






Review

Exploring the Research Challenges and Perspectives in Ecophysiology of Plants Affected by Salinity Stress

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Abstract: Soil salinization processes have increased over the years and affect large parts of agricultural fields. The purpose of this review was to highlight the most important aspects regarding the potential effects of soil salinity on plants. In the current context of climate change, extreme weather and increased drought periods can lead to plant metabolic dysfunctions and accumulation of salt ions because of the increasing need for irrigation. The most important limiting factor, salinity, has a highly negative impact on plant growth independent of the appearance of either natural or anthropic status. The negative aspects include decreased leaf development rate, a low water level in all parts of the plant, reduced cell division and elongation, and low-intensity photosynthetic rate. Other negative aspects are directly related to stomata closure, reduced transpiration, low CO₂ level, and limitations on seed germination. However, there are also some positive aspects to the presence of salinity in soil. The field offers unlimited possibilities of research in order to activate pathways that help plants become resistant to salt stress. Several physiological parameters can benefit from low salt concentration (halopriming), such as germination, vigor, rapid seedling growth, and increased stomata number. Further studies should focus on both the positive and negative aspects of the increase in soil salinity.

Keywords: abiotic stress; climate change; degraded soil; photosynthesis; osmotic stress



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1. Introduction

Soil salinization is the process of excessive salt accumulation that leads to an increase in the concentration of different soluble salt types [1]. It has become a more common phenomenon due to climate change and especially severe droughts, which has resulted in increased need for irrigation [2]. Salinization causes major constraints and reduces crop yield because of limitations on different crops [3]. Soil alkalization or sodification results in an increase in the adsorbed sodium concentration in the soil solution. This process leads to variations in soil pH towards lower values [4]. If they occur simultaneously, salinization and alkalization can lead to the formation of the soil salinization process [5]. Soil degradation, in general, can have **several causes**, including global climate change [6], improper use of agricultural techniques [7], increased and uncontrolled irrigation [8,9], and excessive use of chemical fertilizers [10,11]. In the current context, the soil salinization

process represents a real threat because it negatively affects substrates by changing their physical, chemical, and biological properties. Salinization is caused by soil erosion and is a consequence of cation and anion accumulation in the soil [12]. Cations are represented by Na^+ , Ca^{2+} , Mg^{2+} , while anions include NO_3^- , CO_3^{2-} , SO_4^{2-} , and Cl^- [12,13]. All these minerals and their compounds produce an imbalance in the soil ionic solution. Thus, the soil solution becomes unavailable for plants, leading to negative effects on physiological processes [14]. Chemical reactions in the soil solution can also increase the level of plant osmotic pressure [15]. Another negative effect produced by excess salt in the soil is a reduction in the water potential values, which results in the unavailability of nutrients for plant germination, growth, and development [16]. Although salinity stress is generally considered harmful to plants, there are some potential positive aspects of salinity stress that may be observed in certain plant species or under certain conditions [17–21]. Salinity stress can increase the uptake of certain nutrients, such as potassium and calcium, which are important for plant growth and development under normal conditions [22–24]. Some plants can adjust their osmotic potential in response to salinity stress, which can help them maintain their water balance and survive in saline soils [25] as well as increase their resistance to drought periods. Salinity stress can promote the **biosynthesis of antioxidants** in plants in order to restrain increased levels of reactive oxygen species [26], which can protect plants from oxidative damage and other types of stress.

Soil salinization is a real threat to agriculture as it reduces suitable arable land area for the majority of crops. Moreover, by the year 2050, more than 50% of arable land will be susceptible to salinization [27]. Soil salinity is a global problem, with every continent having multiple affected areas [28–30], although there are large variations between different countries [31]. In Europe, soil salinization requires immediate attention. Romania is included in the short list of countries that are most affected by soil salinization [32], and it is known to have three problematic areas that are susceptible to salinization. The main areas with soils affected by salinization are located along the Danube floodplain in the south and southeast of the country and on the perimeter of the Tisa River Basin in the western part of the country [33]. The soil–plant system is strongly affected in these areas because of salinization and alkalization processes, and the agroecological potential is reduced [34]. All these factors represent a socioeconomic risk for sustainable development of the region and require special attention, research, and adaptive measures.

The methodology used in this study was based on three concurrent searches on the Web of Science Core Collection (last accessed on 9 February 2023), as shown in Figure 1. The first search with the keywords “*physiological changes*” × “*plant under salinity stress*” yielded 1134 results. The second search was performed based on “*salinization stress*” × “*plant organisms*” and yielded 22 articles. The third search was carried out with the keywords “*general aspects*” × “*plants under salinity stress*” and resulted in 12 publications. All three combinations of keywords were set on the basis of holistic research in the field of salinity with the ultimate goal of extracting the most relevant information to establish a complex experimental design. Another aspect to the choice of keywords was the diversity of words used to analyze the same “salinity” phenomenon, with the different combinations chosen based on their potential to expand the search area. Thus, a dual perspective was created on this topic: the first one represented multiple standalone experiments that have analyzed specific plant physiological response, while the second one permitted an ecophysiological vision over multiple results that can be assembled in a holistic overview. The refined criterion was performed by quick filters, and only open-access articles were considered. The open-access filter was selected according to international trends and recommendations for scientific information that are easy to consult. The following filter refined the search on a more granular level (mesolevel) and only included publications from “*Crop Science*” and “*Crop Protection*”. The reason for this second refined database filter was to ensure that only information relevant to food security and sustainable development of agriculture was included. In total, 327 publications were compiled from the first search, of which 38 were review papers. From the second search, four publications were obtained, of which one was

a review. From the third search, two publications were obtained, of which one was a review. The keywords from all publications were analyzed to obtain a general overview of salinity stress from the plant physiology perspective.

