



Review

# Fungal and Fungal-like Diseases of Halophytes in the Mediterranean Basin: A State-of-the-Art Review

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**Abstract:** Halophytes are salt-tolerant plants growing in saline ecosystems and are spread throughout the Mediterranean area. Recently, there has been a renewed interest in agricultural exploitation of halophytes, but poor attention has been given to pest and disease management of these species. The objective of this review is to assess the extent and distribution of pathogenic fungal and fungal-like (Oomycota) organisms on major Mediterranean halophytes. We retrieved 92 references spanning over 100 years, with more than half published since 2000. Ascomycota is the best-represented phylum, and the order *Pleosporales* has the highest species diversity. The order *Pucciniales* prevails in Basidiomycota, whereas *Peronosporales* is the richest order within Oomycota. Most of the pathogenic species have been isolated from aboveground organs, especially from leaves. *Portulaca oleracea* is the species with the most associated pathogens (16) and records (28). *Leveillula* powdery mildew, caused by *Leveillula taurica*, is the most common disease among the selected species. *Cakile maritima* was found to be vulnerable to different mycotoxigenic *Alternaria* species. Strengthening the research on diseases of halophytes is essential to successfully grow these species and to evaluate the risks related to the presence of mycotoxigenic species, which is crucial for the effective exploitation of halophytes as crops.



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## 1. Halophytes for Saline Agriculture

The Mediterranean Basin is considered one of the major hotspots for plant biodiversity in the world, counting more than 25,000 plant species [1]. Hot and dry summers and mild and rainy winters characterize the Mediterranean climate. The Mediterranean Region is particularly vulnerable to climate change [2,3], and coastal areas are particularly prone to saltwater intrusion and tidal inundations [4]. The combination of these extreme events, together with inadequate irrigation practices, makes the Mediterranean soils among the most affected by salinity worldwide [5,6].

Halophytes are salt-adapted plant species that can complete their life cycle in high salt conditions; they can tolerate levels of salinity that salt-sensitive plants, otherwise referred to as glycophytes, cannot tolerate. Various morphological, physiological, and biochemical properties enable halophytes to grow in highly saline environments [7]. The main mechanisms of salt tolerance in halophytes include the development of specialized organs like salt glands, regulation of Na<sup>+</sup> and Cl<sup>-</sup> uptake and excretion, and protection against osmotic stresses [8]. Salt glands originate from the epidermis and consist of multiple vacuolated cells, in which the salt is sequestered in response to salt stress [8]. Through the salt glands, different cations and anions are secreted with a high selectivity for Na<sup>+</sup> and Cl<sup>-</sup> [9]. Furthermore, an important strategy employed by halophytes is the use of specialized transporters to sequester toxic ions, such as Na<sup>+</sup> and Cl<sup>-</sup>, within cellular compartments [8]. Finally, osmotic adjustment, through the accumulation of osmolytes

in the cytoplasm, is a salt tolerance mechanism utilized by halophytes. Low-molecular-weight compounds such as proline, sugar alcohols, sorbitol, and quaternary ammonium compounds act as osmolytes [10]. Additionally, halophytes often exhibit cross-tolerance between salinity and other abiotic stresses [11].

Halophytes play also a crucial ecological role for their ability to grow in salt-affected soils, and the increasing concern for soil salinization in the Mediterranean Basin has revived the interest in these species. Halophytes can restore damaged and underused environments and transform them into productive land for agriculture, improving agrobiodiversity and preventing soil degradation [12].

The Mediterranean halophytes mainly reside in the Amaranthaceae family, which counts several extremely salt-tolerant species [7]. Other representative families are Brassicaceae, Poaceae, and Portulacaceae. They have been traditionally collected in the wild for human consumption and medicinal uses [13,14]. However, plant harvest in the wild (foraging) presents many risks due to possible microbiological and chemical contamination and appears to be incompatible with the quality and safety standards required by the current food market. Furthermore, halophytic plants are often present in protected areas and their collection would therefore be illegal [15]. Some species are protected in Europe, such as *Salicornia veneta*, which is included in the European red list of threatened species as a vulnerable plant [16]. Therefore, the production of these species must be entrusted to professional growers capable of cultivating these plants in controlled conditions and with extensive guarantees regarding sanitary safety and more generally, quality [7].

Moreover, halophytes display a broad range of potentialities that are not limited to human consumption. Many species are widely used as forage, especially *Atriplex* spp. which has proved to provide a better feeding value when cultivated than the spontaneous counterpart [17]. Furthermore, these plants contain many antioxidant metabolites, which contribute to salt tolerance and nutraceutical value [18]. A relatively high content of phenols has been found, among other species, in *Suaeda fruticosa* (shrubby sea-blite) [19], *Atriplex littoralis* (grassleaf orache) [20], and *Portulaca oleracea* (common purslane) [21]. Interestingly, in other species such as *Salicornia perennans* (glasswort), *Lepidium latifolium* (broadleaved pepperweed), and *Suaeda maritima* (sea-blite), the phenolic fraction can be tailored to obtain phenolic-enriched products through saline cultivation [22]. For these reasons, halophytes are now being rediscovered as promising functional food, with notable market perspectives [23].

Some Mediterranean halophytic species are of economic interest. *Salicornia* is probably the most widely cultivated halophyte. Agricultural exploitation of *Salicornia* spp. plant is led by Europe and the Near East, generating hundreds of tons per year in export [24]. In Italy and Spain, *Soda inermis* (Monk's beard or agretti in Italian) is a crop of interest for both poor arable areas and greenhouse operations, while *Crithmum maritimum* (sea fennel) and *Cakile maritima* (sea rocket) are being rediscovered as valuable crops in the Mediterranean Basin [25,26].

