Review

Genomics Advances in olive tree (*Olea europaea* subsp. *europaea* L.) to Mitigate the Effects of Soil Salinisation: Stepping Towards the 'Smart Oliviculture'

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Genomics Advances in olive tree (*Olea europaea* subsp. *europaea* L.) to Mitigate the Effects of Soil Salinisation: Stepping Towards the 'Smart Oliviculture'

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Simple Summary: Soil salinisation must be tackled to mitigate economic losses and difficulties of world food supply under the current climate change. This review revisits the known responses and signs of salt stress in plants, and then focuses on how olive tree can manage salt stress. Morphological and physiological responses are described, together with biochemical adaptations, and the transcriptomic and metagenomic results obtained for different cultivars. A comprehensive list of 97 cultivars classified by salt tolerance is given. The use of soil amendments that induce post-translational modifications in proteins, salt tolerant microbiota, promising modification of metacaspases, as well as the bioinformatics and multi-omics tools that can foster the identification or development of salt-tolerant rootstocks or cultivars is presented. More genomics studies about salt tolerance would be required in olive to reliably integrate future research lines, breeding programs and olivicultural practices in a kind of proof-of-concept for a future 'smart oliviculture'.

Abstract: Soil salinisation is threatening crop sustainability worldwide mainly due to the anthropogenic climate change. To avoid the excessive ion concentration in soils, plants have developed mechanisms, which have been deeply studied in many model plants and widely reviewed in the scientific literature. Nevertheless, the economically relevant olive tree (*Olea europaea* subsp. *europaea* L.), being very exposed to soil salinisation, deserves a specific review, where morphological and biochemical adaptations, signalling pathways involved, and the interplay of transcriptomics and metagenomics adaptations, are described. Variations in the olive tree microbiota due to soil salinisation and usual agricultural practices, and how might biostimulants and chemical amendments may allow the cultivation in salinised soils. Although not concluding, it seems that tolerance in olive cultivars is associated with effective mechanisms of ion exclusion and retention in the root, limiting the accumulation of these ions into actively growing shoots. The emerging importance of post-translational modifications as a source of salt tolerance is highlighted. Also, a comprehensive list of 97 olive cultivars classified by salt tolerance is given. The future advantages of engineering specific metacaspases involved in the programmed cell death and autophagy pathways to rapidly rise salt-tolerant cultivars or rootstocks is considered. An overview of bioinformatic tools focused on olive tree, as well as the machine learning approaches to study plant stress from the multi-omics perspective invites to hypothesise that they can foster the development of salt-tolerant cultivars or rootstocks adapted to soil salinisation and pave the way for a future 'smart oliviculture' in the seeking of more productive and sustainable oliviculture under salt stress.

Keywords: olive; cultivar; salt stress; salinisation; salt tolerance; bioinformatics; multi-omics; machine learning; climate change; post-translational modification; programmed cell death; autophagy

1. Soil Salinisation Is a Major Problem Under Climate Change

1.1. Origins and Consequences of Soil Salinisation

High salts in soil and irrigation water is the more detrimental abiotic factor for agriculture [1,2]. The sixth report of the United Nations Intergovernmental Panel on Climate Change (IPCC) [3] states that deforestation, land degradation, irrigation with brackish or saline water, fertiliser malpractice, and over-exploitation of fresh underground waters, together with the decrease in precipitation, temperature increase and high evapotranspiration due to climate change, are among the main causes of soil salinisation worldwide [2,4–9]. Temperature increase, drought waves, and expansion of drylands are especially concerning in the Mediterranean basin, whose coastal areas suffer seawater intrusion in by over-exploitation of groundwater, which is accelerating the problem [10]. Moreover, the alternative use of wastewater, although provides nutrients that may increase soil fertility, is causing unanticipated, serious salt stress [11]. Predictions point out that soil salinisation will affect 50% of total agricultural lands by 2050 [2], with important economic losses [12]. Adding that 33% of irrigated agricultural lands and 20% of the cultivated lands are highly saline (>40 mM), with an expected increase of 10% annually, drives to the urgent need of fighting against salt accumulation in the root zone [13] or the development of salt-tolerant crops [9]. There are some agronomical practices that may mitigate the salt stress, such as restoration of vegetation cover, changes in irrigation pattern and water quality, appropriate use of fertilisers, application of organic amendments to soil (including microbiota changes, compost, charcoal, chemical compounds...), as well as the cultivation of salt-tolerant crop plants [9]. In conclusion, urgent solutions are required to mitigate the effects of soil salinisation.

1.2. Why the Olive Tree?

The effect of soil salinisation in many crop plants (rice, wheat, maize, sorghum, chickpea, soybean, cotton) as well as in the model plant *Arabidopsis* has been widely studied [14]. But the evergreen sclerophyll olive tree (*Olea europaea* L subsp. *europaea*), typically cultivated in dry lands of Europe and Africa [15,16], has not received the same interest. Olive groves have sculpted the Mediterranean landscape and entails important economic, agronomic and agroecological repercussions due to their olive oil and table olives, appreciated worldwide thanks to the benefits for human health [17]. In fact, these benefits have been proposed to be the main driver of its enormous geographical expansion [18]. Additionally, other parts of the plant are of utility for human use, such as its wood for firewood and its seeds for feed supplements (edible oil, nutraceuticals, and proteins) [19]. Different aspects of olive tree biology have been addressed, including fruit maturation [20–23], oil synthesis [24], alternate bearing [25], juvenility-to-maturity transition [26,27], sexual reproduction and self-incompatibility [28–33], pollen allergy [34–37], pest tolerance [38], etc. Since soil salinisation is also affecting olive fruit yield [39], there are studies about response to salt stress in olive tree (previously reviewed in [15,16,40]). Salt stress is exacerbated in olive groves due to the change from a traditional, extensive, rain-fed crop to intensive or super-intensive groves with high water demands [41]. Hence, it can be hypothesised that soil salinisation might explain why being Europe and Africa the main olive oil producers in the world, are Oceania and America the lands with better yields [15].

In olive tree groves, the soil amendments and salt-tolerant crops are considered the only realistic approaches to mitigate salt stress to date. This is why this review is focused on the biochemical, physiological, genomic and metagenomic studies (in their broadest sense) developed for olive trees to gain molecular insights into its adaptive response to salt stress, the putative roles of microbiota and post-translational modifications in the salt tolerance, as well as the future of approaches based on artificial intelligence, to maintain olive yields in stressed lands.

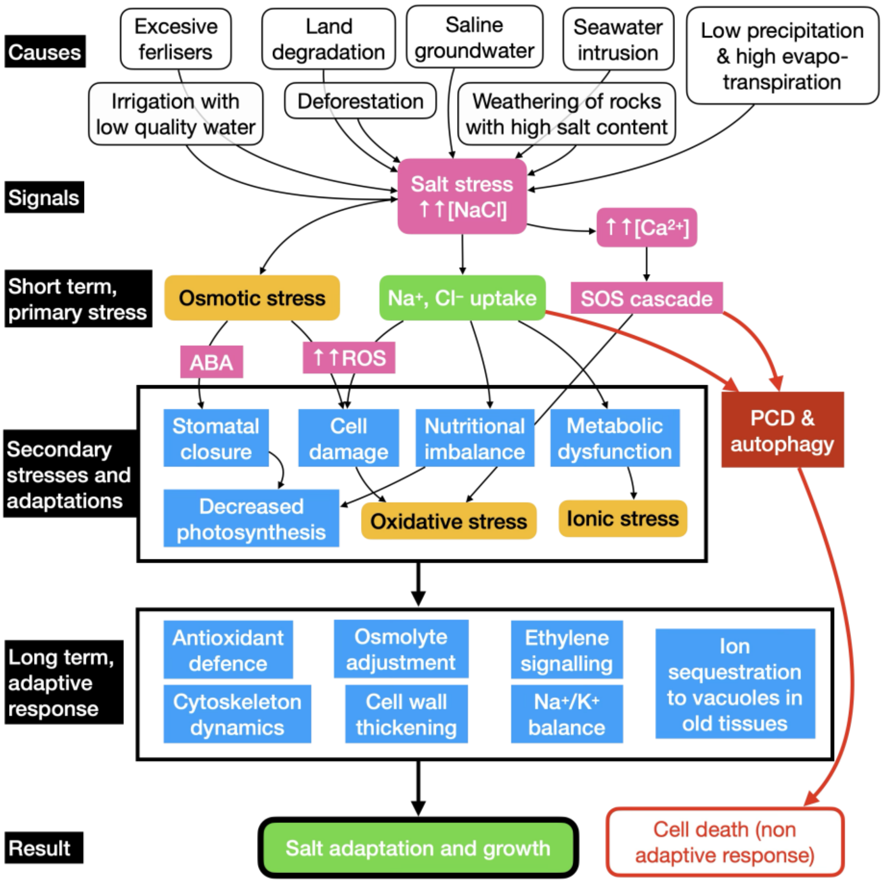

Figure 1. Integrative scheme from the main causes of natural and anthropogenic soil salinisation (white boxes) to the salt adaptation and growth (green box) or non-adaptive response (red lines and boxes). Stresses are represented by orange boxes; the main signals are in pink boxes; adaptive processes are in blue boxes; and arrows depict known cause-effect relations. ABA: abscisic acid; ROS: reactive oxygen species; SOS: salt overly sensitive; PCD: programmed cell death.