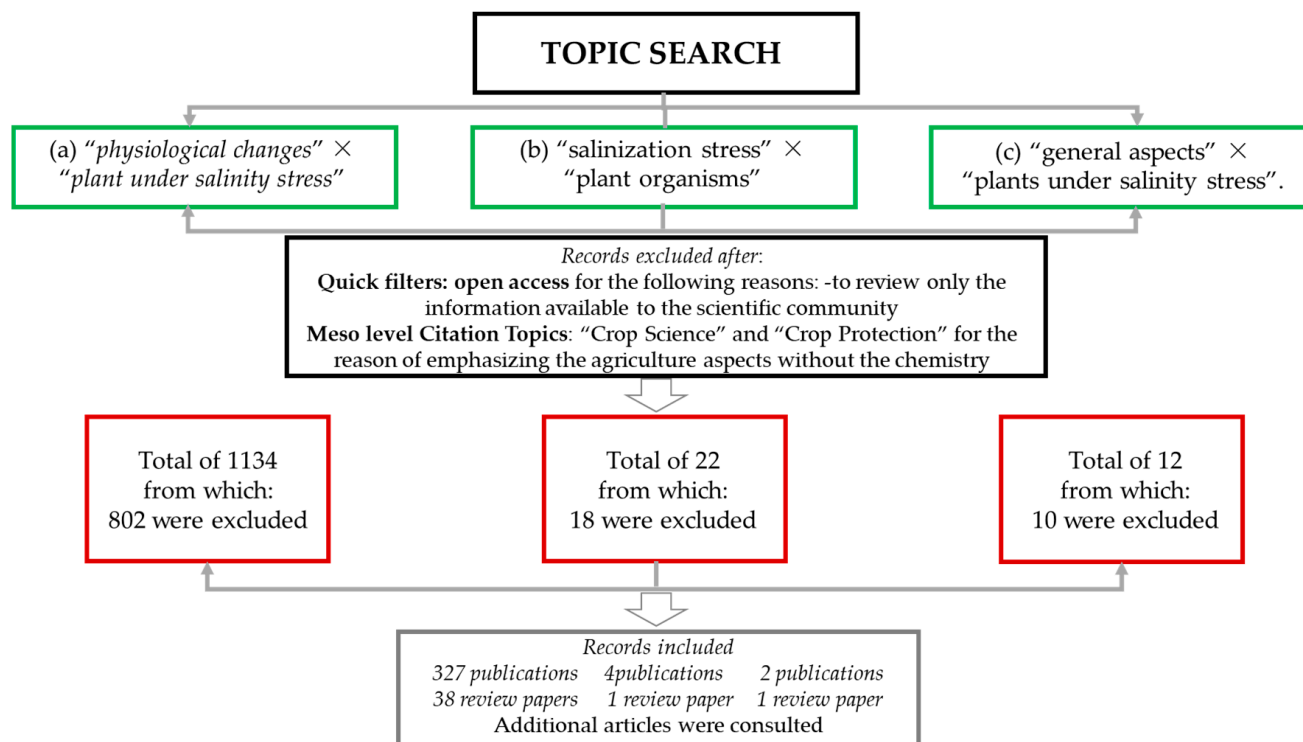


Figure 1. Prisma diagram summarizing the research methodology.

With the help of the filtered data, the aim was to highlight the most important general aspects that need to be explored to determine the effects of salinity stress on plant growth and development. The most important topics related to salinity were explored, with the research relevance and perspective of each one being highlighted. Soil salinity was treated as a phenomenon that occurs in agricultural fields, followed by the assessment of its potential impact. The presence of salinity is a stress that leads to multiple physiological changes in plants, with different responses in terms of resistance and tolerance. Wheat was used as a case study to emphasize the response to salinity stress. The choice of this species was due to its agronomic importance and its tolerance level, which would allow us to assemble multiple studies into a complex one. The final objective was to propose multiple perspective steps in the holistic study of salinity stress.

2. The Phenomenon of Soil Salinization

Soil salinization represents a phenomenon caused by the accumulation of several ions and cations [35]. Soil salinization has **both natural and anthropogenic causes** [36]. The **natural accumulation** of salts in the soil can occur through a series of factors, such as the presence of salt deposits [36], sea depositions [36], and water salinization of the low water table [37]. All these processes can be increased by the nature of the parental rock [38]. Soil fossil salts can be altered in time, thus increasing the local salinity level [5]. Here, the porosity and permeability characteristics of the soil is changed, thus creating major restrictions for associated areas that are susceptible to salinity to different degrees [2]. On the other hand, agricultural techniques and technologies that are inadequately managed and performed, the use of chemical fertilizers, irrigation on a massive scale, improper household water discharges, and use of salt to prevent water freezing in the roads in winter are **anthropogenic** promoters of excess salt accumulation in the soil [36,39]. In agricultural soils, this phenomenon is usually caused by evapotranspiration [40].

