

Review

Revisiting Soil Water Potential: Towards a Better Understanding of Soil and Plant Interactions

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Abstract: Soil water potential (SWP) is vital for controlling the various biological and non-biological processes occurring through and across the soil-plant-atmosphere continuum (SPAC). Although the dynamics and mechanisms of SWP have been investigated for several decades, they are not as widely explored in ecohydrology research as soil moisture, due at least partly to the limitation of field observation methods. This limitation restricts the understanding of the responses of plant physiology and ecological processes to the SWP gradient and the ecohydrological functions of SWP dynamics in different contexts. Hence, in this work, we first briefly revisit the origin and development of the concept of SWP and then analyze the comprehensive factors that influence SWP and the improvement of SWP observation techniques at field scales, as well as strategies for developing new sensors for soil water status. We also propose views of focusing on the response characteristics of plant lateral roots, rather than taproots, to SWP dynamics, and using hormone signaling research to evaluate plant response signals to water stress. We end by providing potential challenges and insights that remain in related research, such as the limitations of the SWP evaluation methods and the future development direction of SWP data collection, management, and analysis. We also emphasize directions for the application of SWP in controlling plant pathogens and promoting the efficiency of resource acquisition by plants. In short, these reflections revisit the unique role of SWP in eco-hydrological processes, provide an update on the development of SWP research, and support the assessment of plant drought vulnerability under current and future climatic conditions.

Keywords: soil water potential; soil moisture; plant physiology; soil-plant-atmosphere continuum; ecohydrological cycle



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1. Introduction

Although the amount of water stored in soil is much less than that stored in the oceans, fluxes of water into and out of soils can be large, making soil water important in the exchange of mass and energy in the soil-plant-atmosphere continuum (SPAC) system. Soil water status is characterized by both the amount of water present (soil water content, SWC) and the energy with which the water is held (soil water potential, SWP) [1,2]. Like all other matter, soil water tends to move from regions of higher SWP to regions of lower SWP, in pursuit of equilibrium with its surroundings [3]. The magnitude of the driving force behind this spontaneous motion is the difference in potential energy across a distance between two points of interest [4]. Accordingly, SWC tells us how much water there is, but SWP gives information about the availability of the water for plant uptake or microbial activity, the movement of the water in the soil, and in particular, how the soil retains and

releases water in the SPAC [5]. It is clear that SWP is an equally critical soil parameter, and a quantitative evaluation of it is needed for almost every aspect of soil and related sciences, from those dealing with soil organisms and plant growth to those dealing with environmental concerns [6]. Historically, however, fewer works have reported on SWP than on SWC, especially in terms of observations and experiments [7], even though the concept of SWP has existed since the early 18th century. This situation is due at least partly to the lack of effective and convenient techniques for measuring SWP [8], but the situation has improved during the last two decades, as various automated and flexible techniques and tools have been developed [9]. In contrast to SWP measurement technologies, SWP modeling—which also has a long history—has been utilized in many more studies [10]. Since Gardner et al. [11] first proposed a model of soil water movement corresponding to the special case using $\psi \propto \theta^{-1/3}$, $K \propto \theta$, and hence $D \propto \theta^{-1/3}$ (ψ , capillary head; θ , water content; K , hydraulic conductivity; D , soil diffusivity), considerable progress has been made in SWP modeling. For example, Richards [12] proposed a partial differential equation for describing water movement in unsaturated soils; Klute [13] rewrote Richards [12] formulation for three-dimensional unsaturated flow in a diffusion form and more recently, SWP was incorporated into the conceptual framework of SPAC, to understand the responses of plant physiology, morphology, phytochemistry, and phytopathology to soil water dynamics [14–17].

Knowledge regarding the improvements in SWP definition and measurement has been advanced by several researchers. For instance, Luo et al. [18] and Novick et al. [6] summarized the comprehensive description of the definition of SWP; Campbell [19] and Clark [20] reviewed the most widely used instruments and theories for determining SWP, and Bittelli [21] and Bianchi et al. [8] reviewed the application of SWP measurement technology and its potential application in agricultural water management. These works, however, are limited as they failed to describe in detail the conditions for SWP dynamics to trigger plant physiological and ecological activities in different water-stressed habitats. These aspects of SWP, in which complex interactions between different stress combinations may arise, remain poorly understood. This oversight brings up new questions; for example, are the changes in plant physiology and ecology dominated by water stress or by plant self-regulation? This question is vital for plants in dry areas where water is scarce but where small changes in SWC often correspond to large changes in SWP [22]. Moreover, slow versus rapid fluctuations of SWP have completely different effects on plants, but how plants interpret the different water signals of SWP and perceive SWP changes remains unknown [23], leading to uncertainty in model outputs. The development of research on plant perception of water potential at the cellular and organ scales in recent years has provided the means to explore this problem—a turning point in the development of SWP research [24]. Besides, not all SWP changes are involved in plant adaptation processes; some of them are short-term adaptations, or even permanent deleterious reactions [25]. Therefore, it is necessary to consider the effects of SWP dynamics on plant physiology and eco-hydrological processes, from the individual-plant scale up to the field or even larger scales (e.g., landscape scales), for example, the as-yet-unknown mechanism of SWP dynamics participating in the interactions between plant and soil [26,27], the quantification of its effect on carbon decomposition and fixation [28], and the kinetic mechanisms of soil organic element migration and nutrient acquisition by plants [29,30]. Thus, we conduct a review of measurement methods and models for evaluating SWP and focus on the role of SWP in ecohydrological cycling. We propose general factors that affect SWP dynamics and special plant strategies in response to the SWP gradient. We also highlight the challenges and provide insights for future research, especially concerning the development of SWP evaluation methods and the role of SWP dynamics in soil-plant-water relationships.