2. Plant Management of Soil Salinisation

Although there are many reviews considering the plant responses to salt stress, such as the one by Hualpa-Ramírez and coworkers [42] focused on possible biotechnological strategies to cope with climate change harsh conditions, a general overview of the main physiological and molecular mechanisms of salt tolerance will be illustrative (Figure 1).

2.1. *Overview of Plant Responses to Salt Exposure*

Natural salt stress is usually due to soil salinisation, characterised by the accumulation of water-soluble salts (mainly Na^+ and Cl^- accompanied by other ions) in the root zone, which provokes a diminution of water uptake [43,44]. This increase induces a short-term osmotic response in plant followed by an long-term response [45,46], as well as other secondary stresses such as nutritional imbalance and oxidative stress (Figure 1). All these factors will limit net photosynthesis rate and consequently plant growth, development, and yield [46]. After long-term salt stress, plants present chlorosis, membrane electrolyte leakage, photosynthesis impairment, reduction of leaf surface and stem diameter, increase of leaf thickness, compartmentalization of salts in old leaves, and stunted growth [47–49]. More severe symptoms include leaf burn, scorching, necrosis and premature defoliation [49]. In spite of the usual robustness of roots, they are very vulnerable to salts [50] and try to cope with salinisation by increasing the root/shoot ratio to diminish the demand for element supply and to improve water absorption and osmotic balance [51].

2.2. *Biochemical Indicators of Salt Adaptation*

The biochemical and molecular adaptation is triggered to evade the adverse effects of salt stress. Most crop plants synthesise and accumulate osmolytes or osmoprotectants (sugars, proline, arginine, glycine betaine, organic acids, etc.) [52] to maintain cellular osmotic potential and turgor, stabilise proteins, and scavenge reactive oxygen species (ROS) that appear at the short-term response (Figure 1). An excess of ROS can produce the oxidative damage of macromolecules [45,53], including cell membrane disorganisation that leads to ion leakage, covalent modifications of chromatin via histone modifications, DNA methylation and alternative splicing [54,55], and alterations in membrane and protein surface charges [54]. Hence, a complex antioxidant defence system is expressed during salt stress, comprising enzymes [56] (e.g., superoxide dismutase [SOD], catalase, peroxidases, glutathione reductase, and glutathione-*S*-transferase) and non-enzymatic components (e.g., ascorbic acid, tocopherol, carotenoids, phenolic compounds, alkaloids, and glutathione) [45,57]. It has been observed that transgenic *Arabidopsis* and rice over-expressing SOD or other antioxidant enzymes switch to salt tolerance (up to 250 mM NaCl) and produce seeds in the presence of 100 mM NaCl [45]. Unfortunately, those genetically modified organisms (GMOs) are difficult to bring to orchards, particularly in Europe, due to the restrictive regulations against GMOs [58].

2.3. Adaptive Signalling to Salt Stress

2.3.1. Hormonal Signalling

It is well known that abscisic acid (ABA) and ethylene play a key role in regulating the response to salt stress [59,60]. ABA is a growth and stress hormone that increases its biosynthesis under salt stress to regulate stomatal closure in order to reduce water loss and prevent further salt uptake, resulting in plant survival [61]. Ethylene is involved in signalling pathways that control cytoskeleton dynamics via microtubule repolymerisation, root development, ion transport, and senescence in response to salt stress. Zhao and coworkers [62] and Zhou and coworkers [63] have recently published exhaustive reviews about hormonal signalling.

2.3.2. Post-Translational Modifications

Another adaptive signalling that is gaining interest is the post-translational modification (PTM) of proteins. Even though the role of PTMs in plant salt tolerance is at a very early stage, it has been demonstrated the ubiquitination and SUMOylation of proteins in pathways regulating salt stress, and the importance of phosphorylation in the ion homeostasis under salt stress [64]. PTMs are described to modulate or even inhibit the activity of numerous enzymes and proteins (including transporters), modify their cell localization or binding capacity, as well as minimise the ROS production to provide some tolerance to salts [64]. Additionally, ROS, reactive nitrogen species (RNS) and other free radicals like reactive sulphur species (RSS) are triggered by salt stress and exert their salt-tolerant signalling functions throughout other PTMs such as carbonylation, *S*- and Tyr-nitration, sulfhydration, persulphidation, and others [65,66]. Lipidation, *N*-acetylation and *N*-glycosylation are also promising PTMs for salt tolerance [64].

Many chemical agents, most of them known to produce PTMs, such as hydrogen sulphide (H_2S), nitric oxide (NO), hydrogen peroxide (H_2O_2) or melatonin, have been shown to enhance the salt tolerance of crop plants when used for priming seeds and seedlings [67], probably by means of the PTMs they cause. In any case, it is important to bear in mind that salt tolerance induced by PTMs would make reusable the salinised lands using these 'primed' crops without the need of GMOs or the time-consuming breeding programs or replanting with salt-tolerant crops.

2.3.3. Signalling Crosstalk

It is well established that cytosolic Ca^{2+} concentration increases rapidly in plants with the exposure to high salt concentrations, suggesting that elevated cytosolic Ca^{2+} may function as second messenger in salt stress [61,68] (Figure 1). However, Ca^{2+} signalling enables information integration and physiological coordination in response to a variety of extracellular cues, such as nutrient deprivation and abiotic stresses, as well as intracellular signals (such as plant cell death [69,70]), which is vital for downstream responses. Interplay between Ca^{2+}, ROS, PTMs, hormones and MAPKs seems to shape the acclimation responses in most plants [71]. An inadequate adaptation to a high ion strength may drive however to premature senescence and programmed cell death [72] (Figure 1, red lines and boxes), as will be discussed below.

2.4. Cell Wall Thickening and Leaf Changes Under Salt Stress

Epidermis is the first line of defence against environmental stresses, but high salt concentrations can severely damage the cell wall to disrupt the normal growth and development of plants by affecting the cortical microtubule polymerisation (governed by Ca^{2+} levels) and the cellulose synthase (CesA) complex assembly. This is why plants respond by altering the synthesis and deposition of epicuticular wax and the main cell wall components to prevent water loss and decrease the transport of ion surplus into the plant. This mainly affects biosynthesis and deposition of cell wall components (cellulose, pectins, hemicelluloses, lignin, suberin and epicuticular waxes) resulting in an increase of both cell wall and leaf thickness when salts are abundant [73,74]. Cell wall suberinisation and lignification becomes a physical root barrier to salts that is regulated by several *MYB* transcription factors as well as members of the *WRKY, ERF* and *NAC* gene families [75]. Other morphological changes described in salt stress are a decreased stomatal density and an increased trichome density [43].

2.5. Avoiding Ion Toxicity

Salt tolerance is a polygenic trait influenced by both genetic and environmental factors [76]. Two main phenotypes can be defined: halophytes (species adapted to perpetually saline conditions of 70-200 mM NaCl [77]) and glycophytes (plants requiring soils with low salt content to maintain low Na^+ and Cl^- levels in their above-ground tissues [78]). The toxicity of different ions also varies according to the plant species and among cultivars, although accumulation of Na^+ in the cytosol is detrimental in both glycophytes and halophytes [46,55,57]. Na^+ is toxic for most terrestrial plants, including many crops [46,48,79,80], and its chemical similarity with K^+ makes that high levels of external Na^+ competitively inhibit K^+ uptake systems and stimulate K^+ efflux, leading to insufficient intracellular K^+ concentrations [81–83]. Therefore, the maintenance of balanced cytosolic Na^+/K^+ ratios has become a key tolerance mechanism in plants, such as *Arabidopsis*, cereals and other crop plants. Transporters probably avert the excessive accumulation of Na^+ and/or prevent the loss of K^+ in the cytosol to keep a high K^+/Na^+ ratio [55,60] by means of (1) NSCC, AKT1, HAK5 and SKOR/GORK, P-H^+-ATPases, involved in selective K^+ *vs* Na^+ uptake in roots; (2) Na^+/H^+ antiporter, SOS1, P-ATPases, mediators in the Na^+ removal to the external medium or to the apoplast; (3) Na^+/H^+ antiporter, NHXs, V-H^+-ATPase, V-H^+-PPase, participating in vacuolar and endosomal compartmentalisation; and (4) HKT1 and SOS1, associated with xylem and phloem loading and unloading. In consequence, ion exclusion, including accumulation in root cells, is used by some plants to prevent the intracellular accumulation in the aerial part.