To fulfill market demand, year-round production must be guaranteed and, in this scenario, greenhouse cultivation, either in soil or in soilless systems, is the most promising cropping technology for these plants [7]. Soil-less cultivation systems have proved to be very suitable for halophytes, and several species have been investigated for their potential to grow hydroponically with considerable yields (reviewed in [7]). Moreover, due to their intrinsic tolerance to high salinity, halophytes are excellent candidates for integrated marine aquaculture systems (i.e., aquaponics), where they can act in the recovery of saline aquaculture effluents [27]. In recent years, many efforts have been carried out to unravel the suitability of these crops in aquaponic systems [28–31] but some crucial aspects are still under-investigated, such as the occurrence and control of plant pathogens. The constant presence of water is an ideal condition for a plethora of plant pathogens and the best adapted are probably those belonging to the phylum Oomycota, which includes genera like *Globisporangium* and *Phytophthora*. Other plant pathogenic fungi can be found in hydroponic systems, e.g., *Fusarium* spp., *Colletotrichum* spp., *Rhizoctonia* spp., and *Verticillium* spp. [32].

Similar to glycophytes, halophytes are susceptible to infectious diseases that can occur either in native environments or throughout the entire production process, thus leading to yield loss or foodstuff contamination. Recently, Calabon et al. [33] have extensively reviewed the fungal biodiversity associated with halophytes in salt marshes worldwide; however, most of these fungal species are saprobic.

Notwithstanding the growing interest in the cultivation of halophytes, the research on pathogenic fungal and fungal-like (Oomycota) organisms of these species is very limited. To fill this knowledge gap, this review aims to systematically analyze and sort the state-of-the-art about infectious diseases of major Mediterranean halophytes. A classification of the pathogenic species, at the order level, is provided together with their distribution among hosts. In addition, for each plant genus or species, a dedicated section will deepen the most well-studied pathosystems, examining the major findings about symptomatology, disease development, and the current taxonomic status of the pathogenic species. The work also intends to provide a critical revision of the records, in conformity with the current taxonomy of Fungi and Oomycota.

The current literature on the topic addressed by this review is very limited. Some halophytic species are still considered weeds and the studies have mainly focused on their eradication with biological methods. For species that can be used as food or non-food crops, however, little or no attention is paid to phytopathological problems, and the case studies are extremely limited. Therefore, due to the lack of information, it was not possible to carry out a comprehensive evaluation including specific aspects (e.g., disease severity in response to growing technique or salinity). The case studies reporting data in this regard have been explored in depth in the appropriate sections of this manuscript.

## 2. Bibliographic Research and Resources Accessed

Fungus–host associations were retrieved using the United States Department of Agriculture Fungal Database [34] as a starting point, and the references were looked at therein. It should be noted that many reports derive from checklists (e.g., lists and indexes of diseases or species annotated in a particular geographic area) and provide no or brief information about disease. Other studies only aimed at addressing species redistribution within a genus and include herbarium specimens previously collected. Therefore, different literature databases (i.e., JSTOR, Google Scholar, SCOPUS, and Web of Science) were searched for research papers regarding pathosystems in halophytic plants, without any temporal limitations. In SCOPUS, we used this searching strategy: TITLE-ABS-KEY (plant species/genus\*) AND TITLE-ABS-KEY (disease\* OR host\* OR pathosystem\*) AND TITLE-ABS-KEY (fungal\* OR fungal-like\*). When no results were found, the input was modified to the more specific string: TITLE-ABS-KEY (plant species/genus\* AND pathogenic species/genus\*). Synonym names for both hosts and pathogens were considered. Similarly, the other databases were searched using plant species/genus and pathogenic species/genus as input words.

We only accepted records that included: (i) disease confirmed through artificial inoculations; (ii) sampling of symptomatic plants followed by the isolation of the putative agent of disease (such as herbarium specimens); and (iii) records of biotrophic pathogens (i.e., rusts, powdery and downy mildews). Furthermore, to provide a study as complete as possible, we included records without any geographical limitations. The plant species in this study refer to recent classifications of the main Mediterranean halophytes [7] and were selected for their distribution and environmental significance in the Mediterranean area. Other halophytic species were included based on their geographical distribution according to the Global Biodiversity Information Facility database [35] and if they were listed in the salt-tolerant plant database eHALOPH [36]. Table 1 summarizes the plant species considered in this review. The taxonomic nomenclature for fungi and fungal-like organisms and for plant species is based, respectively, on Index Fungorum [37] and [7]. Studies on the taxonomic status of pathogens were regarded as research papers.