2. Influencing Factors and Evaluation Methods

2.1. Influencing Factors

The datum for SWP is taken to be the potential of a ‘free’ water surface, subject to atmospheric pressure at the same height as the point of concern in the soil; when the soil water is saturated or in equilibrium with ‘free’ water, it has an SWP of zero; while as the soil dries or the total SWC decreases, the SWP of the soil sample becomes progressively negative [5]. The total SWP can be considered as comprising a component caused by the mutual attraction between water and soil particles, a gravity component, and a soluble-salt component [5] (Figure 1). However, the last two components are negligible in unsaturated soils without salt problems, compared to the first component, making SWC, soil properties, and soil temperature the first-order controlling factors of SWP [31]. The relationship between SWP and the corresponding values of SWC is also called the water release characteristic (in drying soil), the water retention function, and the soil water retention curve, or the pF curve [32]. This relationship is often used to describe the influence of intrinsic soil properties such as texture and structure on the soil moisture regime, e.g., under certain SWC, an increase in clay content usually leads to an increase in suction [33]. Soil temperature also influences this relationship either by controlling the surface tension or by affecting the apparent contact angle, and thus the soil water suction usually decreases with increasing temperature [34]. Other environmental variables, including soil salinity, soil organisms, microbial activities, etc., are second-order factors that affect SWP [35–38] (Figure 2). In salt-affected soils, soluble salts also cause a reduction in SWP similar to the one arising from droughts, mainly through lowering the osmotic potential [35]. Soil organisms (e.g., termites and earthworms) and the physiological activity of plants (e.g., root development and nodule formation) might affect the pF curve by changing the soil macrostructures via physiological activities [5]. The increase in microbial biomass and the corresponding production of exopolysaccharides also affect the pF curve by changing soil microstructures and increasing the stability of soil aggregates [39]. Notably, the combined influence of multiple factors complicates the research of SWP dynamics and is mainly reflected in that some factors (e.g., temperature and biological activities) disturb the evaluation methods of SWP and bring uncertainty to the research results. In recent years, the SWP evaluation methods have improved the evaluation accuracy and reduced the disturbing influence of redundant factors, mainly in the measurement and simulation of SWP, as discussed in the next section.

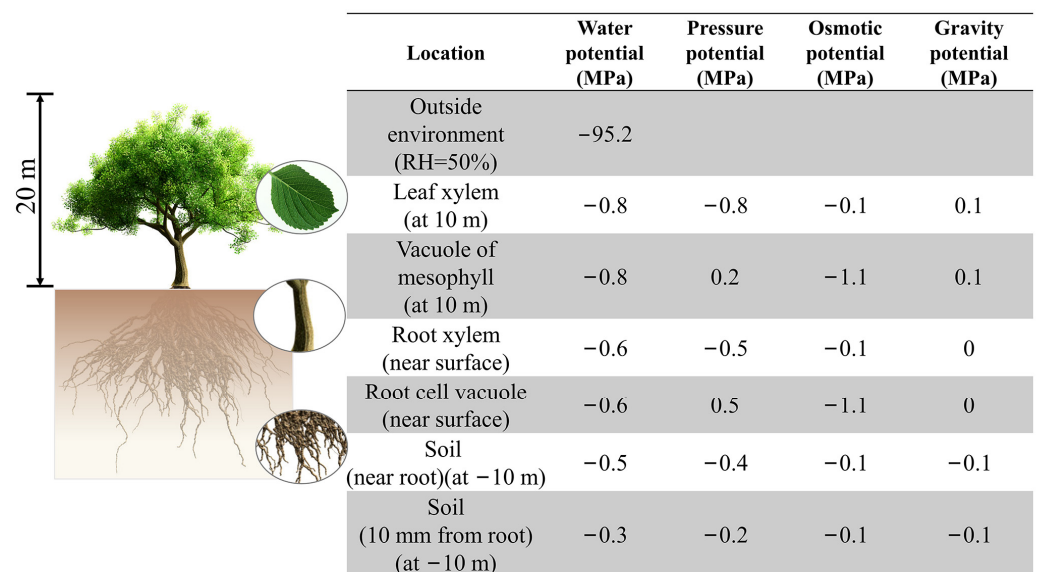


Figure 1. Schematic diagram of typical water potential at different locations during water transfer from soil to the atmosphere, modified from Taiz et al. [40].

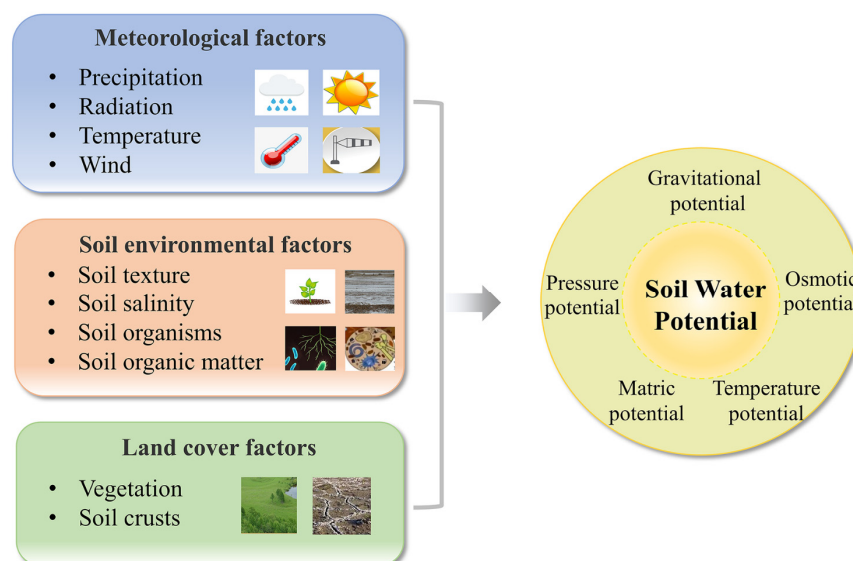


Figure 2. Schematic diagram of factors affecting soil water potential (SWP).