In other crops, such as citrus, grapevine, avocado and persimmon, excessive accumulation of Cl^- (but not Na^+) in leaves correlates with a decrease in crop transpiration, photosynthesis, yield, and quality, eventually leading to plant death [43,84–87]. However, prevention of Cl^- toxicity has been poorly studied in spite of the characterisation of several genes exhibiting Cl^- transport activity (*NPF, NRT2, SLAH, SLAC, CCC, ICln, ALMT, CLC*, or *NAXT* [86,88,89]). Very recently, a new mechanism of Cl^- exclusion has been described in which the chloride channel protein *f* (CLCf) in *Arabidopsis thaliana* moves from Golgi's apparatus to the plasma membrane to remove the excess of chloride ions when plants are treated with NaCl, which increased plant tolerance to salt [90]. This change of location remembers the behaviour of VPEs (vacuolar processing enzymes [91]) involved in the achievement of programmed cell death (PCD, see below).

There are other mechanisms involved in ion detoxification. For example, aquaporins of the PIP (plasma membrane intrinsic proteins) family accumulate in the root cortex to lower the water conductance, and dehydrins increase their expression to prevent cellular damage caused by dehydration [92]. The tetraspanins (integral membrane proteins, characterized by four transmembrane domains) are involved in development, reproduction and immune responses, but also contribute to salt and drought stress tolerance in rice by (1) maintaining an elevated K^+/Na^+ ratio to gain the ionic equilibrium, (2) regulating antioxidant pathway enzymes and (2) promoting the proline accumulation [93]. Biotechnological manipulation of model plants with some of the mentioned ion transporters are providing encouraging results [94], but these plants are difficult to bring to orchards, particularly in Europe, due to the restrictive regulations against GMOs [58] (more hopes can be placed on CRISPR-modified plants after recent resolutions [95,96]).

2.6. Programmed Cell Death and Autophagy Under Salt Stress Conditions

Cell wall structure, cytoskeleton dynamics, phytohormone and ROS signalling, metabolism activation, foliar gas exchange control, morphological changes of leaf anatomy, and growth control have been mentioned above as adaptive processes to alleviate salt stress (Figure 1). PCD, which is usually overlooked in salt stress studies, is also among the evolved plant strategies to tolerate extreme environments by an organised removal of superfluous and damaged cells. In fact, Na^+ toxicity (and not osmotic stress) leads to PCD activation [97] (Figure 1), the Na^+/K^+ imbalance due to salt stress being crucial for triggering the effector enzymes of PCD [98,99]. Salt treatments lead to a rapidly rise in cytosolic Ca^{2+} levels that trigger the Ca^{2+}/SOS cascade, allowing the discrimination of salt stress from mere osmotic stress [70] and resulting in the onset of PCD and death-specific enzymes [69]. PCD depends on caspases as well as on VPEs (located in the apoplast in normal conditions but relocated to the cytoplasm under stress). VEPs have also been recently established as executors of NaCl stress-induced vacuole-mediated PCD [91]. Overexpression of anti-apoptotic proteins such as Bcl-2 drives to the inhibition of salt-induced PCD because it suppresses Ca^{2+} rise and decreases VPE expressions, which eventually improves salt stress tolerance [100]. Since VPEs became key moderators of salt stress-induced PCD in plants, new transporter-independent strategies can be envisaged to enhance the efficiency of salt tolerance.

Salt stress also triggers autophagy to avoid high salt concentrations in cytosol (Figure 1). Thus, NaCl treatments induce transcription of several autophagy-related genes (ATGs) in plants for Na^+ sequestration in the central vacuole, being some of these ATGs and metacaspases required for the autophagosome-vacuole fusion [101]. Hence, plant metacaspases, in addition to be regulators and executors of PCD in a Ca^{2+}-dependent way [102,103], are also involved in a variety of stress responses [104]; for example, metacaspases rapidly enhance their expression in response to salt stress [105]. There are increasing evidences that point out metacaspases as regulators of the autophagy-PCD crosstalk [105,106] since autophagy, together with PCD, is a conserved strategy in plants to resist various environmental stresses [107]. Metacaspases that activate PCD and autophagy, as critical regulators of the balance between cell death and survival, emerge as new biotechnological targets to improve plant salt tolerance. Moreover, manipulation of innate vacuolar PCD pathway emerges as an approach for 'broad stress tolerance'.

2.7. Computer Learning as an Integrative Approach to Study Salt Stress

Generation of new knowledge based on public data becomes the next challenge where the emerging field of artificial intelligence (AI) and its machine learning (ML) and deep learning (DL) subfields are expected to play a key role. A comprehensive understanding of plant response to salt stress would require the combination of image data (source of morphology and phenomics) with genomics datasets in the widest sense [108]. In recent times, the application of ML has gained prominence in the field of plant phenotyping [109,110] as well as in the analysis of plant leaf images to predict the occurrence of biotic and abiotic damage [111]. DL has been successfully applied to identify specific image patterns that can differentiate canopy and non-canopy regions [112] or leaves under stresses [109,110], as well as for the analysis of time-course images to predict plant leaf damages [59,109,110,113,114]. AI techniques, particularly in computer vision, are rapidly progressing in agriculture, encompassing tasks such as counting plants, fruits or leaves, crop classification, phenotyping, vein pattern detection, plant disease diagnosis, weed control, and biotic stress prediction [59,109–111]. Combination of AI models was exploited to diagnose plant stress in greenhouses [115]. Other promising studies reveal that γ-aminobutyric acid (GABA) concentration, type of crop, days of treatment, and level or stress (drought or salt), were able to predict the time for optimal physiological properties in pomegranate [116]. It is clear that integration of physiological, biochemical, and molecular markers with AI techniques for predicting plant stress remains an underexplored area that merits more efforts [108,117,118].

ML models for the identification of genes responsible for six types of abiotic stress (salinisation, oxidation, light, heat, cold and drought) were investigated [119], concluding that SVMs (support vector machines) outperformed other ML approaches including DL. Another successful case was the prediction of miRNAs associated with four specific abiotic stress factors (salt, drought, cold and heat) using SVM models that also surpassed the results obtained by these same authors using more computationally consuming DL algorithms [120]. Yield prediction under salt stress for breeding programmes in alfalfa and many other polyploid crops was another successful use of ML to integrate polymorphisms and genomic context [121,122]. Other ML approach that integrates time-series transcriptome data from various stress types (heat, cold, salt, and drought) drove to more accurate stress classification, with high specificity in the discovery of known stress-related genes [123]. Recently, salt stress was tackled with a multi-omics approach in *Fabaceae* plants (that enabled the development of 'smart farming' with genome-wide marker-assisted breeding and removal of deleterious genes [124]) and rice (with the application of AI to obtain accurate predictions [125]). As a result, more and more pipelines and web tools are emerging designed for multi-omics datasets, such as 'mixOmics' [126], 'OmicsIntegrator' [127] or 'MiBiOmics' [128], as well as AI-driven tools that reduce the need for human intervention such as 'AutoBA' [129] (AI tools and databases to feed algorithms have been recently compiled [108]). Hence multi-omics AI strategies have the potential to revolutionise not only plant stress research but also crop breeding programs [118,130–132].

3. Olive Tree Management of Soil Salinisation

Even though the olive tree has been described as an intermediate tolerant species to salinity compared to other fruit trees (but less resistant than barley, cotton, or sugar beet), a sustained excessive salt exposure may result in a cultivar-dependent, non-adaptive response presenting with reduction of stalk length, leaf surface, dry weight and root length. Easily seen phenotypes of a non-adaptive response are leaf tip burn, leaf chlorosis, leaf rolling, wilting of flowers, and even root necrosis, shoot dieback and defoliation [40]. Identifying and understanding the adaptive response to salts play a pivotal role in enhancing orchard management practices, ultimately contributing to increased yield, cost reduction, and sustainability [133].

3.1. Ion Exclusion and Retention in Olive Tree

The level of tolerance to salts in olive tree is associated with effective mechanisms of ion exclusion and retention of Na^+ and Cl^- in the root to limit the accumulation of these ions into actively growing shoots [134–136]. This suggests that ion concentrations in leaves (mainly Na^+ and Cl^-) is a good indicator of salt stress [136,137], since salt stress damage occurred when the leaf content of Na^+ and Cl^- exceed 0.5% and 0.2% dry weight, respectively [40]. In fact, the tolerance limit for olive trees was established on 137 mM NaCl [138]. As occurs in other plants, the early response of the olive tree is also interlaced with osmotic shock, including a decrease in water potential and plant turgor, leading to ABA-dependent stomata closure and photosynthesis decay. Later, salt-specific effects are deployed depending on the concentration of Na^+ and Cl^- ions, and the stress prolongation, presenting typical phenomics effects, more correlated to Na^+ than to Cl^- accumulation in leaves [139]. Stem elongation and gas exchange in olive leaves may be misleading since they were not highly correlated with Na^+ and Cl^- contents or salt treatments [139,140]. In spite of the decrease in net photosynthesis, leaf chlorophyll content and leaves dry weight [141], there was no relationship between salt accumulation and photosynthesis decay in either young or old leaves, confirming that olive photosynthetic sensitivity to salt did not depend on salt exclusion or compartmentalisation in old leaves [142]. But in agreement with the observed findings in other plants, leaf lignin content is increased in olive tree as response to salt stress [143,144]. Additionally, growing parameters such as shoot elongation, trunk diameter, dry weight of total plant, number of leaves, leaf thickness, stem and roots, internodes length, total leaf area, shoot/root ratio, are good surrogates to determine the salt effects on olive tree [15].