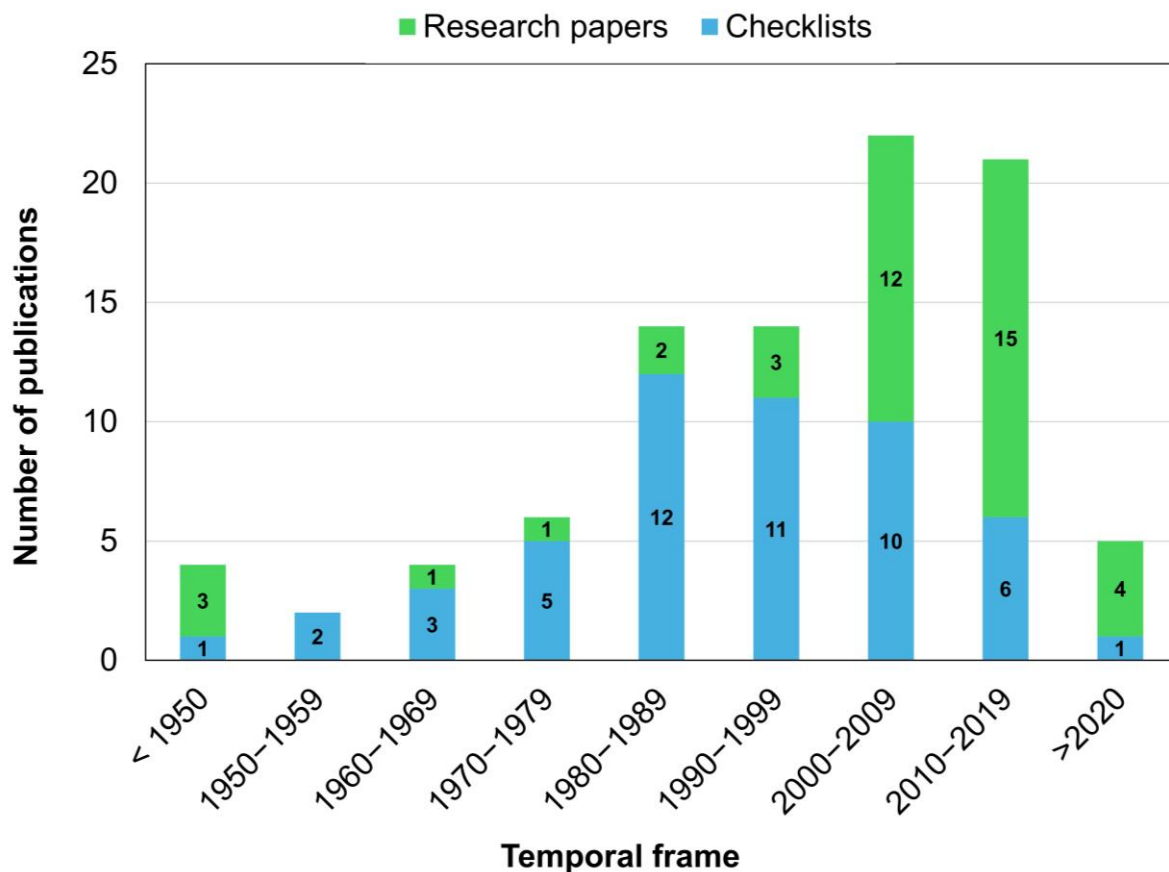
**Table 1.** Halophytic plant species considered in the review. Plant selection was made based on the current literature; other species were added on their geographical distribution (according to the GBIF database) and if present in the eHALOPH salt-tolerant plant database.

Botanical Name	Family	Common Name
<i>Atriplex hortensis</i> L.	Amaranthaceae	Garden orache
<i>Atriplex littoralis</i> L.	Amaranthaceae	Grassleaf orache
<i>Atriplex nummularia</i> Lindl.	Amaranthaceae	Oldman saltbush
<i>Atriplex patula</i> L.	Amaranthaceae	Common orache
<i>Atriplex prostrata</i> Boucher ex DC (=Syn.: <i>Atriplex hastata</i> L. var. <i>prostrata</i> (Boucher ex DC.) Lange)	Amaranthaceae	Hastate orache
<i>Beta vulgaris</i> L. subsp. <i>maritima</i> (L.) Arcang.	Amaranthaceae	Sea beet
<i>Cakile maritima</i> Scop. subsp. <i>maritima</i>	Brassicaceae	Searocket
<i>Crithmum maritimum</i> L.	Apiaceae	Sea fennel
<i>Eryngium maritimum</i> L.	Apiaceae	Sea holly
<i>Lepidium latifolium</i> L.	Brassicaceae	Broadleaved pepperweed
<i>Lepidium perfoliatum</i> L.	Brassicaceae	Clasping pepperweed
<i>Lepidium ruderale</i> L.	Brassicaceae	Stinking pepperweed
<i>Lepidium subulatum</i> L.	Brassicaceae	-
<i>Portulaca oleracea</i> L.	Portulacaceae	Common purslane
<i>Salicornia perennans</i> Willd. subsp. <i>perennans</i> (=Syn.: <i>Salicornia europaea</i> L.)	Amaranthaceae	Glasswort
<i>Salicornia perennis</i> Mill. (=Syn.: <i>Salicornia perennis</i> (Mill.) A.J. Scott subsp. <i>perennis</i> )	Amaranthaceae	Perennial glasswort
<i>Salicornia ramosissima</i> (Hook.f.) J. Woods ex W.A. Clarke & E.S. Marshall	Amaranthaceae	Twiggy glasswort
<i>Salsola kali</i> L. (=Syn.: <i>Kali turgidum</i> (Dumort.) Gutermann)	Amaranthaceae	Common saltwort
<i>Salsola tragus</i> L. (=Syn.: <i>Kali tragus</i> subsp. <i>tragus</i> (L.) Scoop.)	Amaranthaceae	Russian thistle
<i>Salsola soda</i> L. (=Syn.: <i>Soda inermis</i> Fourr.)	Amaranthaceae	Monk's beard
<i>Suaeda maritima</i> (L.) Dumort. (=Syn.: <i>Chenopodium maritimum</i> L.)	Amaranthaceae	Sea-blite
<i>Suaeda vera</i> J.F. Gmel (=Syn.: <i>Suaeda fruticosa</i> (L.) Forssk. subsp. <i>vera</i> (J.F. Gmel.) Maire & Weiller)	Amaranthaceae	Shrubby sea-blite

### 3. Plant Pathogens Associated with Halophytes

Across all the consulted databases, we retrieved a total of 92 references reporting the association of fungal and fungal-like microorganisms that are pathogenic, or potentially pathogenic, to halophytic species. The references cover a time frame from 1911 to 2023, with more than half (48/92, 52.17%) of the documents published since the year 2000. Research papers account for 22.7% (10/44) of the total records before 2000 and 64.6% (31/48) in the following years, thus proving a revived interest in fungal and fungal-like diseases of halophytes (Figure 1).