In the literature, these two classes of soil salinization are also classified as primary and secondary regarding their consequences [41]. The term “**primary**” refers to natural soil salinization and usually occurs in regions characterized by an arid or semiarid climate. Here, soluble salts accumulate because of an intensive soil evaporation index and as a consequence of insufficient precipitation to leach excess salts from natural rocks in the downward soil profile. These salts accumulate in the upper soil profile layers. The “salt cycle” has also been found to be responsible for excess salt in the soil. Here, the ocean salts carried by wind and clouds are delivered by rain into the soils [42]. The term “**secondary**” refers to changes induced as a consequence of anthropic activities originating from agricultural activity or different industries [41]. Irrigation with salt-rich water changes the water solution balance and leads to a decline of perennial crops, which is detrimental to annual intensive cropping systems. Beyond the known causes, accidental salt release from wastewater represents an important source of soil salinity caused by humans.

Climate change has negative impacts on soil salinity levels. Many **regions** around the world are increasingly characterized by aridity, mainly due to unusually extreme events and increased annual temperatures [43]. Therefore, **irrigation systems** in agricultural fields are necessary to obtain high agricultural yields [44]. The use of water in irrigation systems is closely connected with increased salinization processes in the soil. Two years ago, it was declared that salinity-affected areas will increase annually by 10% worldwide [45]. Some 20% of the total cropped fields are already affected by salinity, along with 33% of the total agricultural fields with irrigation systems [45]. Furthermore, this susceptibility is expected to increase with time due to salinization caused by increasing extreme thermal temperatures [42]. It is therefore important to determine the best research direction to deal with this issue. The amount of surfaces affected by salinity represents a real threat, which is why studying the effects of this abiotic stress on plant growth and development requires special attention. Soil salinity is most often expressed by the electrical conductivity of the soil solution or by the form of osmotic potential [46]. The electrical conductivity of the soil solution is derived from the same parameter of irrigation water and precipitation [47]. The most important aspect is the physiological suitability of the crop and yield production in the presence of salinity [48,49]. Without sufficient quantities of biomass, it is difficult to test the chemistry or molecular characteristics [50]. With no biomass at all due to crops suffering under salinity stress and thus becoming dry and dying in the early phenological stages, these tests are impossible to carry out and become irrelevant.

Under saline stress conditions, plants exhibit multiple physiological changes (Figure 2a), which are mostly visible in the rate of photosynthesis and the different physiological parameters [51,52]. Smaller plant leaves present higher chlorophyll content per area but have a reduced amount of photosynthesis rate. Both water consumption and intake are visible by the osmotic stress and the increase in proline levels [53,54].

A restrictive search yielded studies focused on plant tolerance and adaptation capacity in the context of soil salinization stresses (Figure 2b). In early growth stages, plants are more sensitive to salinity [55,56]. The presence of salinity stress overlapping drought periods is one of the most important research topics in the current context of climate change (Figure 2c) [57,58]. Growth regulators can overcome and mitigate salinity stress, which is visible in higher or lower antioxidants found in plants in a species-dependent manner [59,60]. Due to increased salinity levels, it is imperative to observe and monitor vegetation coverage because deep rooting species can prosper and replace [61–64] plants with superficial root systems over time.