A comparative study [145] revealed a lower osmotic potential in salinised olive trees (100 mM NaCl) than in citrus (50 mM NaCl); additionally, the detected increase in Cl^- and Na^+ concentration in leaves and roots of both species caused a decrease in leaf chlorophyll *a* in citrus but not in olive trees. As a result, young olive plantlets do not seem to suffer any apparent damage when treated with 100 mM NaCl for 57 days or even 18 months in field-grown trees irrigated with saline water (6.6 dS/m) [40], while adults growing with moderate salinity (40-60 mM NaCl) reduce viability and germinability of pollen, mean number of perfect flowers per inflorescence, and fruit set [40]. Leaf drop phenomenon was observed from 60 days after high salt treatments [136]. High-salt irrigation water (>6 dS/m) has a detrimental effect by accelerating olive fruit ripening and inhibiting the linoleic desaturase activity, driving to an increase in phenol content and a decrease in the unsaturated/saturated fatty acid content [146].

Olive trees protect their sensitive shoot organs from the detrimental effects of excess toxic-ion concentration by means of a moderate growth and a reduced transport of water that would prevent salt translocation to the aerial part of the plant [140]. Only after a maintained high salt stress (>6-8 dS/m), ions are translocated to and accumulated in the stem and old leaves [139,147]. This exclusion driven by a drastic decline in the water mass flow seems an untenable strategy for most annual crops, but since olive cultivars have evolved under adverse environments, they are able to assimilate CO_2 and produce new growth at considerable rate, allowing a rapid recovery of plant performance when good-quality water is available to the roots [148]. High salt also reduces the number and length of roots, increases the root turnover, and rises the concentration of Na^+ and Cl^- 5 to 10 times greater compared to leaf tissues, indicating that the protection of aerial tissues from salt ends up having a high cost to roots [137].

3.2. Biochemical Adaptations to Salt in Olive Cultivars

Although is well established that, as occurs in 'Frantoio', long-term salt tolerance is mediated by Na^+ exclusion in leaves and accumulation in roots, there are other possibilities. For example, in one study, 'Frantoio' presents a higher mobilisation of Ca^{2+}, with expression of transporter activities in cytoplasmic membrane instead of tonoplast [149]. This setting may remember the recently described tolerance mechanism involving CLCf in *A. thaliana* [90].

A Croatian wild olive tree genotype was considered salt-resilient due to several factors: its ability to accumulate a huge amount of Na^+ and Cl^- in leaves, avoid the loss of K^+, and deploy adaptable antioxidative mechanisms [150]. It is known that ROS are increased in olive trees due to salt stress, with a concomitant increase in the activity of antioxidant enzymes that differs between cultivars [141]. In fact, some degree of salt tolerance in olive trees is depending on the time required to increase SOD levels in plant tissues, since more sensitive olive tree genotypes accumulate higher concentrations of SOD over a shorter time [151].

Another way of defence against oxidation due to salt stress is the accumulation of phenolic compounds, including the highly abundant oleuropein, especially in leaves, due to the highly significant correlation observed between total phenol content and antioxidant activity in both leaves and roots in different olive cultivars [152]. It has also been observed a strong up-regulation of key genes of the phenylpropanoid pathway in salt-sensitive 'Leccino' under salt stress while salt-tolerant 'Frantoio' showed a less intense up-regulation of the phenylpropanoid genes but overall higher content of phenolic compounds, suggesting that 'Frantoio' faces NaCl toxicity not only with mechanisms of Na^+ exclusion, but also through activating antioxidant defences [153,154].

Regarding osmoprotection, in some cultivars such as 'Picual', 'Gemlik' or 'Chemlali', proline accumulates in roots and leaves in response to salts due to its high hydration capacity so that it can bind proteins to prevent their denaturation [144,155–157]. However, a decrease in proline levels under salt stress has been described for cultivars 'Chétoui', 'Arbequina', 'Koroneiki', 'Royal de Cazorla' and 'Fadak 86' [141,143]. Other osmoprotectant adjustments in olive trees to counteract oxidative damage under salt stress involved mannitol, violaxanthin-cycle pigment, and flavonoid accumulation [148].

Exploring the Italian olive germplasm also allowed to compare 'Canino' (salt-tolerant) and 'Sirole' (salt-sensitive) transgenic olive trees overexpressing a tobacco osmotin gene with control non-transgenic plants [158]. After four weeks of treatment with 200 mM NaCl, stunted growth and ultimate leaf drop was observed in both cultivars, but not in the transgenic lines. The authors provide evidence that the S assimilation pathway plays a key role in adaptive response of olive trees under salt stress conditions. Tobacco transgenic plants overexpressing *OeSCR1* gene, which encodes a Ks-type dehydrin, also showed an increased tolerance to salt and drought stresses [159].

3.3. Salt Tolerance of Olive Tree is Cultivar-Dependent

Since the natural habitat of olive trees are calcareous soils, the available Ca^{2+} limits the toxic effects of Na^+ on plasma membrane integrity and avoids the transport of Na^+ and Cl^- to sensitive shoots and leaves [147], explaining at least partially why olive trees appear more tolerant to salts than other fruit trees. Additionally, olive grooves based on salt tolerant cultivars may have positive consequences for soil fertilisation, since salt-sensitive trees have difficulties in capturing the available nitrogen compounds in salinised soils while salt-tolerant trees can capture them [160], resulting in a clear improvement of plant growth in high salt. As occurs in other fruit trees, the use of salt-tolerant rootstocks grafted with salt-sensitive cultivars can mitigate salt stress issues. To avoid the time-consuming efforts for improving salt tolerance in cultivars or rootstocks, the use of salt tolerant cultivars can be encouraged on salinised soils. The knowledge of the salt-tolerance levels of olive cultivars is then helpful since this trait is cultivar-dependent [138]. Hence, we have collected this information from literature and presented it in Tables 1 and 2. As a result, 89 cultivars have been unambiguously described as salt-tolerant (30), intermediate tolerance (33) and salt-sensitive (26) nowadays (Table 1), even if they have been analysed in different reports (such as 'Chemlali', 'Frantoio', 'Kalamon', 'Megaritiki', 'Royal de Cazorla', 'Manzanillo', ' Chondrolia Chalkidikis' and 'Leccino' in Table 1). 'Frantoio' is commonly considered a salt-tolerant cultivar despite the fact that in one study [157] the authors found that 'Ocal' (Table 1) and 'Picudo' (Table 2) were more salt-tolerant cultivars than 'Frantoio'. 'Changlot Real' was included in the intermediate tolerance group in Table 1, but nurseries (https://gardencenterejea.com/olivos/382-olivo-changlot-realacebuche-c1.html) and the experience of the authors indicate that it can tolerate high salts. Treatment time has been very variable in the different studies, as well as the strength of the salt treatment. More surprisingly, the salt concentration is not described in some cases (ND in Table 1).

Table 1. Unambiguous classification of 89 olive cultivars according to their salt tolerance.

Cultivar	Reference	Country	Salt treatment	Treatment time
		Salt-tolerant cultivars		
Abou-Satl	[161]	Syria	12 dS/m NaCl	90 days
Amigdalilolia	[162]	Iran	12 dS/m NaCl	90 days
Ayvalık	[163]	Turkey	300 mM NaCl	30 days
Barnea	[164]	Israel	7.5 dS/m EC	9 years
Cañivano	[165]	Spain	100 mM NaCl	49 days
Chemlali	[164]	Tunisia	brackish water	8 months
	[166]		200 mM NaCl	5 months
Dakal	[162]	Iran	12 dS/m NaCl	90 days
Empeltre	[167]	Spain	10 dS/m Eciw	4 years
Escarabajuelo	[165]	Spain	100 mM NaCl	49 days
Frantoio	[168]	Italy	200 mM NaCl	60 days
	[169]		100 molc/m^3 SIW	ND
	[157]		200 mM NaCl	84 days
	[154]		200 mM NaCl	56 days