2.2. Evaluation Methods

Various techniques and methods have been developed during the past decades to determine SWP. These can be roughly categorized into (i) traditional techniques, (ii) new modern techniques, and (iii) simulation methods [21]. The traditional SWP measurement techniques include tensiometers, piezometers, dielectric sensors, heat dissipation sensors, etc. The new modern techniques utilize microbial sensors and micro SWP sensors, as described in the following. However, both traditional and modern techniques exhibit uncertainty related to their precision, coverage, and sensitivity of measurement under the influence of many factors (e.g., soil temperature and salt concentration), which can also cause deviations in the results of the simulation methods.

2.2.1. Measurement Methods

Traditional methods for SWP measurement include field measurement and laboratory-based methods. Although these methods have undergone tremendous development—from Buckingham [41], who carried out the first measurement of SWP some 100 years ago, up to the present day—all of them have shortcomings, such as limited measurement range (Figure 3), low accuracy, and complicated installation (Table 1). The basic instrument for field measurement, the tensimeter, was first described by Gardner et al. [11]; it is portable, inexpensive, and easy to install, but has a limited range and is insensitive to infiltration of dissolved salts in soil solutions [32]. Psychrometers overcome the upper limit of the tensiometer of about -0.1 MPa and prompt measurements based on the equilibrium of the vapor phase. It can be used in situ or in a sample chamber but is extremely sensitive to temperature [42]. Heat dissipation sensors (HDS) measure the water potential through the heat pulse dissipation in porous membranes and have a wide range of measurement (<-1 MPa). The sensors are not affected by salinity, but they have a limited upper range of SWP—close to saturation [21]. Comparatively new devices, such as dielectric water potential sensors, which were created based on time-domain reflectometry [43], can now provide a wider range of measurement (<-100 MPa), while the water potential is inferred from calibration curves and is restricted due to the hysteresis effect problem [44]. The expansion of measurement range can also be obtained with laboratory methods, such as the filter paper technique, but this is time-consuming (just like resistance sensors) and limited by temperature (just like the dew point potentiometer) [45,46]. In short, the measurement range of every available method is limited, and there is no method that can cover the whole dynamic range of water potential from wet to dry [47].

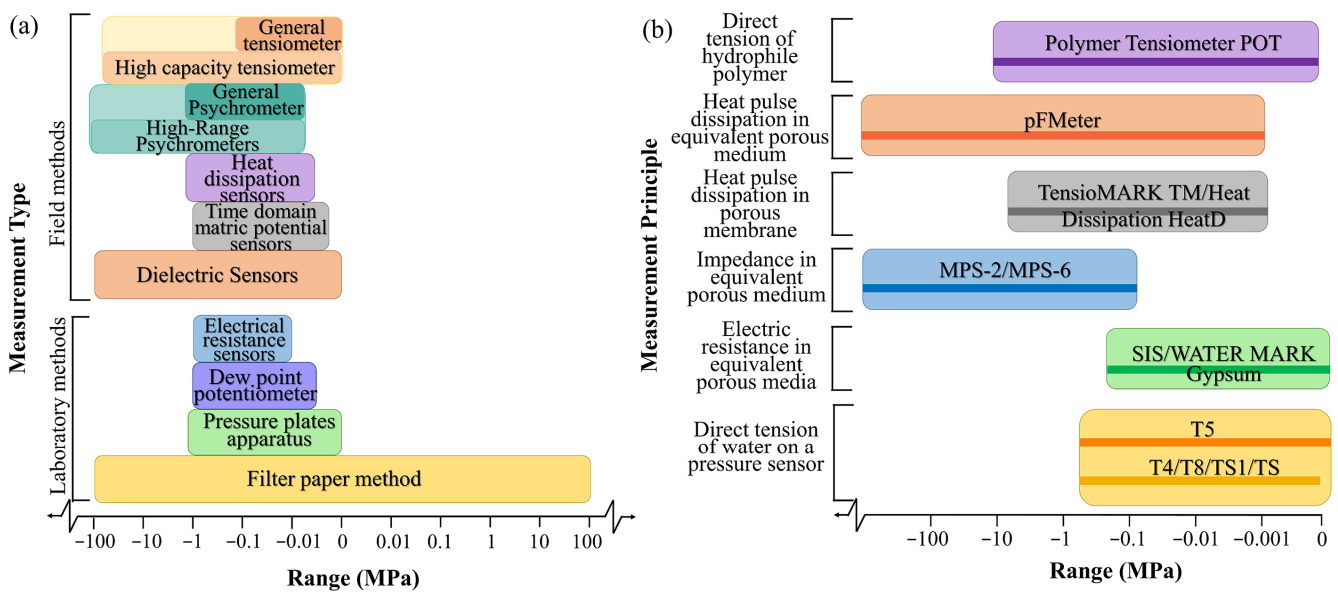


Figure 3. Primary SMP measurement methods (a) and some new SWP sensors (b), modified from Jackisch et al. [9] and Vereecken et al. [48].

Table 1. Comparison of SWP measurement methods.

Measurement	Device	Operational Range/MPa	In Situ Calibration	Measurement Principle	Main Features	References
Field methods	Tensiometer	-0.1~0	Not required	Equilibrium of the liquid phase	Low range and long response time	[49]
	Psychrometer	-1.5~-0.08	Depends on the accuracy	Equilibrium of the vapor phase	Extremely sensitive to temperature	[50]
	Piezometer		Depends on the accuracy	Equilibrium of the liquid phase	Used in saturated material	[51,52]
	Dielectric sensors	-100~0	Depends on the accuracy	Dielectric capacity of the porous cup	Short response time; but subject to hysteresis	[43,44]
	Heat dissipation sensors	-1.5~-0.005	Require separate calibration	Heat pulse dissipation in porous membrane	Not sensitive to the salt content of the solution	[47]
	Frequency Domain and Time Domain Matric Potential Sensors	-1~-0.002	Depends on the accuracy	Equilibrium of the liquid phase	Subject to hysteresis and very wet range	[53]

Table 1. Cont.