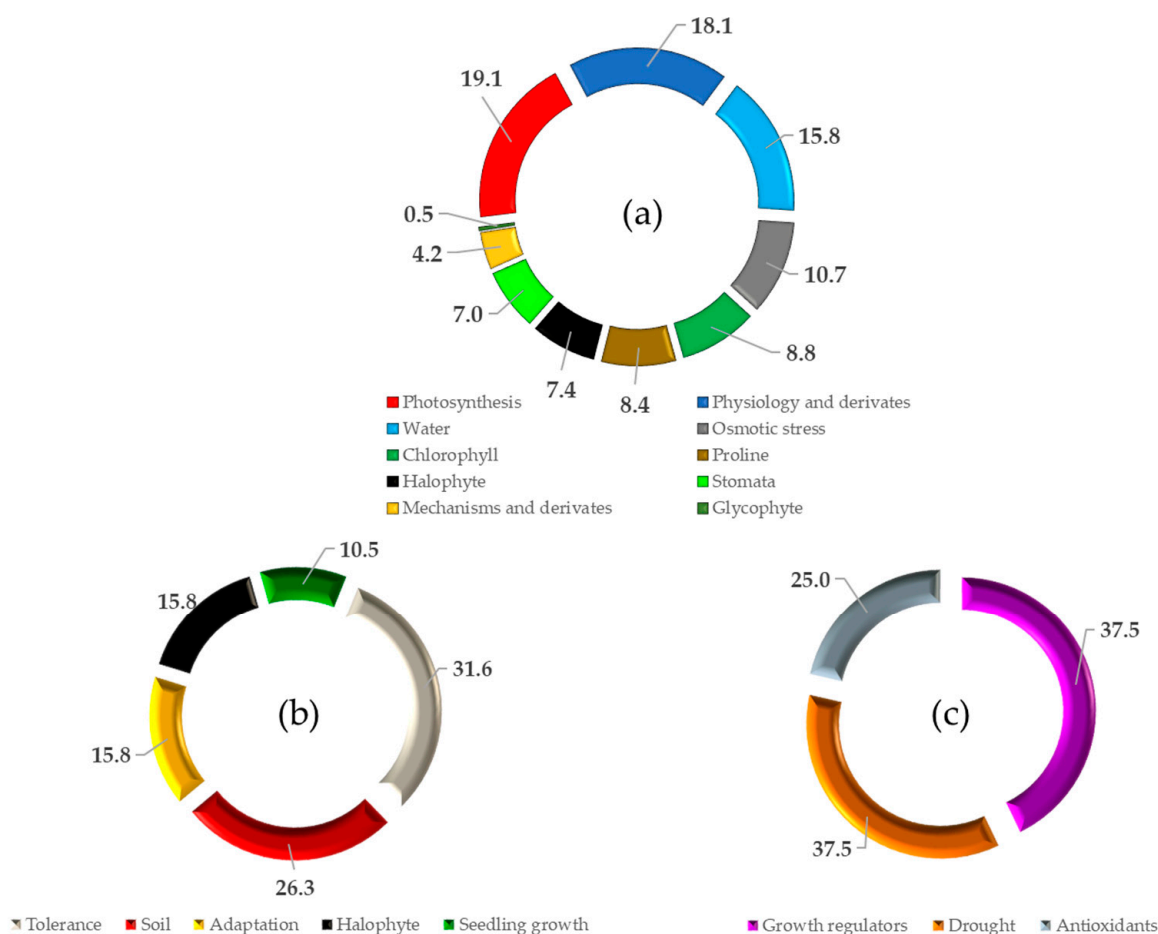


Figure 2. The results obtained by selected keywords of three searches in the Web of Science (a) “physiological changes” × “plant under salinity stress”; (b) “salinization stress” × “plant organisms”; (c) “general aspects” × “plants under salinity stress”.

3. The Impact of High Salinity Levels on Plant Growth and Development

Salinity is the most serious threat to agriculture as it is a limiting factor for crop growth and development and thus crop yield [65]. The consequences that can occur as a result of soil salinization are varied. A high level of salt in the soil influences the **osmotic** pressure of the solution, which becomes unavailable to the cultivated plant, thus causing water deficit [66]. Therefore, plants cannot grow and develop optimally by benefitting from the extraction of substrate water. Through alkalization, salinization causes an increase in soil pH. However, the soil solution can become acidic when the cation exchange between Na^+ and H^+ leads to increased H^+ concentration in the soil solution, thus lowering the pH. Soils with a more acidic pH can negatively influence plants and have **toxic effects** [5].

Crop salt tolerance can be influenced by a series of environmental and edaphic factors. The most important climatic factors with a direct influence on plant response to salinity are temperature, air pollution, and relative humidity [67].

The excess accumulation of salts originating from Na^+ , Ca^{2+} , and Mg^{2+} cations and Cl^- , CO_3^{3-} , and NO_3^- anions have negative effects on plant growth and development (Figure 3), with changes especially seen in the plant size.

Plant organisms can be divided into two large categories depending on how they are affected by salinity (Figure 3): the **adapted** ones, called native **halophytes**, and the sensitive ones, called **glycophytes** [68]. The highly tolerant species can possess a halophytic mechanism and translocate salts collected by roots directly to some salt glands with the attribute of onward excretion [69]. Excess salt in the soil has negative consequences on plants through two processes: decreasing the water potential and increasing the osmotic

pressure [70]. Disturbance of these parameters makes the soil solution inaccessible to plants, which has negative effects on various factors and processes. A decrease in the photosynthesis intensity rate, a decrease in the leaf development rate, and stomata closure are other negative effects of soil salinization. Soil salinity influences cell elongation and division, affects seed germination, lowers water levels, and increases the cellulose content of leaves. These phenomena lead to the poor development of leaves and eventually cause a decrease in the plant height [71]. On the other hand, native salt-resistant species exhibit multiple mechanism of growth and development, even at higher salinity levels [72,73]. These plants tolerate changes in the external concentration of salts while maintaining the internal osmotic potential at low values [74]. Germination rates are maintained or decrease in value under different saline conditions, with a higher sensitivity in the early growth stages than in the vegetative ones [75]. A crop rotation system that alternate nonhalophytes (conventional species) and halophytes may reduce the salinity and help maintain yield [76].