Hamed	[164]	Egypt	6000 ppm NaCl, NaSO$_4$, CaCl$_2$ and MgSO$_4$	2 years
Istarska bjelica	[170]	Croatia	100 mM NaCl	70 days
Jabaluna	[165]	Spain	100 mM NaCl	49 days
Jlot	[171]	Syria	8000 ppm NaCl	ND
Kalamata	[164]	Greece	200 mM NaCl	5 months
Kalamon	[172]	Greece	120 mM NaCl	90 days
	[173]		120 mM NaCl	90 days
Kerkiras	[164]	Greece	ND	ND
Kilis	[163]	Turkey	300 mM NaCl	30 days
Kilis Yağlık	[174]	Turkey	150 mM NaCl	4 months
Koroneiki I38	[175]	Spain	200 mM NaCl	5 months
Kothreiki	[164]	Greece	200 mM NaCl	5 months
Lechín de Sevilla	[165]	Spain	100 mM NaCl	49 days
Lianolia	[164]	Greece	ND	ND
Megaritiki	[168]	Greece	150 meq NaCl	4 months
	[135]		200 mM NaCl	5 months
Nevadillo	[165]	Spain	100 mM NaCl	49 days
Oblica	[170]	Croatia	100 mM NaCl	70 days
Ocal	[157]	Spain	200 mM NaCl	84 days
Pocama	[176]	Egypt	6000 ppm NaCl, NaSO$_4$, CaCl$_2$ and MgSO$_4$	2 years
Royal de Cazorla	[141]	Spain	100 mM and 200 mM NaCl	8 months
	[159]		100 mM and 200 mM NaCl	60 days
	[177]		200 mM NaCl	8 months
Verdale	[176]	France	6000 ppm NaCl, NaSO$_4$, CaCl$_2$ and MgSO$_4$	2 years
Intermediate tolerance to salt				
Adramitini	[164]	Greece	ND	ND
Aggezi	[164]	Egypt	6000 ppm NaCl, NaSO$_4$, CaCl$_2$ and MgSO$_4$	2 years
Alameño	[165]	Spain	100 mM NaCl	49 days
Arbosana I43	[166]	Spain	200 mM NaCl	5 months
Blanqueta	[165]	Spain	100 mM NaCl	49 days
Cañivano Negro	[165]	Spain	100 mM NaCl	49 days
Carolea	[168]	Italy	14.97 mS/cm	11 months
Casta Cabra	[157]	Spain	200 mM NaCl	84 days
Changlot Real	[165]	Spain	100 mM NaCl	49 days
Chorruo	[165]	Spain	100 mM NaCl	49 days
Coratina	[168]	Italy	200 mM NaCl	60 days
Cornicabra	[157]	Spain	200 mM NaCl	84 days
Dezful	[162]	Iran	12 dS/m NaCl	90 days
Gordal Sevillana	[165]	Spain	100 mM NaCl	49 days
Hojiblanca	[165]	Spain	100 mM NaCl	49 days
Khaisi	[171]	Syria	8000 ppm NaCl	ND
Lechín de Granada	[165]	Spain	100 mM NaCl	49 days
Manzanilla de Sevilla	[165]	Spain	100 mM NaCl	49 days
Manzanillo	[168]	Spain	60 mM NaCl	115 days
	[178]		4000 mg/L MgSO$_4$, CaSO$_4$, NaCl, MgCl$_2$ and CaCO$_3$	9 months
	[176]		6000 ppm NaCl, NaSO$_4$, CaCl$_2$ and MgSO$_4$	2 years
Maraiolo	[164]	Italy	ND	ND
Maurino	[164]	Italy	200 mM NaCl	60 days
Moraiolo	[168]	Italy	200 mM NaCl	60 days
Mostazal	[164]	Peru	6000 ppm NaCl, NaSO$_4$, CaCl$_2$ and MgSO$_4$	2 years

Nabali Muhassan	[164]	Jordan	100 molc/m^3 SIW	ND
Nizip Yağlik	[174]	Turkey	150 mM NaCl	4 months
Oblonga	[165]	Italy	100 mM NaCl	49 days
Redondil	[165]	Spain	100 mM NaCl	49 days
Toffahi	[164]	Egypt	6000 ppm NaCl, $NaSO_4$, $CaCl_2$ and $MgSO_4$	2 years
Tokhm-e-Kabki	[162]	Iran	12 dS/m NaCl	90 days
Valanolia	[164]	Greece	ND	ND
Verdial de Vélez-Málaga	[165]	Spain	100 mM NaCl	49 days
Wardan	[164]	Egypt	6000 ppm NaCl, $NaSO_4$, $CaCl_2$ and $MgSO_4$	2 years
Zorzariega	[165]	Spain	100 mM NaCl	49 days
Salt-sensitive cultivars				
Aggezi Shami	[178]	Egypt	4000 mg/L $MgSO_4$, $CaSO_4$, NaCl, $MgCl_2$ and $CaCO_3$	275 days
Aguromanaki	[164]	Greece	ND	ND
Arbequina I18	[166]	Spain	200 mM NaCl	5 months
Arbosana	[175]	Spain	200 mM NaCl	5 months
Bezeri	[171]	Syria	8000 ppm NaCl	ND
Bouteillan	[164]	France	6000 ppm NaCl, $NaSO_4$, $CaCl_2$ and $MgSO_4$	2 years
Buža	[170]	Croatia	100 mM NaCl	70 days
Chondrolia Chalkidikis	[172]	Greece	120 mM NaCl	90 days
	[179]		150 meq NaCl	4 months
	[172]		120 mM NaCl	90 days
	[180]		75 mM NaCl	45 days
	[181]		75 mM and 150 mM NaCl	45 days
Cobrançosa	[165]	Portugal	100 mM NaCl	49 days
Conservalia	[162]	Iran	12 dS/m NaCl	90 days
Drobnica	[170]	Croatia	100 mM NaCl	70 days
Fadaq86	[177]	Iran	200 mM NaCl	8 months
Galego	[165]	Spain	100 mM NaCl	49 days
Khederi	[171]	Syria	8000 ppm NaCl	ND
Lastovka	[170]	Croatia	100 mM NaCl	70 days
Leccino	[168]	Italy	200 mM NaCl	60 days
	[170]		100 mM NaCl	70 days
	[154]		200 mM NaCl	56 days
Mastoidis	[134]	Greece	200 mM NaCl	5 months
Meski	[165]	Tunisia	100 mM NaCl	49 days
Mission	[176]	US	6000 ppm NaCl, $NaSO_4$, $CaCl_2$ and $MgSO_4$	2 years
Nabal	[164]	Egypt	6000 ppm NaCl, $NaSO_4$, $CaCl_2$ and $MgSO_4$	2 years
Nocellara del Belice	[182]	Italy	14.97 mS/cm	11 months
Pajarero	[168]	Spain	100 mM NaCl	49 days
Rosciola	[176]	Italy	6000 ppm NaCl, $NaSO_4$, $CaCl_2$ and $MgSO_4$	2 years
Shiraz	[162]	Iran	12 dS/m NaCl	90 days
Sourani	[171]	Syria	8000 ppm NaCl	ND
Throubolia	[164]	Greece	ND	ND

ND: no data available.

Further 8 cultivars (including the very common 'Arbequina', 'Koronieki' and 'Picual') have been assigned to different levels of salt tolerance depending on the published studies (Table 2). Surprisingly inconsistent cases are 'Arbequina' and 'Picual (qualified as tolerant, intermediate and sensitive), or 'Chétoui' and 'Gemlik'' (qualified as sensitive or tolerant). Divergences in salt

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concentration and treatment time, in addition to the research laboratory, might partially explain the inconsistencies in the tolerance qualification.

Table 2. Inconsistent classification of 8 olive cultivars according to their salt tolerance.

Cultivar	Tolerant	Intermediate	Sensitive	Country	Salt treatment	Treatment time
Amphissis		[179]		Greece	150 meq NaCl	4 months
			[134]		200 mM NaCl	5 months
Arbequina	[168]			Spain	100 mM NaCl	49 days
	[167]				10 dS/m Eciw	4 years
		[175]			200 mM NaCl	5 months
		[159]			100 mM and 200 mM NaCl	60 days
			[161]		12 dS/m NaCl	90 days
Chétoui	[166]			Tunisia	200 mM NaCl	5 months
			[165]		100 mM NaCl	49 days
Gemlik	[163]			Turkey	300 mM NaCl	30 days
			[174]		150 mM NaCl	4 months
Koroneiki		[176]		Greece	6000 ppm NaCl, NaSO$_4$, CaCl$_2$ and MgSO$_4$	2 years
		[179]			150 meq NaCl	4 months
			[159]		100 mM and 200 mM NaCl	60 days
			[141]		100 mM and 200 mM NaCl	8 months
			[177]		200 mM NaCl	8 months
			[166]		200 mM NaCl	5 months
			[134]		200 mM NaCl	5 months
Picual	[168]			Spain	100 mM NaCl	49 days
	[178]				4000 mg/L MgSO$_4$, CaSO$_4$, NaCl, MgCl$_2$ and CaCO$_3$	9 months
	[176]				6000 ppm NaCl, NaSO$_4$, CaCl$_2$ and MgSO$_4$	2 years
		[159]			100 mM and 200 mM NaCl	60 days
			[177]		200 mM NaCl	8 months
			[157]		200 mM NaCl	84 days
Picudo	[157]			Spain	200 mM NaCl	84 days
		[165]			100 mM NaCl	49 days
Zard	[161]			Iran	12 dS/m NaCl	90 days
		[162]			12 dS/m NaCl	90 days