Overall, 62 different species residing in 16 distinctive orders and three Phyla (Ascomycota, Basidiomycota, and Oomycota) were retrieved (Figure 2). Ascomycota is the most represented and diverse phylum, with the highest number of orders (9) and species (37), followed by Basidiomycota (five different orders and 11 species), and Oomycota (two different orders and 14 species). Among the phylum Ascomycota, the order *Pleosporales* is the richest one, counting 12 different species, and the genus *Alternaria* is the most represented with five species (*A. alternata*, *A. arborescens*, *A. brassicae*, *A. brassicicola*, and *A. mali*). The order *Pleosporales* is the largest within the class Dothideomycetes and includes 23 families, 332 genera, and more than 4700 species [38].

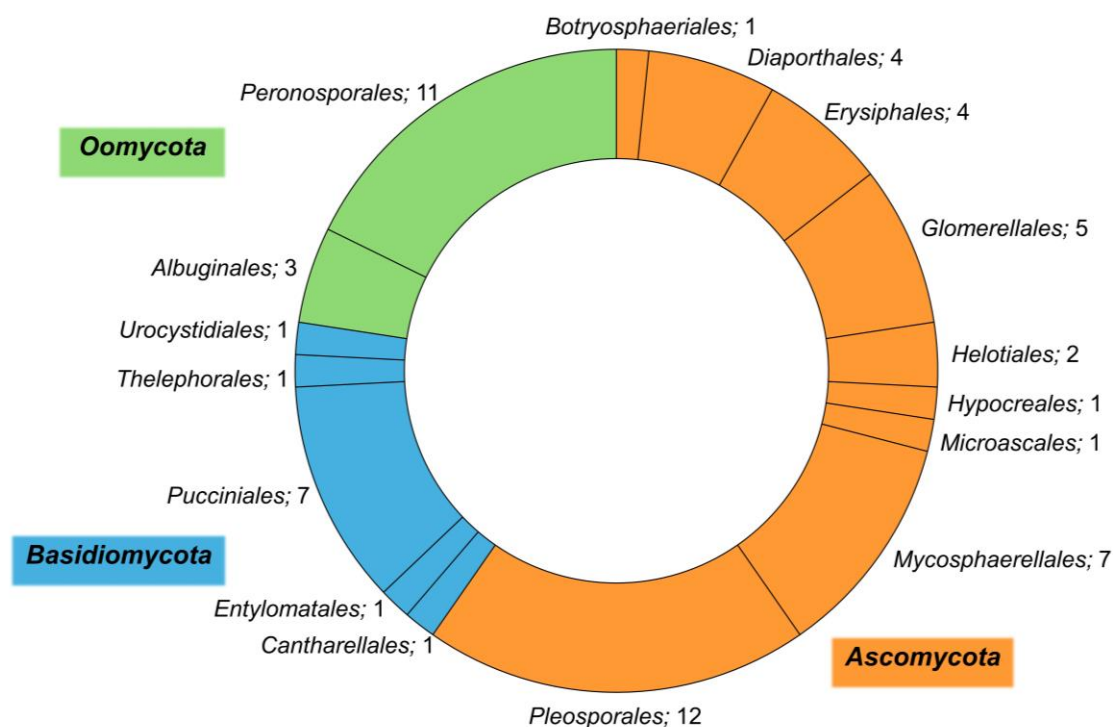


**Figure 1.** Documents published over time, distinguished in research papers and checklists on fungi or fungal-like pathogens of Mediterranean halophytic species. Documents are chronologically grouped by decades; those published before 1950 are gathered under the same period. Studies addressing the taxonomy of species were considered research papers. Data were collected using the USDA Fungal Database and different literature databases (i.e., JSTOR, Google Scholar, SCOPUS, and Web of Science).

Several studies were mostly restricted to endophyte communities and reported *Pleosporales* as the main order associated with halophytes worldwide. Calabon et al. [33] found that *Pleosporales* was the most recurring order among the fungi inhabiting salt marshes, with 178 taxa recorded.

Similarly, *Pleosporales* accounted for 28.9% of the total operational taxonomic units found in endophytic and rhizospheric fungal communities associated with roots of *Limbarda crithmoides* (golden samphire) [39], interestingly, the fraction of *Pleosporales* increases when moving from the upper dune to the salt marsh. *Pleosporales* may prevail in the endophytic community regardless of the location. The genera *Phoma* (order *Pleosporales*) and *Fusarium* (order *Hypocreales*) were reported to be the most frequent in both coastal and inland sites in the province of Alicante (Southeast Spain) [40]. In the nearby region of Andalusia, more than half of the isolates (208 out of 349) collected from different hosts belonged to *Pleosporales*, with *Neocamarosporium*, *Alternaria*, and *Preussia* being the most frequently isolated genera [41]. Finally, *A. alternata* was one of the most frequently isolated species from the roots of halophytic species in the Red Sea coast of Egypt [42].