Measurement	Device	Operational Range/MPa	In Situ Calibration	Measurement Principle	Main Features	References
Laboratory methods	Filter paper method	Entire range	Required	Equilibrium of the liquid phase	Long equilibration time	[45,46]
	Pressure plate apparatus	−1.5~0	Depends on the accuracy	Equilibrium of the liquid phase	Only used in the laboratory	[46,54]
	Electrical resistance sensors	−1~−0.01	Depends on the accuracy	Electric resistance in equivalent-porous medium	Interface easily with data loggers; but subject to hysteresis	[55]
	Dew point potentiometer	−1~−0.005	Not required	Equilibrium of the vapor phase	Needs temperature control	[53]

In recent years, water potential sensors have been developed, showing some potential for convenience, miniaturization, and intelligence. For example, in order to extend the measurement range, the wide-range psychrometer and the high-capacity tensiometer were developed [56]. The dihedral tensiometer overcomes the major limits of common tensiometers [57]. Microbial sensors can be used to visualize millimeter-scale water potential gradients in the soil around plant root tips by producing green fluorescent protein (GFP) as a function of total water potential in nonsterile soil [58]. Non-contact measurement methods, such as a new tool based on a power-law relationship between sound velocity and water potential, have also received attention [59]. The development of new sensors, such as pFMeter, Polymer Tensiometer (POT), MPS-6 and TensioMark (TM), provides more options for SWP measurement with improved operability and more convenient features, as Jackisch et al. [9] reviewed (Figure 3b). However, the lack of commonly agreed-upon calibration procedures makes the capability and reliability of specific sensing methods controversial.

2.2.2. Simulation Methods

Modeling methods related to SWP dynamics can partially compensate for the defects in traditional measurement methods. Many models involve the relationship between SWP and environmental factors [60]. As mentioned above, the relationship between SWP and SWC is the most useful way to infer SWP and remains an indispensable input for models, to simulate the soil water balance [5]. Saxton et al. [33] studied the statistical correlation between soil texture and SWP, based on water retention characteristics, and established a model that could reflect the impact of different textures on SWP dynamics. Leong and Rahardjo [61] proposed a nonlinear model for the change of SWP over time in sandy loam and clay loam soil, but it cannot cover other soil textures. The preliminary research on the relationship between temperature and SWP is attributed to Philip and De Vries [62]; they proposed the expression of the temperature effect of SWP under given water content based on the effect of temperature on the surface tension of water; this was called surface tension and viscous-flow (STVF) by Nimmo and Miller [63]. However, the STVF model does not consider the change in soil-sealed gas volume caused by temperature change. Nimmo and Miller [63] produced a functional model and well described the temperature effects of SWP. Under the dynamic change of salinity, osmotic potential dynamics are often used as a variable in crop-growth and salt-stress models. Richards [64] established a regression equation between the electrical conductivity (EC) of salt solutions and osmotic potential, but it is difficult to measure the relationship between osmotic potential and EC with instruments. A log-linear relationship between SWP and microbial activity was described by Orchard and Cook [65] in order to provide a more representative average

function; the model provided by Moyano et al. [66] can be used to approximate the effect of water potential on soil organic matter decomposition, but it is empirical in nature and difficult to use when studying the effects of different settings and conditions.

Although both measurement and simulation methods have been developed, to our knowledge, the methods of directly measuring SWP at millimeter scales or even at the micro-scale have not yet become popularly accepted [67]. Especially for the investigation of the interaction between plant root physiological activities and SWP dynamics, the root release of organic matter (such as organic acids) and root hair growth and elongation are all affected by SWP fluctuations, and these changes need to be analyzed at the millimeter scales [68]. However, it is still difficult to study the change of potential energy at the organ or even the cellular level. Furthermore, developing landscape-scale continuous SWP measurements remains a challenge. Since SWP uniquely reflects changes in soil water energy, especially in arid and semi-arid regions, it is very sensitive to SWC fluctuations and plays an indicative role in community dynamics under climate change. Therefore, landscape-scale studies on SWP will contribute to the research of surface water energy change and land-air simulation under climate change.

3. Plant Biological Responses to Varied SWP

The dynamic change of SWP directly affects the physiological and ecological activities of plants. Moderate SWP fluctuations can promote the germination and growth of plant seeds, and the ripening of fruits, while a drastic change in SWP may lead to the collapse or death of plants. This subsection analyzes the effects of SWP dynamic changes on individual plant physiology, morphology, phytochemistry, and pathology (Figure 4).