4. Studies About Salt Stress Genomics in Olive Tree

4.1. More and More Genome Sequences of Olive Cultivars Are Available

In recent years, olive tree genome sequences started to populate databases. The first one corresponded to the genome of a very old tree of cultivar 'Farga' [183], whose assembly and annotation have been recently improved [184]. Next was the wild olive or oleaster (*O. europaea* L.

subsp. *europaea* var. *sylvestris*) from a Turkey-located individual [18], although it was recently suggested that it would be more consistent with a feral genome [184]. The 'Picual' cultivar, widely used in Spain but without a clear salt-tolerance phenotype (Table 2), was published on the scaffold stage [185], chromosomes being pending. Another widely used cultivar in Spain and throughout the world called 'Arbequina', whose salt tolerance also seems inconsistent (Table 2), was recently sequenced at the level of chromosomes combining short- and long-reads [186]. Finally, using the most recent advances in sequencing platforms, the first gap-free, telomere-to-telomere, olive tree genome has been published for the salt-sensitive cultivar 'Leccino' (Table 1) [187], representing the highest contiguous and complete olive genome to date. There are two other *Olea europaea* sequenced genomes corresponding to *Olea europaea* subsp. *cuspidata*, a wild olive tree present from northeast Africa and southwest Asia to drier parts of Yunnan and Sichuan in China. This subspecies, considered the ancestor of the European olive, was also originally introduced into Australia and New Zealand as ornamental plant, but now it is considered relevant as rootstock because of its fungal resistance, growth strength and the survival rate of olive cultivar grafts [188–190].

4.2. Transcriptional Response to Salt Stress in Olive Tree

Over the last decade, many key genes for salt tolerance were reported in plants, many of them relating to oxidation-reduction processes, ion transport and chloride channels, cell wall synthesis, as well as hormone-related genes, supporting the above introduced idea that salt tolerance is a multigenic response [60]. Genes related to transcription factor families such as MYB, WRKY, basic leucine zipper (bZIPs), basic helix–loop–helix (bHLH), NAC, homeobox (HB) and GATA are key in the early response to salt stress [193,194]. This can explains why transgenic plants overexpressing transcription factors such as DREB6 [52] or SNAC1 [195], among others, gain salt tolerance under controlled conditions. Unfortunately, a limited success was obtained when these strategies were translated from laboratory to field [196].

Olive breeding was only initiated in the second half of the twentieth century and currently represents the most promising strategy to provide farmers with new, well adapted cultivars or rootstocks [197]. Since (1) genomics tools can shorten the protracted crossbreeding process [118], and (2) high-throughput analyses of differentially expressed genes in horticultural plants support the already known physiological findings [198], genomic information from olive tree regarding salt stress is required to foster new salt-tolerant varieties or rootstocks. A pioneer transcriptomic study was carried out by Bazakos and coworkers [172], using 'Kalamon' (salt tolerant) and 'Chondrolia Chalkidikis' (salt sensitive) cultivars treated with 120 mM NaCl for 90 days. In the salt tolerant cultivar 'Kalamon', up to 159 genes were up-regulated in response salt treatment and 50 transcripts were synthesized *de novo* after 45 days of treatment, all of them decreasing their levels after plants recovered from stress. However, only 20 genes responded to salt stress in the salt sensitive cultivar. This lack of transcriptional activation might be partly responsible for the sensitivity of 'Chondrolia Chalkidikis' compared to 'Kalamon'. The same authors analysed leaves and roots of the salt-tolerant olive cultivar 'Kalamon' using 454-pyrosequencing [173]. Only 24 genes in roots (15 up- and 8 down-regulated) and 70 in leaves (56 up- and 14 down-regulated) were differentially expressed in salt stress. Among them, the typical responsive transcription factors were reported, but also other salt-responsive genes including *AP2/ERF, NF-Y, JERF, HMG* and *GRAS*, ABA-related transcripts, a vacuole-type H^+-ATPase, a Na^+/H^+ antiporter to accumulate Na^+ in the vacuole, and the plasma membrane antiporter SOS1. The presence of solute transporters and enzymes involved in the synthesis of osmoprotectants corroborates that salt stress in olive trees triggers an osmotic response at early stages.

In another study involving only the salt-sensitive cultivar 'Chondrolia Chalkidikis', concentration of metabolites was contrasted with expression levels of genes involved in tyrosine (*OePPO, OehisC*), flavonoid (*OeAtF3H, OeFNSII, OeCA4H*), lignan (*OePLRTp2*) and secoiridoid (*OeGTF*) metabolism during 45 days at 75 mM NaCl to reveal salt-responsive tissue-specific metabolic pathways [180]. Tyrosine and flavonoid metabolism-related genes were clearly modulated by salt in old leaves, while *OeGTF* gene up-regulation in new leaves suggests that oleuropein metabolism was modified by salt stress. The same authors studied the molecular basis of the priming response in roots and leaves to moderate salt (75 mM NaCl for 45 days) in the same cultivar following a proteogenomic approach [181]. This study revealed major differences between primed and non-primed tissues mainly associated with hormone signalling and defence-related interactions, as well as the key role of protein PTMs, particularly phosphorylation, carbonylation and *S*-nitrosylation, in promoting salt priming. Salt stress also produces a significant reduction of *OeFAD6* transcript levels together with a synergic up-regulation of *OeSAD1* gene, increasing the oleic/linoleic ratio in the maturing fruit mesocarp of salt-sensitive cultivar 'Leccino' [146].

Up to ten salt-responsive candidate genes were tested in shoots of high- and medium-tolerant Spanish cultivars ('Royal de Cazorla' and 'Picual', respectively), and compared with low-tolerant Greek ('Koroneiki') and Iranian ('Fadak86') varieties [177]. Only *OeNHX7*, *OeP5CS*, *OeRD19A* and *OePetD* genes were up-regulated in salt tolerant cultivars. These data suggest that the maintenance of ionic homeostasis, the increase of turgor pressure, the modulation of electron transport and generation of ATP, and the induction of stress-related proteins (SRPs) are key processes to cope with salt stress. Moreover, expression of *OePIP1.1* (an aquaporin), *OePetD* (a cytochrome b6), *OePI4Kg4* (a phosphatidylinositol 4-kinase) and *OeXylA* (a xylose isomerase) genes was differentially regulated by DNA methylation among cultivars, suggesting that this mechanism could be also involved in the adaptation to high salt of the salt-tolerant cultivar 'Royal de Cazorla' [159]. In another study, the differential expression of novel salt-responsive genes (*OeMO1*, *OeSTO*, *OePMP3*, *OeUSP2*, *OeAP-4*, *OeWRKY1*, *OeCCX1* and *OeKT2*) was detected when comparing ‘Picual’ (tolerant) and ‘Nabali’ (moderately tolerant) cultivars [199], suggesting that different sets of salt-responsive genes are triggered depending both on the stress level (i.e. salt concentration) and the cultivar genotype.

These very early high-throughput studies on the response to salt-stress in olive tree seem to corroborate the general findings described for most plants. However, after the early onset of an osmotic response secondary to salt stress, the number of genes that significantly change their expression in sensitive and tolerant cultivars is very low, suggesting that seed priming, epigenetics and PTMs may be playing an important role in salt response that would merit the effort to analyse. In addition, more comparative studies with more cultivars should be undertaken to have the complete range of olive tree responses to salt stress.

5. Microbiota Changes in Salinised Soils of Olive Groves

5.1. Distribution of Plant-Associated Microorganisms

Plant-associated microorganisms consist of large numbers of bacteria, fungi and archaea taxa potentially interacting among them. They live either inside the plant tissue (endophytes) or on the surface of plant organs (epiphytes) in both the aerial part (phyllosphere or 'above-ground' microbiota) and root region (the 'below-ground' microbiota). The below-ground microbiota, considered as the key hot-spot for plant–microbe interactions, is usually divided in four compartments: the bulk soil, the rhizosphere (outside the root), the rhizoplane (the root surface) and the endosphere (inside the root), each compartment sustaining distinctive microbial communities. The compartments are not isolated since some endophytes are vertically-transmitted to reach the endosphere of the phyllosphere [200]. This has also been described in olive tree, where the phyllosphere seems to come from the soil and reaches aerial plant parts through xylem sap [201] and also protects the plant from diseases and stresses [202]. Plant root-associated microbiota hosts a reservoir of beneficial microorganisms that improve growth, nutritional status, development, and fitness of the host plants, including tolerance to drought and salt stresses; those enhancements are achieved directly by improving nutrient assimilation and protection against the stressing factor [203–205] and indirectly by shaping agronomically relevant traits [206,207].