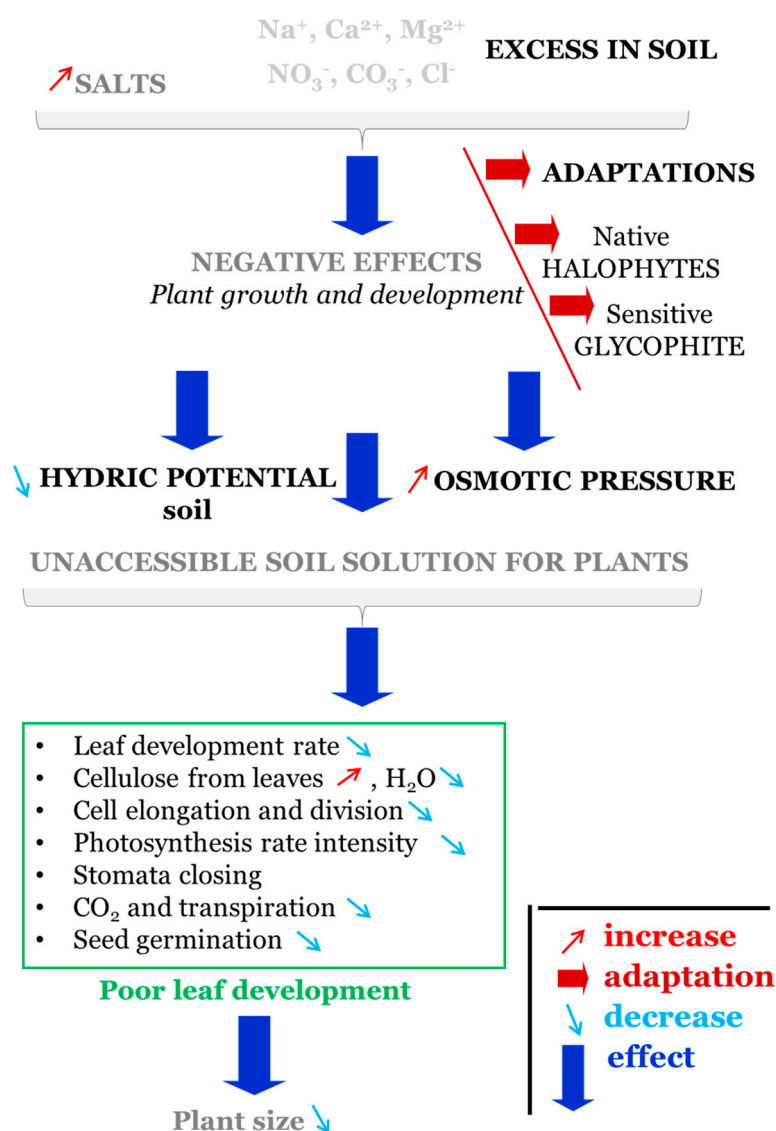


Figure 3. Scheme of the principal impact of salinity stress.

4. Salinity Stress as a Driver in Plant Physiological and Biochemical Process

Increased soil salinity can cause unbalanced physiological and **biochemical processes** due to nutritional imbalance, osmotic stress, water deficit, and oxidative stress [52]. The primary biochemical defense reaction of plants to salinity is represented by the modification of the adaptation mechanism to osmotic stress [77]. This results in the accumulation of

proline, proteins, and soluble carbohydrates but also a decrease in the phenolic content of the plants [78]. The low level of phenols results in a reduction of the antioxidant potential of plants [78]. Salt stress produces various reactions in the plant metabolic system by increasing the level of soluble organic compounds inside the cell, also called compatible solutes [79]. Moreover, the disturbance of the metabolism at the cellular level leads to damage of the antioxidant capacity of plant organisms sensitive to salinity due to the decreasing level of anthocyanins [80]. On the contrary, in halophyte species, the anthocyanins level is increased by the stimulation of metabolism induced by saline stress [81]. The increasing cell wall lignin content and restraining root growth are processes that plants use to adapt against saline stress [82]. The exposure of plants to salt stress facilitates the biosynthesis of reactive oxygen species (ROS). Ethylene, which is a plant stress hormone, and ROS function as signal markers that intervene in the remediation of numerous processes in different plant organs, including the resistance to salinity as an abiotic stress [83]. Pectin content and composition are other biochemical parameters that are increased and modified under saline conditions. Being an important constituent of the cell wall matrix, its content variation can affect root growth and dry biomass [84].

In addition, metabolic changes induced by high salinity levels impact other organic compounds in the cellular level, known as osmoprotectants [85]. These compounds, such as oligosaccharides and amino acids, of which proline [86] is especially dominant, act as one of the signaling markers for the presence of environmental stress [81]. Glycine betaine is also an osmolyte involved in plant metabolism, similar to proline, whose presence is correlated with exposure to high levels of salinity [87]. Synthesized under the effect of already installed hydric stress, glycine betaine is involved in maintaining the resistance of cell membrane and its components and provides osmotic adjustments [88]. Substances such as RFO, known as Raffinose family oligosaccharides, are synthesized from sucrose and represent another group of compatible solutes or osmolytes that can adapt plant mechanisms in order to cope with the changes produced by salt stress [89].

Germination is a **physiological process** strongly influenced by salt accumulation in the substrate [90]. Previous studies have shown that low concentrations of salts can also improve the germination of some species, such as *Capsicum annuum* and *Solanum lycopersicum*, *Brasica oleracea* [91]. For *Lolium rigidum* and *Triticum aestivum*, there can be both positive and negative effects [92].

Plant emergence represents one of the most critical growth stages when a stable root system is developing close to the soil surface, usually where salts accumulate. Depending on their genetics, agricultural crop species can be susceptible to specific salts or particular management practices, such as irrigation. Therefore, when irrigation water contains salts, plant leaves can suffer injuries. When these conditions appear, the best solution is to select salinity-resistant crop varieties or rootstocks to maximize the use of zones representative of saline water [93].