The second most represented order within the phylum Ascomycota is *Mycosphaerellales*, which belongs to the class *Dothideomycetes* and includes important plant pathogens typically causing leaf spots. Within this order, the most represented genera are *Cercospora* and *Passalora*, both counting two species (*C. beticola* and *C. bizzoeriana*, and *P. dubia*, and *P. spgazzinii*, respectively)



**Figure 2.** Diversity of fungal and fungal-like orders reported on major Mediterranean halophytes according to the literature search on different databases (JSTOR, Google Scholar, SCOPUS, and Web of Science). Each color corresponds to the specific phylum (orange: Ascomycota; blue: Basidiomycota; green: Oomycota). Numbers indicate the different pathogenic species within each order.

In the phylum Basidiomycota, the order counting the highest number of species (seven) is *Pucciniales*, represented by two genera: *Puccinia* (two species, *P. aristidae*, and *P. isiacae*) and *Uromyces* (five species, *U. betae*, *U. chenopodii*, *U. peckianus*, *U. salicorniae*, and *U. salsolae*). Members of the *Pucciniales* are widely known as rusts; they can infect a broad range of economically important crops and display a biotrophic lifestyle.

Finally, the Oomycota, a phylum of fungus-like organisms in the Kingdom Straminipila, counts 14 different species of two different orders (*Albuginales*, and *Peronosporales*). The genus *Peronospora* is the most represented one, with five different species: *P. atriplicis-hastatae*, *P. atriplicis-hortensis*, *P. minor*, *P. litoralis*, and *P. schachtii*. This genus consists of species mainly responsible for downy mildew, a foliar disease that is promoted by wet weather conditions and is characterized by whitish patches on the underside of leaves and discolorations on the upper leaf surface.

#### 4. Diversity of Plant Pathogens among Halophytes of the Mediterranean Basin

Overall, we considered 11 plant genera commonly found in the Mediterranean Basin, accounting for 22 different plant species belonging to four families: Amaranthaceae, Apiaceae, Brassicaceae, and Portulacaceae. Amaranthaceae is the most represented family, with six genera: *Atriplex*, *Beta*, *Salicornia*, *Salsola*, *Soda*, and *Suaeda*. In the Apiaceae family, *Crithmum* and *Eryngium* are the genera examined, whereas Brassicaceae counts two different genera: *Cakile* and *Lepidium*. Finally, *Portulaca oleracea* (purslane) was considered in the Portulacaceae family. The diversity of plant pathogen orders among the halophytic plant genera is reported in Figure 3.

The order *Pucciniales* is the most common among all the plant genera, as it is described in seven out of eleven genera, although hosts only belong to Amaranthaceae and Brassicaceae (restricted to the genus *Lepidium*). Interestingly, these biotrophic pathogens were found in every examined plant genus in Amaranthaceae.



are described on *Atriplex*, *Beta*, *Salicornia* (Amaranthaceae), *Cakile*, *Lepidium* (Brassicaceae), and *Beta*, *Salsola*, *Soda* (Amaranthaceae), *Cakile*, *Lepidium* (Brassicaceae), and *Crithmum* (Apiaceae).

Leaf spot agents in the order *Mycosphaerellales* are reported on plants belonging to Amaranthaceae (*Atriplex* and *Beta*), Apiaceae (*Eryngium*), and Brassicaceae (*Cakile* and *Lepidium*). Surprisingly, despite being the richest order in terms of species diversity, fungal species in the *Pleosporales* are only recorded on four plant genera: *Atriplex*, *Beta*, *Cakile*, and *Portulaca*. Genera *Cakile* and *Portulaca* count the highest number (four) of distinctive species within this order.

Members of the *Diaporthales* are present on Amaranthaceae (*Atriplex* and *Salsola*), Apiaceae (*Eryngium*), and Brassicaceae (*Lepidium*), while species belonging to *Glomerellales* are present on Amaranthaceae (*Salsola*), Brassicaceae (*Lepidium*) and Portulacaceae.

White rusts in the *Albuginales* are exclusive to the Brassicaceae and Portulacaceae families, while species within the order *Helotiales* are reported on genera *Eryngium* and *Portulaca*. Finally, the remaining orders (*Botryosphaeriales*, *Hypocreales*, *Microascales*—phylum Ascomycota—*Cantharellales*, *Entylomatales*, *Thelephorales*, and *Urocystidiales*—phylum Basidiomycota) are exclusive to only one host species.

Table 2 shows the association between a pathogenic (or potentially pathogenic) species and its host, reporting the diseases caused by the pathogen and thus providing an overview of the diseases. For those reports providing no information about the pathosystems, the putative disease was inferred by the pathogen itself.

**Table 2.** Plant pathogenic species associated with major Mediterranean halophytes. Host species, diseases caused, origin of the specimens, and bibliographic references are reported.