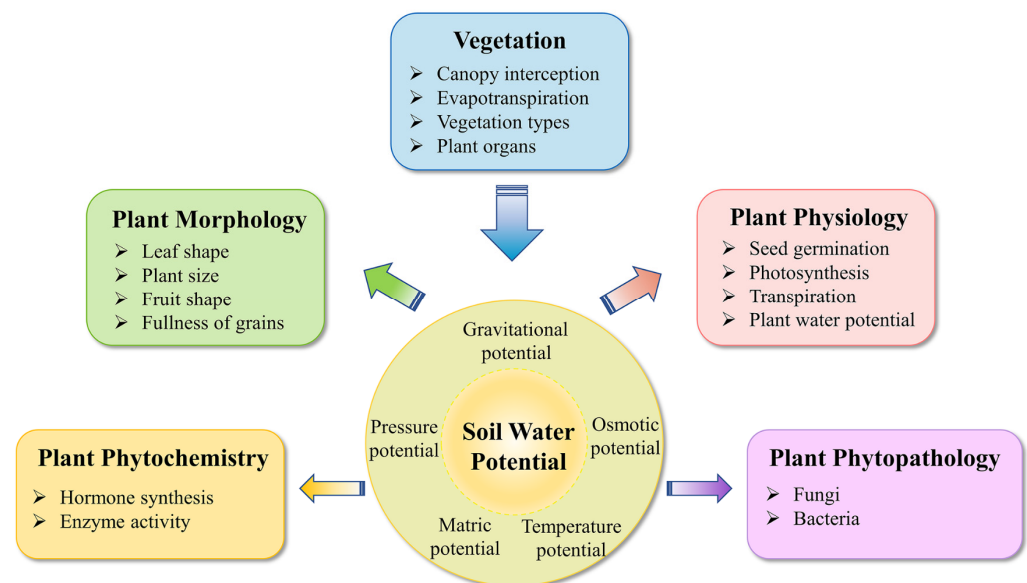


Figure 4. Factors influencing the interaction between SWP and vegetation.

3.1. Physiology

Physiological activities such as seed germination, root activity, transpiration, and photosynthesis are affected by the dynamic changes of SWP. Knowledge of SWP is critical to quantifying soil water availability and plant water requirements [21]. As the initial physiological stage of plant growth and development, seed germination is related to matric potential and osmotic potential. Germination depends on the amount of water the seeds can absorb, which is a function of SWP and hydraulic soil properties [69]. Doneen and MacGillivray [70] stated that the rate of germination and the final germination percentage both decrease with decreasing SWP. The combination of low water potentials and high temperatures even reduces the germination rate to an extreme level [71]. For the plants themselves, this phenomenon is a protective mechanism to avoid exposing the seedling to

untenable environments [72]. Therefore, seeds will germinate only when certain favorable conditions are met (Table 2). For example, *Thespesia populnea* and *Celosia cristata* require adequate wetting conditions to achieve the maximum germination rate [69]. Interestingly, the result of some species' need for high temperatures with low water potential in European countries where soil moisture is lowest when temperatures are highest, was unexpected [73]. Accordingly, plant germination parameters can be modeled as functions of SWP and temperature, to predict germination dates and classifications of diverse plants [74]. In ecological restoration areas, this relationship can be used to determine the key time for plant germination and growth, so as to improve the efficiency of ecological restoration.

Because roots are the main organ for water absorption and have hydrophilic characteristics, plant root development is also highly related to the water potential gradient in the soil [75]. When SWP decreases (soil drying), cell activity in roots decreases, leading to a corresponding decrease in root water conductivity [76]. In addition, very low SWP can cause root shrinkage, loss of root water uptake, and even plant death. Roots are the main organs for plants to perceive soil water dynamics. The root cap contains cells that sense gradients in water potential, e.g., the roots of a pea can respond to a gradient less than 0.5 MPa by growing toward the higher SWP [77]. Some studies have found that lateral roots have different geotropism set point angles and are less responsive to gravity than taproots, increasing the response to the water potential gradient [75]. Nevertheless, the water potential threshold varies among plant species, and the physiological mechanisms by which plants sense and respond to changes in SWP are unclear. This problem can be solved to some extent by exploring the response of plant lateral roots rather than taproots at small scales.

The difference in water potential between soil near roots and in the atmosphere is the driving force of transpiration [78]. Stomata in the leaf, which are primarily involved in transpiration, are controlled by the hydraulic gradient of the water potential. A moderate decrease in SWP can increase stomatal length, width, density, and opening, while a very low SWP can lead to stomatal closure and leaf water potential decline [79]. The stomatal limitation also leads to a decrease in photosynthetic rate. Low water potential decreases stomatal conductance, increases stomatal resistance, and decreases the photosynthetic rate and transpiration rate of wheat [80]. The latest research suggests that the closure of stomata also prevents the formation of large gradients in SWP around the roots [81], which provides new insights into hydraulic processes at the root-soil interface [82]. However, this conclusion needs to be tested in different plant species, soil types and variable atmospheric conditions to further understand the coordination between stomata and soil desiccation.

Table 2. Basal water potential of germination of some plants.

Species	Base Water Potential/MPa	Reference
<i>Cercidium praecox</i>	−0.41	[83]
<i>Neobuxbaumia tetetzo</i>	−0.66~−0.2	[83]
<i>Yucca periculosa</i>	−0.41~−0.2	[83]
<i>Ambrosia artemisiifolia</i>	−0.8	[84]
<i>Sinapis alba</i>	−1	[85]
<i>Vigna radiata</i>	−0.5	[86]
<i>Allium cepa</i>	−1.1	[87]

3.2. Morphology

Plants enhance their adaptability to decreased SWP not only through internal physiological regulation but also by changing the morphological and functional characteristics of roots, stems, and leaves, so as to guarantee their life activities and reproduction. Leaves are the primary organs for photosynthesis and transpiration. Leaf area is an important indicator for judging whether plants are water-deficient, and the main reasons for leaf area change, in response to low SWP, are decreases in the photosynthetic rate and leaf turgor pressure [88]. A significant decrease in SWP, in addition to causing leaf area reduction,

leaf curl, and the production of highly pubescent leaves, can also lead to an increase in leaf tissue density and thickness, and the formation of a thick keratin membrane, or leaf edge elongation, in plants such as *Encelia farinose*, sugarcane, wheat, and conifers [40,79]. Apart from the leaves, plant roots undergo morphological changes to adapt to low water potential environments. The root structure is changed, resulting in phenomena such as root hair elongation, fine root thinning, decreases in root branch angle and lateral root branch density, and a change in the root/shoot ratio. Under low SWP, maize root elongation and rooting depth increase, while *Cunninghamia lanceolata* increases root complexity and reduces its root branching angle, thus obtaining more water from arid soil [79]. It can also result in the elongation and further differentiation of the fine roots of cotton, significantly increasing the root length density, decreasing the average rhizoid, shortening the life span of some fine roots, and promoting the elongation of fine root hairs [89]. Low SWP can also influence other aspects of morphological change, e.g., lower plant height, smaller stem girth, less shoot and root biomass, lower fresh and dry weights, and higher crown roughness [79]. For instance, the tiller number, plant height, and internode length of rice are obviously changed and associated with cell enlargement and leaf senescence under low water potential environments [90]. The shedding and death of branches of birch and poplar can occur, enabling them to adjust root-shoot ratios [91,92]. The transparency and roughness of some trees' crowns (e.g., Norway spruce) will increase [92]. Furthermore, under low SWP, highly competitive trees reduce their already small canopy size to the minimum necessary for efficient survival, when competition and environmental stress occur at the same time.