5.2. The Olive Grove Microbiota

Soil microbial composition of olive groves varies depending on the genotype and the studied plant compartment [208–211], and seems to be modulated by other factors like edaphic condition and soil management [201,212,213], as well as domestication [214]. Microbiota in olive tree roots across different seasonal patterns is highly stable in taxa composition except in cold-susceptible genotypes [206], although a vast amount of novel diversity remains to be discovered in olive grove soils [210].

Proteobacteria, Actinobacteria, Firmicutes and Bacteriodetes dominated the olive tree bacterial microbiota, and in many cases Planctomycetes, Acidobacteria, Myxococcota, Verrucomicrobiota, Gemmatimonadetes, Betaproteobacteria can also be relevant [206,208,214]. It seems that the presence of Proteobacteria in the soil is an indicator of high soil nutrient-content [201]. Proteobacteria and its class Grammaproteobacteria, Firmicutes and Actinobacteria were also highly represented in the olive tree phyllosphere [208,214] while Bacteroidetes were more variable [208,215]. Going deeper in the taxonomy level, the most common genus in soil, leaves and xylem sap [201] were Alphaproteobacteria (more abundant in soil and leaves), Actinobacteria, Sphingobacteria, Bacilli (more abundant in xylem), Gammaproteobacteria and Betaproteobacteria. The most abundant classes in the root endosphere were Alphaproteobacteria, Gammaproteobacteria and Deltaproteobacteria, belonging to Proteobacteria, with (i) Actinophytocola spp. especially relevant for olive tree fitness and health, (ii) Streptomyces, Pseudonocardia, all belonging to Actinobacteria, the most abundant genus in rhyzosphere, and (iii) α-Proteobacteria, Rhizobium, Sphingomonas and Sphingomonas (all Proteobacteria) and Acinetobacter the most abundant in soil [209,210,216].

Concerning the mycobiota whose symbiotic relationships is beneficial under salt stress [217], minor differences were found between the olive tree root endosphere and the soil rhizosphere while there were significant differences between above- and below-ground communities [209,211,218], with predominance of *Basidiomycota* and inconsistent data about *Ascomycota*, with four genera (*Canalisporium, Macrophomina, Aspergillus* and *Malassezia*) constituting the belowground fungal core [206,208,214]. S*ordariomycetes* was also the most abundant class found in olive tree fruits and roots [209,218].

The presence of Archaea is not described in many metataxonomic studies, but there are reports describing *Thaumarchaeota, Crenarchaeota* and *Euryarchaeota* in the root and leaves endosphere, indicating that olive cultivars select specific groups of Archaea as endophytes [212,214].

5.3. Decrease of Microbiota Biodiversity due to Agricultural Practices

Recent studies support the idea that plant microbiota is a consequence of millions of years of coevolution, where plants likely seek cooperation with microorganisms by means of chemical stimuli as a kind of 'cry for help' strategy to fight stresses [203]. In other level of co-evolution, the beneficial effects of the natural above- and below-ground microbiota are threatened by human agricultural practices related to pesticides, fertilisers or tillage, since they tend to decrease microbiota biodiversity [219]. This prompted to propose a defensebiome [203] to guide the design and construction of beneficial microbial synthetic communities. Low-quality soils of olive groves make endosphere and rhizosphere highly affected by the agronomic practices in a cultivar-dependent way [201,208,220,221]. For example, it was reported in three olive groves with differences in soil and climate (Jaén, Córdoba and Málaga) that *Proteobacteria, Actinobacteria* and *Bacteroidetes* were the most abundant bacteria, and that *Ascomycota* and *Basidiomycota* were the most abundant fungi. Moreover, *Actinophytocola, Streptomyces* and *Pseudonocardia* are the most abundant bacterial genera in the olive tree root endosphere in the Spanish germplasm bank, *Actinophytocola* being the most prevalent genus by far [209].

5.4. The Olive Tree Microbiota Changes Under Salt Stress

It is known that salt stress affects microbial diversity, community structure, and their functions in many crops [222]: bacterial diversity decreases in high salt, whereas the response of fungi to this stress is more complex. In general, soil salinisation leads to the replacement of salt-sensitive taxons by salt-tolerant ones [223], resulting in a salt-resistant microbial community that may sustain and even promote plant growth [72,224]. The microbiota contributes to plant growth in salinised soils by means of biofilm formation, extracellular polymeric substance production, nitrogen fixation, phytohormone production, nutrient uptake promotion and homeostasis [72,223] in addition to the above mentioned response of phytohormone biosynthesis, signalling pathways, accumulation of osmoprotectants, and regulation of ion transporters. Other microorganisms induce the expression of salt-responsive genes via the action of transcription factors, as well as by post-transcriptional modifications and PTMs [223].

Moderate levels of salt stress can favour bacterial diversity of soil microbial communities instead of their rapid replacement by salt-resistant fungus at high salt levels, suggesting that the interaction of the epigenetic adaptation process in the plant and the microbiota occurs under high salt stress but not at mild salt stress. In olive tree there is a shift of the phyllosphere bacterial communities, with a significant increase of *Burkholderia* and *Ralstonia* taxa (both belonging to *Burkholderiales*) and a decrease of their antagonistic counterpart *Pseudomonas* (a genus that improves salt tolerance in plants [222,225,226] and is the main taxon of native olive leaf microbiota [215]). In summary, there are many evidences that salt tolerant bacteria can protect plants (including olive tree) from salinisation and would improve productivity and yield under salt stress regimes.

5.5. Soil Amendments and Salt Stress

Restoring the quality of degraded soils by salinisation is a challenging task, especially in arid and semi-arid regions, even though soil health restoration has recently gained increased attention to recover the global biodiversity and habitat (loss driven by human activities and climate change) and rebuild ecosystem resilience and sustainability [227]. Biostimulants (materials of biological origin that enhance plant growth or development when applied to the soil) as well as chemical compounds (such as biochar [228], melatonin [229], silicon or ascorbic acid [67]) have been used in crop (including olive tree) groves as cost-effective soil amendments to increase plant yield, stress tolerance and even soil health and fertility [230]. In some cases, the amendments induce microbial cells to counteract the osmotic stress with the production of osmolytes that mitigate the effects of salinisation [231], demonstrating a close crosstalk between plants and the inhabitant microbiota favoured by the amendment [216]. Chemical amendments have also been used with olive tree cultivars Koroneiki and Mastoidis showing that salt-toxicity symptoms are partially reverted in the presence of 100 mM K^+ [232]. Other chemical compounds with $CaCl_2$, $MgCl_2$, H_2SO_4 (the three added to the saline irrigation water), and gypsiferous material (added to the soil) were able to maintain the tree productivity, although high Mg^{2+} concentration led to some nutrient imbalances [233]. Adverse effects of salinisation were partially ameliorated by proline in 'Arbequina', 'Arbosana', and 'Koroneiki' [175]. The use of compost, olive mill wastewater and legume cover crops was also beneficial for 'Chemlali' irrigated with saline water under semi-arid conditions [234]. Since Zn^{2+} is required for ROS detoxification, its supplement improves the antioxidative defence and increases the salt tolerance in many plants, including the olive cultivars Frontoio and Conservolea, by alleviating oxidative injuries [235]. Hence, chemical amendments can be beneficial to olive fruit production when other salt-toxicity mitigation strategies are not available.

When the described conventional strategies cannot alleviate the ion toxicity, are difficult to implement, or are harmful for soil health [236], enhancing biodiversity to promote pedosphere processes appears as an alternative. This is why the manipulation of plant microbiota is an emerging practice to mitigate salt stress, even in olive tree [237]. Several studies have demonstrated that, when inoculated to soils, growth-promoting rhizobacteria (PGPR) from genera *Klebsiella*, *Streptomyces*, *Pseudomonas*, *Agrobacterium*, *Bacillus*, *Enterobacter*, *Stenotrophomonas*, *Rhizobium*, and *Ochromobacter* avoided the over-accumulation of Na^+ and maintained the ion homeostasis under salt stress, resulting in an improved crop yield [238]. Several successful studies have identified soil and rhizosphere bacteria (and in less extent fungal taxa) as potential plant growth-promoting microorganism (PGPM) able to reduce the impact of salt stress in crops [222,226,239]. Regarding olive tree, it was described that *Glomus mosseae* was the most efficient fungus in reducing the detrimental effects of salts in olive plantlets, concomitant with an enhanced K^+ concentration in the plant [240], its inoculation in olive tree pot soils being a current practice in nurseries.