Other physiological parameters that are modified by salt stress are the water content at the root and stem levels of plants and the relative water content at the foliar level [94]. Previous studies on *Lactuca sativa* as a test plant have shown that at low salt concentrations (up to 50 mM NaCl), root and stem water content and relative leaf water content do not vary significantly but are significantly affected by higher salt concentrations (100–200 mM NaCl) [95]. Salinity has a direct effect on the plant–water relationship, transpiration, and transpiration use efficiency [96]. Plant turgor decreases when stress is present, and it can influence stomatal opening and cell division and expansion [97]. Other turgor pressure from plants can have no influence on water transport because of osmotic adjustment, which is the change in osmotic potential by alteration of salt concentration, thus resulting in reduction of the potential pressure. The effects of salinity on ions can be highlighted by an increase in organic solutes compatible with high salinity levels [96]. These compatible solutes, such as proline and glycine betaine, are responsible for water balance from the cytoplasm because of the decrease in water potential from the vacuole due to ion accumulation [98].

The effects of salinity on photosynthesis is represented by a reduction of it. Salinity induces a reduction in plant leaves with higher number of chloroplast density per leaf area unit [99]. The impact of salinity on limitations occurring in the fundamental process of photosynthesis is determined by membrane dehydration, which leads to a decrease in cell permeability for carbon dioxide. A high soil osmotic potential has negative effects on the water potential of plants and decreases the osmotic potential of membranes. Therefore, photosynthetic electron transport is negatively influenced. Normally, in a vegetal cell, the salt concentration is around 1.5%. An increased soil salt concentration can also block access to water in the root cells by disturbing the osmosis mechanism [100].

The effects of salinity on plant senescence can be calculated with imaging analysis of salt-induced senescence areas [96]. At the seedling stage, plants can be classified as follows: normal growth and no leaf symptoms; nearly normal growth with some leaves and tips being whitish and rolled; growth severely retarded with most leaves rolled and only a few elongated; complete growth arrest with most of the leaves dried and some plants dead and almost all plants dead or dying [101].

The **morphological parameters** of interest are root length, stem length, leaf length, total plant mass, dry mass, and plant fresh mass. They vary according to the concentration of the applied saline treatment, which has significant effects in the case of high salt concentrations [102]. The most visible symptom of the effect of salinity on plants is a yellowing of leaves due to leaf senescence, then brown color at death [96]. Leaf shedding was the first symptom when purslane (*Portulaca oleracea* L.) was subjected to saline stress [103], followed by lower fresh and dry biomass weights and reduced number of flowers. Principally, the shoots suffer from Na accumulation. This aspect is most visible in older leaves because they accumulate Na for longer. The photosynthetic rate and leaf greenness are species dependent, with some plants being able to maintain these parameters for a longer time in the presence of salt stress than others [96].

5. Tolerance as a Plant Salinity Stress Response

Soil salinity is most often expressed by the electrical conductivity of the soil solution or by the form of osmotic potential [104]. The electrical conductivity of the soil solution derives from the same parameter of irrigation water and precipitation [105]. The soil solution is the result of the interaction between water and salts from the soil. Depending on the electrical conductivity of the soil solution, the soil can be divided into several categories that more or less limit the growth and development of plants [106]. A soil with electrical conductivity between 0 and 2 (mS/cm) is considered to be nonsaline and has a negligible effect on plants [107]. Electrical conductivity within values of 2 and 4 mS/cm integrates the soil into the weak salinization class and results in yield reduction of some sensitive plants. Medium salinization includes soils with an electrical conductivity between 4 and 8 mS/cm, which can result in a reduction in yield for the majority of plants. Electrical conductivity between 8 and 12 mS/cm characterizes the class of soils with very high salinity, where only the growth and development of salt-tolerant plants are possible [107]. The extreme salinization class includes soils that have an electrical conductivity higher than 16 mS/cm, and it can only produce reasonable harvest for very salt-tolerant plants [107]. The most common vegetables and fruit crops can be classified into the following classes: salinity sensitive, moderately sensitive, moderately tolerant, and tolerant plants [67,108,109] (Table 1). Based on the selected literature, 20 plants were classified in the four classes. The sensitive ones were found to be pea and bean, while the moderately sensitive ones included clover, alfalfa, sunflower, cabbage, potato, and spinach. Maize was declared as both moderately sensitive [67,109] and moderately tolerant [108]. Soybean followed the same pattern as maize and was framed as MS [108] and MT [67,109]. The third crop with opposite classification was cowpea with MS [109] and MT [67] qualities. The moderately tolerant species included wheat, forage barley, rape, sorghum, and forage rye, while the tolerant class included durum wheat, barley for grain, and sugar beet.

Table 1. The degree of salt tolerance level for different crops.