Plant Genus	Plant Species	Disease	Pathogenic Species	Order	Origin	Reference(s)
<i>Atriplex</i>	<i>A. hortensis</i>	Downy mildew	<i>Peronospora atriplicis-hortensis</i>	<i>Peronosporales</i>	Herbarium specimen(s)	[43]
		Leaf spot	<i>Ascochyta caulina</i>	<i>Pleosporales</i>	Herbarium specimen(s)	[44]
			<i>Passalora spegazzinii</i>	<i>Mycosphaerellales</i>	Wild	[45]
			<i>Stagonospora atriplicis</i>	<i>Pleosporales</i>	Herbarium specimen(s)	[46]
	<i>A. littoralis</i>	Downy mildew	<i>Peronospora littoralis</i>	<i>Peronosporales</i>	Herbarium specimen(s)	[43,47]
		Leaf spot	<i>Ascochyta caulina</i>	<i>Pleosporales</i>	Herbarium specimen(s)	[44]
			<i>Stagonospora atriplicis</i>	<i>Pleosporales</i>	Herbarium specimen(s)	[46]
	<i>A. nummularia</i>	Shoot blight	<i>Diaporthe inconspicua</i>	<i>Diaporthales</i>	Wild	[48]
	<i>A. patula</i>	Downy mildew	<i>Peronospora minor.</i>	<i>Peronosporales</i>	Herbarium specimen(s)	[43,47]
			Wild			[49–53]
		Leaf spot	<i>Ascochyta caulina</i>	<i>Pleosporales</i>	Herbarium specimen(s)	[44]
			<i>Passalora dubia</i>	<i>Mycosphaerellales</i>	-	[54,55]
Wild					[56–58]	
Rust		<i>Passalora spegazzinii</i>	<i>Mycosphaerellales</i>	-	[55,59]	
	<i>Stagonospora atriplicis</i>	<i>Pleosporales</i>	Herbarium specimen(s)	[46,60]		
		<i>Uromyces peckianus</i>	<i>Pucciniales</i>	Wild	[61]	
<i>A. prostrata</i> (=Syn.: <i>A. hastata</i> )	Downy mildew	<i>Peronospora atriplicis-hastatae</i>	<i>Peronosporales</i>	Herbarium specimen(s)	[43,47]	
	Leaf spot	<i>Ascochyta atriplicis</i>	<i>Pleosporales</i>	-	[54]	
		<i>Ascochyta caulina</i>	<i>Pleosporales</i>	Herbarium specimen(s)	[62]	
		<i>Stagonospora atriplicis</i>	<i>Pleosporales</i>	Herbarium specimen(s)	[44]	
<i>Beta</i>	<i>B. vulgaris</i> subsp. <i>maritima</i>	Downy mildew	<i>Peronospora schachtii</i>	<i>Peronosporales</i>	Wild	[53]
		Leaf blotch	<i>Septoria betae</i>	<i>Mycosphaerellales</i>	-	[60]
		Leaf spot	<i>Cercospora beticola</i>	<i>Mycosphaerellales</i>	Wild	[63]
		Powdery mildew	<i>Leveillula taurica</i>	<i>Erysiphales</i>	-	[64]
		Rust	<i>Uromyces betae</i>	<i>Pucciniales</i>	Wild	[65,66]



Table 2. Cont.

Plant Genus	Plant Species	Disease	Pathogenic Species	Order	Origin	Reference(s)	
Cakile	C. maritima	Black leaf spot	Alternaria alternata	Pleosporales	Wild	[67]	
						Wild and pot (artificial inoculation on detached leaves)	[68]
						Pot (artificial inoculation in salinity-NaCl 200 mM)	[69]
			Alternaria arborescens	Pleosporales	Wild and pot (artificial inoculation on detached leaves)	[68]	
				Alternaria brassicicola	Pleosporales	Wild	[67,70]
				Alternaria mali	Pleosporales	Wild and pot (artificial inoculation on detached leaves)	[68]
			Downy mildew	Hyaloperonospora parasitica	Peronosporales	Wild	[71]
	Powdery mildew	Erysiphe cruciferarum	Erysiphales	-	[64]		
	Ring spot	Mycosphaerella brassicicola	Mycosphaerellales	Herbarium specimen(s)	[72]		
	White rust	Albugo candida	Albuginales	Wild	[50,73,74]		
Crithmum	C. maritimum	Powdery mildew	Leveillula taurica	Erysiphales	-	[64,75]	
			Leveillula lanuginosa	Erysiphales	Wild	[76]	
Eryngium	E. maritimum	Leaf spot	Cylindrosporium eryngii	Helotiales	-	[77]	
			Pseudocercospora eryngii	Mycosphaerellales	-	[54]	
		Leaf smut	Entyloma eryngii-maritimi	Entylomatales	Wild and herbarium specimen(s)	[78]	
		Stem necrosis	Diaporthe angelicae	Diaporthales	Herbarium specimen(s)	[79]	
					-	[80]	
			Wild	[81]			
Lepidium	L. latifolium	Canker and dieback	Cytospora ribis	Diaporthales	Wild	[82]	
		Downy mildew	Perofascia lepidii	Peronosporales	Herbarium specimen(s)	[83]	
		Leaf spot	Alternaria brassicae	Pleosporales	Herbarium specimen(s)	[84]	
			Cercospora bizzozzeriana	Mycosphaerellales	Herbarium specimen(s)	[85]	
		Powdery mildew	Erysiphe cruciferarum	Erysiphales	-	[54,64]	
					Wild	[62,76,86,87]	
				Leveillula taurica	Erysiphales	-	[64]
		Rust	Puccinia isiacae	Pucciniales	-	[88]	
		White rust	Albugo candida	Albuginales	Wild	[74]	
					Wild and pot (artificial inoculation)	[89]	
			Albugo lepidii	Albuginales	Wild and growth chamber (artificial inoculation)	[90]	
	L. perfoliatum	Downy mildew	Hyaloperonospora lepidii-perfoliati	Peronosporales	Herbarium specimen(s)	[43]	
		Leaf smut	Urocystis coralloides	Urocystidiales	-	[91]	
		Powdery mildew	Erysiphe cruciferarum	Erysiphales	-	[64]	
					Wild	[76]	
Rust		Puccinia aristidae	Pucciniales	-	[59]		
Stunting	Verticillium dahliae	Glomerellales	Greenhouses, gardens, fields, and orchards	[92]			
L. ruderale	Downy mildew	Hyaloperonospora parasitica	Peronosporales	Herbarium specimen(s)	[51]		
		Perofascia lepidii	Peronosporales	Herbarium specimen(s)	[51,83]		
	Leaf smut	Urocystis coralloides	Urocystidiales	-	[91]		
	Powdery mildew	Erysiphe cruciferarum	Erysiphales	-	[54,64]		
White rust	Albugo candida	Albuginales	Wild	[76,93]			
			-	[54]			
L. subulatum	Downy mildew	Perofascia lepidii	Peronosporales	Wild	[53]		