6. Bioinformatics Studies in Olive Tree Concerning Salt Stress

6.1. From Olive Tree Transcriptome to OliveAtlas

The first sequencing studies concerning olive tree were performed in the 21th century to obtain information, among other aspects, about the response to biotic and abiotic stresses [241]. The high-throughput sequencing data were later collected to produce the first olive tree transcriptome [242] and then a database for the transcriptome of olive tree reproductive tissues [28]. Microarrays and 454/Roche pyrosequencing were also used, including studies regarding the salt–tolerant and salt–sensitive olive tree cultivars [172,173] discussed above. The authors of the present review have also developed olive-focused bioinformatic tools that were also useful to study salt stress in citrus [243]: (1) RSeqFlow [33] to study differential gene expression that is currently in use to study salt and drought stresses, (2) a comprehensive list of *Arabidopsis* orthologues to 'Picual' [33] adapted for functional analyses based on the clusterProfiler package (https://github.com/bullones/FunRichR), (3) an R markdown pipeline for new olive allergen detection (https://github.com/bullones/AllergenDetectR), and (4) an R markdown pipeline to detect gene co-expression based on WGCNA package (https://github.com/Javiersdr/Co-expression_analysis).

The continuous growth of high-throughput sequencing data, the availability of five olive cultivar genome sequences and the continuous advances of artificial intelligence algorithms required new bioinformatics approaches. It is time for expression atlas, that (1) integrates expression data from different sources such as RNA-seq, proteomics, metabolomics, expression microarrays, etc., (2) precomputes many analyses using standardised methods, and (3) incorporates multiple interactive visualization methods to explore and analyse expression data. Successful cases of atlas in plants are the Tomato Expression Atlas (TEA) [244], the atlas of the Norway spruce needle seasonal transcriptome [245] and many plants in ePlants (http://bar.utoronto.ca) at BAR [246], PEATmoss for *Physcomitrium patens* [247], and MangoBase for *Mangifera indica* [248]. The OliveAtlas (https://www.oliveatlas.uma.es/) for *Olea europaea* subsp. *europaea* cultivar Picual was recently published [249] integrating information of 70 RNA-seq experiments, organised by datasets that include, among others, the response to biotic and abiotic stresses. Our ongoing multi-omics data about responses to salt stress of four olive cultivars will be soon integrated in the OliveAtlas. Expression data from other research groups, as well as other olive tree genome references, will be integrated and subjected to ML approaches to provide clues (i.e. genes, biomarkers) for selection of the most suitable cultivars tolerating salt stress. Researchers can find the gene expression levels under different environmental conditions without performing expensive, time-consuming experiments. This would help to select biomarkers and biosensors (genes, polymorphism/alleles, phenotypes, and even microbiota) that can guide both research and agricultural practices to include by introgression the desired tolerance traits in new olive rootstocks or cultivars. Hence, OliveAtlas can be considered the first step towards a future smart (or digital) breeding under the current climate change scenario.

6.2. Machine Learning to Study the Olive Tree

AI in general and ML in particular are virtually unexplored fields in olive tree. A pioneer study developed an algorithm to detect symptoms of olive quick decline syndrome on leaves infected by *Xylella fastidiosa* from leaf images [250]. The method was able to discover veins and colours that lead to symptomatic leaves. Authors also demonstrate that transfer learning (the use of other model plants where more data can be found to obtain models that will then be tested in another organism) of the same disease in other plants can be leveraged when it is not possible to collect thousands of new leaf images in olive trees, with a promising true positive rate of 98.60 ± 1.47%. A more recent approach was able to detect symptoms of this infection using image processing techniques applied to high-resolution visible and multispectral images [251]. Detection was not only fast but high sensitive (98%) and precise (93%). Another study described the accurate (89.57%) identification of olive cultivars using a combination of morphological characteristics and ISSR (Inter Simple Sequence Repeats) markers analysed through DL [252]. However, studies about salt stress in olive trees remains to be done, in spite of its high potential for elucidating the salt tolerance mechanisms that would foster the selection of salt tolerant rootstock and cultivars [132], as well as optimal microbiota, for salinised soils.

7. Conclusions: Stepping Towards a 'Smart Oliviculture'

There is an urgent need of combat soil salinisation to mitigate the future economic losses and the difficulties of world food supply under the current climate change. The usual agronomical practices to fight against soil salinisation are many times difficult to apply to orchards, particularly olive groves, leaving the use of soil amendments (including microbiota) and salt-tolerant crops as the only realistic approaches for salt stress mitigation. The exploitation of salt tolerant bacteria, both natural and adapted populations, as well as other biostimulants or amendments can protect sensitive plants from salt stress, may improve productivity and yield under salt stress regimes, and would enable the use of salinised lands as olive groves. The use of salt tolerant cultivars or the restoration of the microbial community in salinised soils also protects biodiversity, that is another way to mitigate soil salinisation under climate change. It must be considered that non adaptive responses to salt trigger the mechanisms of PCD and the plant dies. However, metacaspases involved in PCD and autophagy can be the target of new, CRISPR-based biotechnological strategies that can enhance salt tolerance (and likely other stresses) in crop cultivars.

The economical and nutritional interest of olive oil, the abundance of olive groves in lands affected by soil salinisation, and its resilience to ion toxicity makes olive tree a good model to study salt tolerance from the genomics, and preferably multi-omics, point of view. An agricultural advantage of natural or induced salt tolerant olive cultivars is that they exhibited an improved growth and probably required less fertilisers because their roots can better take up nitrogen, while salt-sensitive cultivars did not and required more fertilisers, which exacerbates soil salinisation. The use of salt-tolerant olive rootstocks or cultivars is a good way to mitigate salt stress issues without the need of develop new salt-tolerant cultivars, since most olive cultivars are clones grafted on wild olive trees (any of *Olea europaea* subsp. *europaea* var. *sylvestris* or *Olea europaea* subsp. *cuspidata*). When such rootstocks are not available, treatment of olive seed, seedling or even soils with organic amendments that induce PTMs is a promising alternative.

There are many successful cases of transgenic plants becoming salt tolerant by the insertion of one ion transporter in the genome, but this approach is not currently suitable due to the laboratory difficulties to produce transgenic olive plants and to the restrictive regulations about GMOs, even though other biotechnological approaches such as CRISPR-Cas have more opportunities in future field cultures. In any case, it is compulsory that breeding programs aiming to produce new salt-tolerant cultivars or rootstocks know what genome loci will affect the phenotype, so that the availability of genome sequences would facilitate the genetic dissection of complex traits. The olive tree genomics studies are congruent with the morphological and phenomical findings reported for this species in the literature. However, it is a little bit surprising the limited number of genes that were differentially expressed after long-term salt treatments in olive trees and other fruit trees, suggesting that studies about epigenetics and PTMs may be accomplished in olive tree to have the complete picture of salt stress. If the involvement of these processes is clearly demonstrated, new biotechnological approaches may be designed in place to increase the salt tolerance of olive groves.

Future research in the field of salinisation should explore more remote sensors of soil and plant properties besides the analytical and imaging methods already available. The use of AI, particularly ML and SVMs, should guide future research lines and oliviculture practices to cope with climate change in a kind of 'smart oliviculture'. Unfortunately, AI requires an arsenal of data compiled in a compatible way that is unavailable nowadays for olive tree. Transfer learning would fill the gap, but future research should include the collection of large amounts of olive tree-specific data and their integration in an open science resource (for example, by means of the OliveAtlas) that would give scientists and growers a powerful way to find information about basic and applied knowledge related to the soil salinisation and the consequent olive damages. Application of AI to salt stress in olive tree remains an unexplored field yet. Recent advances in sensors, imaging and automation technologies combined with AI have promoted the development of platforms that will facilitate the multi-omics integrations and predictions. The proposed central role of AI in olive tree research, rootstock genetic improvement, microbiota selection and PTM targets should also integrate data from agrisensors, physical mapping, and any other smart agriculture technology to increase the productivity of farmers' operations, minimising risks through more accurate predictions, resulting in improvement of biodiversity, productivity, sustainability and resilience of oliviculture practices and post-harvest processing. This is not science fiction speculation, since Arable (https://www.arable.com) and Semios (https://semios.com/es/) already offer in-field remote sensors to provide farmers real-time data on factors affecting crop health and overall yield, such as soil quality, leaf water potential, and precipitation to help them to manage supply to meet crop demands, identify disease and infection in their crops, and earlier treatment interventions. As a result, the combination of multi-omics (and beyond the realm of omics) data and in-field data with the aid of AI is expected to stimulate sustainable and resilient 'smart oliviculture' by (1) providing clues to manage olive cultivars and groves to cope with salinisation to maintain or increase productivity; and (2) providing information about the possibility to maintain current cultivars irrigated with poor quality water while waiting for new rootstocks that support salt stress, which is known to require less nitric fertilisers (diminishing their leaching into underground water).

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Abbreviations: ABA: abscisic acid; AI, artificial intelligence; ATG, autophagy-related gene; DL, deep learning; GMO, genetically modified organism; ISSR, inter simple sequence repeats; ML, machine learning; PCD, programmed cell death; PTM, post-translational modification; RNS, reactive nitrogen species; ROS, reactive oxygen species; RSS, reactive sulphur species; SOD, superoxide dismutase; SOS, salt overly sensitive; SUMO, small ubiquitin-like modifier; SVM, support vector machine; VPEs, vacuolar processing enzymes.

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