No.	Common Name	Botanical Name	S	MS	MT	T	Supplementary References
1	Wheat	<i>Triticum aestivum</i>			■		[110–112]
2	Durum wheat	<i>Triticum turgidum</i>				■ ■	[113,114]
3	Maize	<i>Zea mays</i>		■ ■	■		[115–117]
4	Soybean	<i>Glycine max</i>		■	■ ■		[118–121]
5	Barley (grain)	<i>Hordeum vulgare</i>				■ ■	[122–124]
6	Barley (forage)	<i>Hordeum vulgare</i>			■ ■		[125–127]
7	Bean	<i>Phaseolus vulgaris</i>	■ ■				[128–130]
8	Broadband	<i>Vicia faba</i>		■ ■			[131–133]
9	Clover	<i>Trifolium repens</i>		■ ■			[134–136]
10	Alfalfa	<i>Medicago sativa</i>		■ ■			[137–139]
11	Sugarbeet	<i>Beta vulgaris</i>				■ ■ ■	[140,141]
12	Cowpea	<i>Vigna unguiculata</i>			■ ■		[142–144]
13	Sunflower	<i>Helianthus annuus</i>		■ ■			[145–147]
14	Rape	<i>Brassica napus</i>			■ ■		[148–150]
15	Sorghum	<i>Sorghum bicolor</i>			■ ■		[151–153]
16	Cabbage	<i>Brassica oleracea capitata</i>		■ ■			[154]
17	Potato	<i>Solanum tuberosum</i>		■ ■			[155,156]
18	Spinach	<i>Spinacia oleracea</i>		■ ■			
19	Pea	<i>Pisum sativum</i>	■ ■				
20	Rye (forage)	<i>Secale cereale</i>			■ ■		

Note. S: salinity sensitive, MS: moderately sensitive, MT: moderately tolerant, T: tolerant plants. The representative colors indicate the consulted references in green [67], red [108], and gray [109]. Supplementary references represent the latest specific studies in the topic of salinity for each species.

In addition to the ones presented in Figure 3, other **salinity-sensitive** plants include strawberry *Fragaria x Ananassa*, Angola pea *Cajanus cajan*, parsnip *Pastinaca sativa*, onion bulb *Allium cepa*, mung bean *Phaseolus mungo*, and fennel *Foeniculum vulgare* [26]. Plants that are **moderately sensitive** to salinity also include watermelon *Citrullus lanatus*, tomatoes *Lycopersicon lycopersicum*, sweet potato *Ipomea batatas*, spinach *Spinacia oleracea*, radish *Raphanus sativus*, potato *Solanum tuberosum*, pepper *Capsicum annuum*, peas *Pisum sativum*, onion seeds *Allium cepa*, lettuce *Lactuca sativa*, kale *Brassica oleracea*, garlic *Allium sativum*, eggplant *Solanum melongena* variety *esculentum*, cucumber *Cucumis sativus* Brussels sprouts *Brassica oleracea*, cauliflower *Brassica oleracea*, and sweet corn *Zea mays* [26]. Plants that are **moderately tolerant** to salinity include *Psophocarpus tetragomolobus* winged bean, *Cucurbita pepo* pumpkin, *Portulaca oleracea* fat grass, *Vigna unguiculata* black-eyed bean, *Apium graveolens* var. sweet, broccoli *Brassica oleracea*, beetroot *Beta vulgaris*, lima bean *Phaseolus lunatus*, and artichoke *Cynara scolymus* [26]. **Plants tolerant** to salinity include asparagus *Asparagus officinalis* and chard *Beta vulgaris* subs. *Cicla* [26].

6. The Case Study of Wheat, a Major Cereal Crop, with Regard to Salinity Tolerance

Wheat is a major crop that is present in almost all crop rotations in agricultural ecosystems worldwide [157–159]. In the literature, there is evidence that different varieties of the same cereal species react differently to salinity stress [160,161]. Therefore, future research should focus on finding the most tolerant genotypes from international and national varieties. Wheat varieties with increased salinity tolerance can also be bred, with chlorophyll content, yield, and harvest quality among the important factors [161]. To improve wheat growth, different methods have been tested, such as water regime by applying optimal irrigation or soil reclamation. Both measures are expensive or time-consuming and provide very short-term solutions to counter the negative effects of salinity [162]. Experiments in field conditions are recommended to establish the degree of resistance to salinity of wheat genotypes because other environmental factors, such as soil properties, climatic regime, and spatial heterogeneity, can have an impact, especially on the generative stages [161]. Experiments in controlled conditions, where the influence of abiotic factors is missing compared to the field conditions, can produce faster results but may contain increased biases. The biases can appear because all the set conditions for optimal growth and development can produce good salinity responses in the vegetative stages but with no corresponding effect in practice in the field [161,163]. Under saline environments, plant characteristics can differ greatly depending on their tolerance class. In this case, a measure of interactions between seed yield and yield biomass can give a better indication of wheat genotype resistance [164].