Table 2. Cont.

Plant Genus	Plant Species	Disease	Pathogenic Species	Order	Origin	Reference(s)	
<i>Portulaca</i>	<i>P. oleracea</i>	Anthracnose	<i>Colletotrichum fructicola</i>	Glomerellales	-	[94]	
			<i>Colletotrichum gleosporioides</i> species complex	Glomerellales	-	[94]	
	Black root rot	Basal stem rot	<i>Colletotrichum spinaciae</i>	Glomerellales	Herbarium specimen(s)	[95]	
			<i>Berkeleyomyces basicola</i>	Microascales	Tobacco field	[96]	
	Crown rot	Leaf blight	<i>Rhizoctonia solani</i>	Cantharellales	Wild	[97]	
			<i>Sclerotium rolfsii</i>	Thelephorales	-	[94]	
	Leaf spot	Root dieback	<i>Sclerotinia sclerotiorum</i>	Helotiales	Wild	[98]	
			<i>Stemphylium vesicarium</i>	Pleosporales	Onion field and growth chamber (artificial inoculation)	[99]	
	Stem rot	White rust	<i>Dichotomophthora lutea</i>	Pleosporales	Field and pot (artificial inoculation)	[100]	
			<i>Phyllosticta portulacae</i>	Botryosphaeriales	Herbarium specimen(s)	[101,102]	
	<i>Salicornia</i>	<i>S. perennans</i> (=Syn.: <i>S. europaea</i> )	Black lesions on leaves	<i>Globisporangium intermedium</i>	Peronosporales	Wild	[103]
				<i>Globisporangium irregulare</i>	Peronosporales	Carrot field	[104]
		Rust	Stunting	<i>Dichotomophthora portulacae</i>	Pleosporales	Carrot field	[104]
				<i>Curvularia portulacae</i>	Pleosporales	Cultivated (not specified) and pot in glasshouse (artificial inoculation)	[105]
		Rust	White rust	<i>Verticillium dahliae</i>	Pleosporales	Wild	[106,107]
				<i>Wilsoniana portulacae</i>	Albuginales	Wild and greenhouse (artificial inoculation)	[108]
		<i>S. perennis</i>	Rust	<i>Curvularia portulacae</i>	Pleosporales	Wild and pots in growth chamber (artificial inoculation)	[109]
				<i>Verticillium dahliae</i>	Glomerellales	Field and greenhouse	[110]
		<i>S. ramosissima</i>	Rust	<i>Curvularia portulacae</i>	Pleosporales	Not specified	[111]
				<i>Verticillium dahliae</i>	Glomerellales	Greenhouses, gardens, fields, and orchards	[92]
<i>Salsola</i>	<i>S. kali</i>	Black foot	<i>Wilsoniana portulacae</i>	Albuginales	-	[51,77,112]	
			<i>Phytophthora inundata</i>	Peronosporales	Herbarium specimen(s)	[113]	
	Powdery mildew	Rust	<i>Uromyces salicorniae</i>	Pucciniales	Maize, soybean, sugar beet, and sunflower fields	[114]	
			<i>Uromyces salicorniae</i>	Pucciniales	Wild	[74,98,103,115,116]	
	Rust	Stunting	<i>Uromyces salicorniae</i>	Pucciniales	Wild and maize and sunflower fields	[117]	
			<i>Uromyces salicorniae</i>	Pucciniales	Wild	[118]	
	<i>S. tragus</i>	Anthracnose	<i>Uromyces salicorniae</i>	Pucciniales	Wild	[119–121]	
			<i>Uromyces salicorniae</i>	Pucciniales	Wild	[121]	
	<i>S. tragus</i>	Stem canker	<i>Uromyces salicorniae</i>	Pucciniales	Wild	[121]	
			<i>Uromyces salicorniae</i>	Pucciniales	Wild	[121]	
<i>S. kali</i>	Black foot	<i>Dactylonectria macrodidyma</i>	Hypocreales	Grapevine field	[122]		
		<i>Leveillula cylindrospora</i>	Erysiphales	Wild	[123]		
Powdery mildew	Rust	<i>Leveillula taurica</i>	Erysiphales	-	[64]		
		<i>Puccinia aristidae</i>	Pucciniales	Herbarium specimen(s)	[124]		
Rust	Stunting	<i>Uromyces chenopodii</i>	Pucciniales	Wild	[66,98,125]		
		<i>Uromyces salsolae</i>	Pucciniales	Pots under greenhouse	[126]		
<i>S. tragus</i>	Anthracnose	<i>Uromyces salsolae</i>	Pucciniales	Wild	[127]		
		<i>Verticillium dahliae</i>	Glomerellales	Greenhouses, gardens, fields, and orchards	[92]		
<i>S. tragus</i>	Stem canker	<i>Colletotrichum salsolae</i>	Glomerellales	Wild and greenhouse (artificial inoculation)	[128–130]		
		<i>Diaporthe eres</i>	Diaporthales	Field	[131]		
<i>S. tragus</i>	Stem canker	<i>Diaporthe eres</i>	Diaporthales	Wild and greenhouse (artificial inoculation)	[132]		
		<i>Diaporthe eres</i>	Diaporthales	Wild and greenhouse (artificial inoculation)	[132]		

Table 2. Cont.