3.3. Phytochemistry and Phytopathology

Low SWP triggers chemical signals (e.g., abscisic acid, inositol-1,4,5-triphosphate, etc.) and increases the concentration of secondary metabolites, to prevent plant tissue damage [25,79]. Dynamic changes in secondary metabolites induced by these chemical signals vary from plant to plant. For example, the content of total flavonoids in *Glechoma longituba* under low SWP conditions increases, whereas the concentration of phenolic compounds in grape plants decreases considerably [93]. Moderate drought stress increases the content of carotenoids and phenolic compounds in *Carthamus tinctorius*, while under severe drought stress this content decreases significantly [94]. The dynamic change in SWP can also lead to the rapid multiplication of pathogenic bacteria and the occurrence of plant diseases; for example, active flora was composed almost entirely of *Aspergillus* and *Penicillium* when the suction was between 145 bar and 400 bar, whereas *Actinomycetes* were active only at suction values of less than 55 bar [95]. In addition, the temporal dynamics of SWP could lead to considerable variability in the incidence of common scab disease [96]. Conversely, changes in SWP also promote the growth and reproduction of beneficial fungi. For instance, plant rhizosphere growth-promoting bacteria (PGPR) improve plant tolerance to abiotic stress through various mechanisms, making a positive contribution to the morphological, physiological, and phytochemical traits of *Fenugreek* plants [97]. At present, it is not clear what the specific mechanism is, of the response of pathogenic or beneficial bacteria to SWP, especially how to induce a dynamic change of SWP in the direction of promoting the propagation of beneficial bacteria or inhibiting pathogenic bacteria.

4. The Responses of Ecohydrological Processes to Varied SWP

The dynamics of SWP act at the plant level but also contribute to changes in community structure and function and ecosystem cycling. In this section, we discuss the influence of SWP on eco-hydrological processes, including its role in water processes, carbon processes, and nutrient processes.

4.1. Water Processes

Water potential differences at different positions in the soil-plant-atmosphere continuum (SPAC) determine a series of water potential gradients and drive water movement. Water flows from the soil to the roots, through the xylem, mesophyll, and parietal cells, evaporates through the substomatal cavity and diffuses the stoma, and enters the atmosphere through the leaves and canopy (Figure 5). The water process with the participation of the SWP gradient at the field scales primarily includes hydraulic lifting and deep drainage. Hydraulic lifting refers to the passive movement of water from the root to the layers with lower SWP [98] which expressively influences field water balances [99]. Since most plants have limited water storage capacity, hydraulic lifting provides a mechanism for the temporary storage of water in the topsoil. The evidence for the process of hydraulic lifting originally came from experiments with SWP, which have shown that water taken up by the deeper roots from the moist soil is transferred to the dry upper soil at night [98]. Therefore, the temporal and spatial instability of the water potential gradient should be considered when estimating the water balance of the system. If a striking hydraulic lift occurs nightly, the timing and position of SWP measurements become an element in systematic water measurement. The reverse phenomenon to hydraulic lifting—when the surface SWP is higher than the bottom soil, water moves from the shallow lateral roots to the deeper taproots—has also been observed. Especially during the change of seasons, the topsoil is moistened again, and water is carried from the top layers to the deeper ones through the roots [100]. Moreover, beyond that the SWP gradient can also directly lead to hydraulic migration between different soil layers, excluding the roles of plant roots.

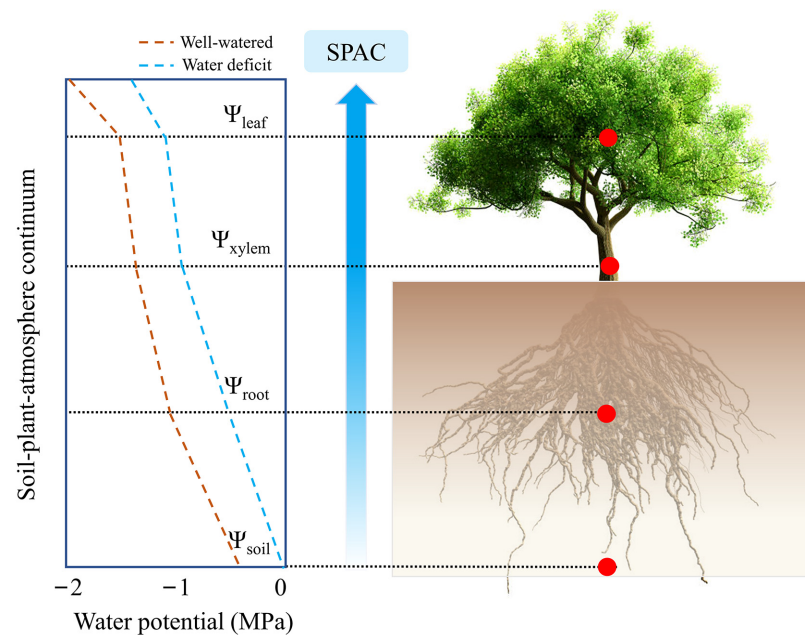


Figure 5. Soil-plant-atmosphere continuum (SPAC) water fluxes, adapted from Scharwies and Dinneny [101] and Boanares et al. [102].