As a starting measure before setting up a crop in saline field conditions, different seed priming methods, such as halopriming [165], can be used. This can result in improved values for above- and belowground fresh and dry biomass or shoot and root length [166]. Furthermore, some specific morphophysiological parameters can highlight salt tolerance and stress. This is an easy assessment method for quantifying the phenotypic response of plants and organogenesis features [167] because of their adaptive mechanism to salinity [165,168]. In saline conditions, using seed priming methods, remarkable variations were observed in the period from start of germination to physiological maturity [166]. The principal reason for weak aboveground development of wheat can be explained by water deficiency, ionic toxicity, and unavailable photosynthates [169]. Wheat reaction varies with different salinity values, which is visible in yield reduction of 6 to 8 dS m⁻¹ [170]. However, some varieties succeed in alleviating excess salinity by activating the mechanisms of osmoregulation, sodium exclusion, or potassium retention [171]. The most commonly affected physiological mechanisms include water absorption depending on the amount of sodium and chloride ions, homeostasis, and the osmotic potential, which can be negatively impacted by enzymatic activity and hormonal disorders [172]. Stress tolerance is genetically inherited by descendants through a key stress gene locus (QTL) [173], a research area that needs attention in the future, especially for ensuring a comparable yield [174]. High

concentrations of salts directly affect the leaves of different ages by accumulating a high level of ions [175]. Plants can also activate specific mechanisms to restrict ions from the xylem through the Casparian strip, thus protecting the shoots and leaves [176]. Another mechanism that restricts the Na^+ ions in root cell vacuoles [174] was studied in an ancestral germplasm wheat, which acts as protection from Na^+ in aboveground tissues [171,177].

7. Ecophysiological Perspectives in Salinity Stress

The entire salinity issue should be viewed through a holistic perspective, both by integrating the knowledge with the newest advances in agronomy, soil science, and climatology and by creating new indicators relevant for the current challenges in this field [178–180]. The first step is to create a strong connection between already developed climatic scenarios and salinity scenarios that still need to be developed. This approach uses both mathematical models and satellite or drone surveys to constantly update information regarding the models. It offers a survey area around the world, with the most important points displayed at a high resolution.

A second step that is critical for the correct understanding of salinity stress related to crops is the proposal and validation of new ecophysiological indices that will increase knowledge of this phenomenon and will be very useful in breeding programs [181–184]. The indices need to be easy to use and cheap enough to be replicated in the field, even by individuals with low to medium level of training. Additionally, new studies on plant physiology with detailed analysis of each phenological stage should be carried out. This type of research represents a vital point in the understanding of sensitivity related to salinity at the phenological stage, which will lead to more detailed knowledge on the entire growth and development period. By identifying the most sensitive phenological stages, new agronomic techniques can be proposed to mitigate salinity stress.

Another step is to externalize studies from laboratories and controlled experiments, where the results are limited to model plants or variables proposed and observed by the researchers [185–190]. A system of farm networks can be identified for areas where salinity is currently a problem or will present a problem in the near future. Involving farmers along with scientists will increase the amount of data collected from the field, the modeling and forecasting potential, and the overall speed of studies on agronomic issues related to salinity stress. This approach will also increase knowledge of farmers themselves, and most importantly, all the observations will be recorded in a similar manner that will reduce the time necessary for synchronizing the data. Both plants and the soil where they are cultivated need to be constantly monitored, which will ensure a large database with a diverse gradient of salinity that will allow realistic comparison.

Furthermore, both rhizosphere and phyllosphere microbiomes should be studied in the search for microorganisms adapted or tolerant to salinity [191–197]. This research will respond to current requirements of microbial specificity for crops, with microbial communities acting as a support for plants during the entire growth and development period. The use of microbial consortia to reduce salinity level is a good biological approach during cropping. An important focus of microbiome research should be the fallow periods, where cover crops can be directed to increase microbial activity, resulting in reduction of salinity values.

The final step in this holistic, complex process is to synchronize all the information and to create new scales for the assessment of crop status during the vegetation period. New scenarios based on integrative models will respond faster and better to the requirements and the constant increase in this phenomenon.

8. Conclusions

The salinity phenomenon represents a hot topic for researchers given the current challenges posed by climate change. Ambitious targets should be set to observe plant growth in the entire growth period, especially highlighting the key phenological developmental stages. Within an interconnection analysis between different morphological and

physiological parameters, some crop associations can be proposed to form sustainable cropping systems under saline soil conditions. This measure represents a heterogeneous system based on soil analysis.

In order to mitigate this abiotic stress, it is important to understand the effects of soil salinity on plant growth and development and the consequent changes in physiological parameters. By understanding the effects of different levels of salinity on plants, adjustments to agricultural practices can be made, such as implementing crop rotation systems that alternate nonhalophytes and halophytes in order to reduce soil salinity and maintain yield. Plants adapt to salinity by modifying their mechanisms, which can result in decreased phenolic content and antioxidant potential. Water content, turgor, and photosynthesis are also affected and lead to decreased plant growth and development. Future research should focus on finding the most tolerant genotypes, and field experiments are recommended to establish the degree of resistance to salinity. Seed priming methods, especially halopriming, have shown potential in improving growth and development in saline environments.

Soil salinity could offer the opportunity to carry out new studies aimed at implementing new agronomic practices and strategies. All the mechanisms that restrict the effects of salinity outside the aboveground biomass need to be intensively studied. Another perspective is a research focused on ancient germplasm collections, which may lead to the identification of alternative survival mechanisms and genetic resources that can be used in breeding programs. Agricultural production worldwide is significantly limited by soil salinity, and studies should be oriented to mitigate its effect and to even create new varieties of plants adapted to saline soils conditions.

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