nat. Rev. Genet.* **2015**, *16*, 237–251. [CrossRef]
74. Baillo, E.H.; Kimotho, R.N.; Zhang, Z.; Xu, P. Transcription Factors Associated with Abiotic and Biotic Stress Tolerance and Their Potential for Crops Improvement. *Genes* **2019**, *10*, 771. [CrossRef]
75. Galloway, A.F.; Knox, P.; Krause, K. Sticky Mucilages and Exudates of Plants: Putative Microenvironmental Design Elements with Biotechnological Value. *New Phytol.* **2020**, *225*, 1461–1469. [CrossRef]
76. Young, I.M. Variation in Moisture Contents between Bulk Soil and the Rhizosheath of Wheat (*Triticum aestivum* L. Cv. Wembley). *New Phytol.* **1995**, *130*, 135–139. [CrossRef]
77. North, G.B.; Nobel, P.S. Drought-induced changes in soil contact and hydraulic conductivity for roots of Opuntia ficus-indica with and without rhizosheaths. *Plant Soil* **1997**, *191*, 249–258. [CrossRef]
78. Ahmed, M.A.; Kroener, E.; Benard, P.; Zarebanadkouki, M.; Kaestner, A.; Carminati, A. Drying of Mucilage Causes Water Repellency in the Rhizosphere of Maize: Measurements and Modelling. *Plant Soil* **2016**, *407*, 161–171. [CrossRef]
79. Marasco, R.; Fusi, M.; Ramond, J.-B.; Van Goethem, M.W.; Seferji, K.; Maggs-Kölling, G.; Cowan, D.A.; Daffonchio, D. The Plant Rhizosheath–Root Niche Is an Edaphic "Mini-Oasis" in Hyperarid Deserts with Enhanced Microbial Competition. *ISME Commun.* **2022**, *2*, 47. [CrossRef] [PubMed]
80. Teixeira, P.P.C.; Trautmann, S.; Buegger, F.; Felde, V.J.M.N.L.; Pausch, J.; Müller, C.W.; Kögel-Knabner, I. Role of Root Hair Elongation in Rhizosheath Aggregation and in the Carbon Flow into the Soil. *Biol. Fertil. Soils* **2023**, *59*, 351–361. [CrossRef]
81. Pathan, S.I.; Ceccherini, M.T.; Sunseri, F.; Lupini, A. Rhizosphere as Hotspot for Plant-Soil-Microbe Interaction. In *Carbon and Nitrogen Cycling in Soil*; Datta, R., Meena, R.S., Pathan, S.I., Ceccherini, M.T., Eds.; Springer: Singapore, 2020; pp. 17–43, ISBN 9789811372636.
82. Ndour, P.M.S.; Gueye, M.; Barakat, M.; Ortet, P.; Bertrand-Huleux, M.; Pablo, A.-L.; Dezette, D.; Chapuis-Lardy, L.; Assigbetsé, K.; Kane, N.A.; et al. Pearl Millet Genetic Traits Shape Rhizobacterial Diversity and Modulate Rhizosphere Aggregation. *Front. Plant Sci.* **2017**, *8*, 1288. [CrossRef] [PubMed]
83. Delhaize, E.; Rathjen, T.M.; Cavanagh, C.R. The Genetics of Rhizosheath Size in a Multiparent Mapping Population of Wheat. *J. Exp. Bot.* **2015**, *66*, 4527–4536. [CrossRef] [PubMed]
84. Aslam, M.M.; Pueyo, J.J.; Pang, J.; Yang, J.; Chen, W.; Chen, H.; Waseem, M.; Li, Y.; Zhang, J.; Xu, W. Root Acid Phosphatases and Rhizobacteria Synergistically Enhance White Lupin and Rice Phosphorus Acquisition. *Plant Physiol.* **2022**, *190*, 2449–2465. [CrossRef]
85. Streit, W.R.; Schmitz, R.A. Metagenomics—The Key to the Uncultured Microbes. *Curr. Opin. Microbiol.* **2004**, *7*, 492–498. [CrossRef]

86. Baldrian, P. The Known and the Unknown in Soil Microbial Ecology. *FEMS Microbiol. Ecol.* **2019**, *95*, fiz005. [CrossRef]
87. Zhang, R.; Vivanco, J.M.; Shen, Q. The Unseen Rhizosphere Root–Soil–Microbe Interactions for Crop Production. *Curr. Opin. Microbiol.* **2017**, *37*, 8–14. [CrossRef] [PubMed]