4.2. Carbon Processes

SWP dynamics are a vital element that indirectly controls field carbon cycling by regulating plant photosynthesis, soil microbial activity, and soil respiration. Low SWP and high temperature are extreme stresses governing carbon allocation in plants. Especially under drought stress, the organic matter produced by photosynthesis is reduced, resulting in decreased carbon accumulation in plant leaves and changes in carbon allocation. With low SWP, photosynthate distribution to the root system in spring wheat is increased, leading to an increase in the root/shoot ratio [103]. Soil microbial activity also is sensitive to SWP dynamics and is the key component of carbon balance. When SWP is low, the

metabolic activity of most microorganisms decreases, resulting in reduced respiration and nutrient mineralization [104]. Microbial respiration stops below -15 MPa water potential. Subsequent rewetting events mobilize the physically protected carbon in the aggregate, enhancing metabolism and enzymes, and thus increasing respiration [105,106]; this is known as the “birch effect” [107]. For instance, with the increase in intermittent precipitation in arid and semi-arid regions, the respiration pulse and the release of its related elements will intensify and become more variable, thus affecting the carbon cycle [108]. In addition, an increase in soil respiration is also affected by an increase in SWP, and during the early wet period following rewetting, soil respiration increases the most [65]. However, due to inadequate measurement methods, SWP is not considered in most studies for evaluating soil moisture effects on soil carbon dioxide emissions [28]. Therefore, future research should focus on improving the accuracy and convenience of SWP measurement, and organically combine SWP with soil carbon cycle research.

4.3. Nutrient Processes

Soil is a major reservoir of nutrients, and relatively high SWP positively affects circulation and accumulation of nutrients (e.g., nitrogen and phosphorus). Biological nitrogen fixation is one of the crucial sources of soil nitrogen and is sensitive to SWP dynamics [109]. Low SWP directly influences nitrogenase activity, leading to a decrease in nitrogen accumulation in legume crops [29]. However, nitrogen-fixing bacteria strains in arid areas are specially adapted to dry climates and can fix nitrogen under the condition of very low SWP. The SWP fluctuations control the nitrogen uptake and release by plants and microorganisms in diverse ways; the increased precipitation pulse events may lead to nitrogen cycles and losses in arid and semi-arid regions [105]. When SWP values are low, microbes involved in the nitrogen cycle remain active for a shorter time (compared to plants) after water pulses [110]. After rewetting, a rapid change in SWP could lead to the lysis of microbial cells or the release of intracellular solutes, increasing the net release rate of plant inorganic nitrogen but not improving the absorption rate of plant inorganic nitrogen, resulting in a short pulse of soil inorganic nitrogen and nitrogen loss. This nitrogen loss is likely to worsen with climate change [105]. The phosphorus cycle is also dynamically influenced by SWP, and with the increase in SWP, the activity of a microorganism related to phosphorus decomposition and migration increases [111]. Bacterial communities dominate most nutrient cycles such as soil carbohydrate metabolism and phosphorus dissolution, while fungi promote soil phosphorus dissolution and plant-root interaction. Sinigani and Mahohi [112] proffered the improvement of soil productivity by organic waste and concluded that microbial phosphorus and phosphatase activities increased significantly with the increase in SWP. Wells et al. [113] also demonstrated that changes in SWP affect mycelia’s ability to obtain phosphorus from the soil and the degree of phosphorus migration through the mycelia network. In terms of phosphate mineralization, Grierson et al. [114] found that specific phosphate mineralization was most sensitive when SWP was high. The sensitivity decreases logarithmically with a decrease in water potential. When water potential is less than -0.008 MPa, phosphate mineralization is insensitive to SWP. Therefore, an improved understanding of the relationship between SWP, microorganisms and nutrient pairs is helpful to promote plant uptake and utilization of nutrient elements and plant growth.

5. Challenges and Insights for Future Research

SWP research has taken a giant leap forward in the last decades (Figure 6). However, there are still challenges to overcome in SWP evaluation methods, and in understanding its roles in soil-plant-water relationships [115]. To adequately perceive the ecological effects of SWP dynamics, improved measurement instruments are needed. Although the established techniques, including solid-, liquid-, and vapor-based methods as discussed above, can be used to monitor a diversified range of SWP (Table 1), they are restricted in in-situ or plot-scale evaluations in the spatial dimension. Indeed, data of larger scales (i.e., within-field to landscape scales) may provide insights that can be interesting for the interpretation of the

spatial patterns of water status and the behavioral heterogeneity of vegetation. However, few methods could be applied on these scales so far. In the future, the coupling of in-situ technology and non-invasive methods (e.g., acoustic techniques and spectroscopy techniques [59] take advantage of ‘signals of sound and light’, theoretically allowing for more extensive and frequent observations, but with an affordable price), is expected to be utilized for the solving of this issue. Besides developing instruments for large-scale measurement of SWP, broader observation systems or networks are more likely a solution for getting information on SWP at large scales. However, such datasets are rarely available—even at most field stations across LTER (Long-term Ecological Research Network), CERN (Chinese Ecosystem Research Network), and other research networks [116,117]. Therefore, we suggest including SWP observation in the regular monitoring schedules at those field sites in the future. Observation networks of water potential or energy state in the SPAC across different landscapes and ecological settings are also highly expected to fulfill the demands of model validation, data assimilation, and drought monitoring at larger scales [118,119].

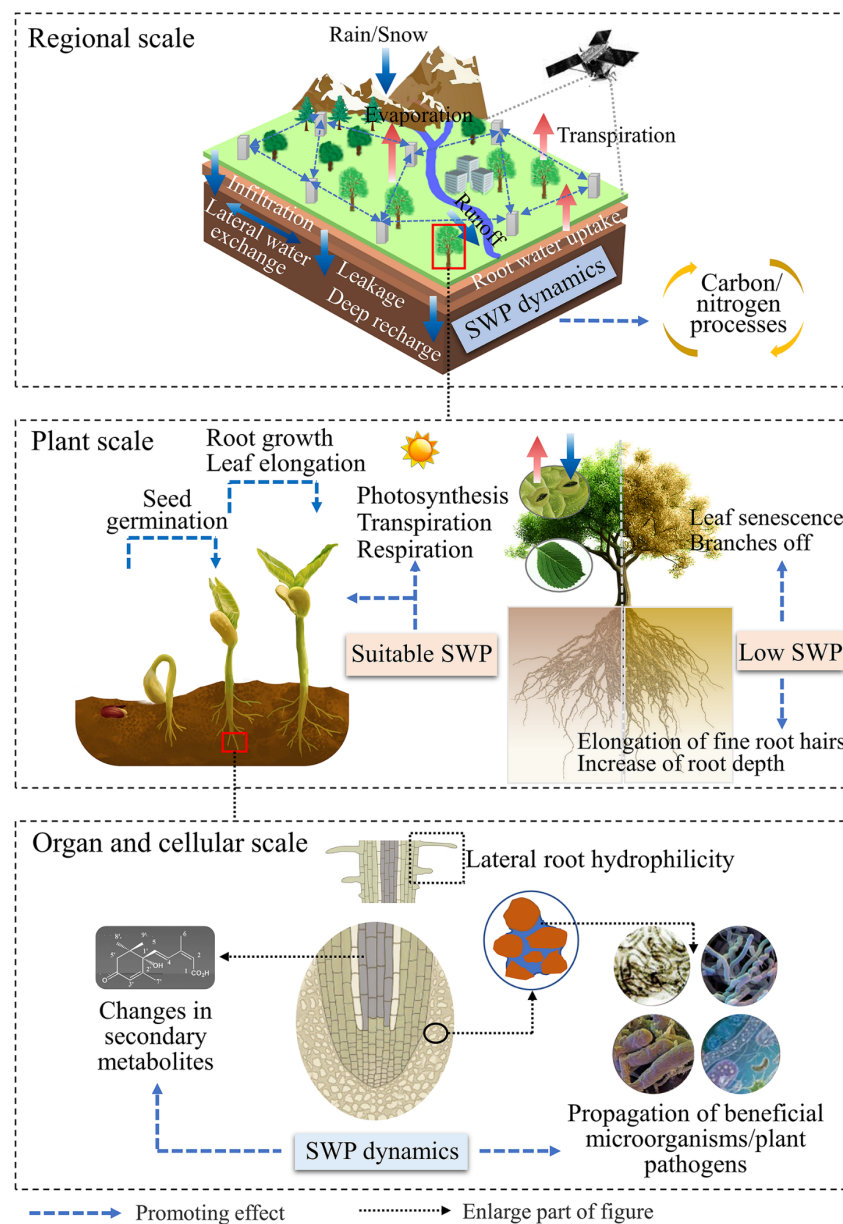


Figure 6. Effects of SWP at the landscape, plant, organ, and cellular scales.

SWP dynamics plays a crucial role in the soil-plant-water relationship, which has been confirmed to control plant development and phenology, such as germination or flowering time [69], and root elongation or leaf area change [88,89], especially in water-limited environments. However, the physiological mechanisms by which plants sense and respond to changes in SWP remain unclear, e.g., the response mechanism of plant roots to changes in hydraulic characteristics at the root-soil interface is undefined, which limits our understanding of plant water use strategies in water-stressed environments. In addition, it is also not clear what is the specific mechanism of soil microbe response to SWP, especially how to induce the dynamic change of SWP toward the direction of promoting beneficial bacteria reproduction or inhibiting pathogenic bacteria. Due to inadequate measurement and research methods, SWP dynamics are not considered in most studies for evaluating the ecohydrological effects, such as the carbon and nitrogen cycles, particularly in the absorption of nutrients (e.g., nitrogen and phosphorus) by plants and the impact of climate change on soil carbon storage. Therefore, future SWP research should focus more on the ecohydrological effects of dynamic changes in SWP under climate change and take advantage of the water potential dynamics in the application, such as the proper SWP dynamics for promoting the propagation of beneficial bacteria, the utilization of nutrient elements in plants, and the physiological activities of plants. In addition, the perception of SWP dynamics by plants and microorganisms should be further investigated in conjunction with the lateral root cells, plant hormone signals, etc., based on disciplines of plant cytology, microbiology, and biochemistry.

6. Conclusions

This paper revisited the research on SWP from the influencing factors, evaluation methods, and the impact of SWP on plant biology and eco-hydrological processes. This literature review indicates that SWP plays an important role in controlling plant biological functioning, and eco-hydrological interactions, especially in water-limited environments. Our knowledge of plant-level effects was improved by incorporating SWP dynamics into plant physiological ecological experiments and model research, but challenges remain in the signal recognition of root responses to SWP, the role of plant morphological indicators under drought stress, and the application of SWP in preventing plant diseases. In order to obtain SWP data more efficiently, we argue that it is necessary to combine various established technologies (e.g., solid-, liquid-, and vapor-based technology) and novel technologies (e.g., sonic technology and spectroscopic technology) for the large-scale measurement of SWP and integrate the observation of SWP and even energy states in the SPAC across different landscapes and ecological settings, into soil hydrology and ecosystem observation networks. For a better understanding of soil and plant interactions, we also propose to study the dynamic changes in SWP in the context of climate change and combine the disciplines of plant cytology, microbiology, and biochemistry to explore new hotspots in the application research of SWP. These challenges and insights gained through our review efforts are expected to provide inspiration for future research regarding drought management and climate adaptation.

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