Plant Genus	Plant Species	Disease	Pathogenic Species	Order	Origin	Reference(s)
Soda	<i>S. inermis</i> (=Syn.: <i>Salsola soda</i> )	Powdery mildew	<i>Leveillula cylindrospora</i>	<i>Erysiphales</i>	Wild	[76]
		Rust	<i>Uromyces salsolae</i>	<i>Pucciniales</i>	-	[133]
Suaeda	<i>S. maritima</i>	Rust	<i>Uromyces chenopodii</i>	<i>Pucciniales</i>	-	[134]
					Wild	[103,135]
	<i>S. vera</i>	Rust	<i>Uromyces chenopodii</i>	<i>Pucciniales</i>	-	[77,136]
					Wild	[66,120]

#### 4.1. *Atriplex* spp.

In the genus *Atriplex* (Amaranthaceae), five different species are considered: *A. hortensis* (garden orache), *A. littoralis* (grassleaf orache), *A. nummularia* (oldman saltbush), *A. patula* (common orache), and *A. prostrata* (hastate orache). Except for *A. nummularia*, all the species are native to the Mediterranean area. *A. nummularia* was introduced in Tunisia from Australia and rapidly became one of the most distributed exotic *Atriplex* species in the whole Mediterranean Region [137]. Fourteen different species are reported on this genus, belonging to the orders *Diaporthales*, *Mycosphaerellales*, *Peronosporales*, *Pleosporales*, and *Pucciniales*. The order *Peronosporales* is the richest one, with four different species described among the selected hosts, each of them resulting to be species-specific.

Interestingly, the different species within the *Peronosporales* order reside in the genus *Peronospora*. This genus is the largest in the Oomycota phylum, comprises about 400 species [43], and is responsible for downy mildew on several crops. *Atriplex* spp. are particularly susceptible to downy mildew. The species separation within the genus *Peronospora* has undergone several revisions during the decades. Fries [138] first published in *Systema Mycologicum* the name *Botrytis farinosa* to indicate an organism found on an undefined species of *Atriplex* in Sweden before moving it to the genus *Peronospora*, and therefore establishing the name *P. farinosa* Fr. [139]. Later, Gaumann [140] described *P. littoralis* Gäum. on *A. littoralis* and *P. minor* Gäum. on *A. patula*. In 1932, Săvulescu and Rayss [141] described *P. atriplicis-hastatae* Săvul. & Rayss on *A. prostrata* (indicated as *A. hastata*) and *P. atriplicis-hortensis* Săvul. & Rayss on *A. hortensis*. Constantinescu [43] kept their original names when annotating an exhaustive list of species in *Peronosporales* and described 11 species on *Atriplex* spp. However, Yerkes and Shaw [142] gathered the different *Peronospora* species, including the parasitic species on other plant hosts in the Amaranthaceae, under the synonym *P. farinosa*, which was erroneously considered as the sole downy mildew agent on Amaranthaceae. Nonetheless, molecular phylogenetics demonstrated that downy mildews are extremely host-specific and that species from different plants represent different lineages according to their host genus or species [143–145]. Taxonomic revisions can lead to the reclassification of particular species and their placement in different taxonomic groups. This affects how pathogenic species are identified. By accurately classifying species within their taxonomic groups, evolutionary history, transmission dynamics, and host range of pathogens can be better defined.

Pathogenic species described on *Atriplex* spp. are not related to other pathogens revealed on important crops in the Amaranthaceae, such as spinach, beet, and quinoa [146]. Different names were proposed to indicate downy mildew agents on these crops: *P. effusa* (Grev.) Rabenh. on spinach [144], *P. schachtii* Fuckel on beet [47], and *P. variabilis* Gäum. on quinoa [147]. The name *P. farinosa* was proposed for rejection [148], and the proposal was accepted in 2017 by the Nomenclature Committee on Fungi and the General Committee on Nomenclature [149,150]. Consequently, reports annotating the occurrence of *P. farinosa* on *Atriplex* were not included in this study. Through multi-locus phylogenetic analysis, Choi et al. [47] were able to discriminate different downy mildew species associated with Amaranthaceae. The authors discriminated different *Peronospora* species (including three

species on *Atriplex* spp.) consistently with the narrow species concept, that a downy mildew species is specific to a host plant genus or species. On *Atriplex*, two distinct lineages were found representing *P. littoralis* and *P. minor*/*P. atriplicis-hastatae*. The study found that the isolates from *Atriplex* were closely related but received low support for monophyly. They were divided into three clades (i.e., monophyletic groups, comprising members descending from a single ancestor), corresponding to a specific *Atriplex* species, namely *A. littoralis*, *A. prostrata*, and *A. patula*. Therefore, we only included records aligned with these findings. It should be noted that the identity of *P. atriplicis-hortensis* was not investigated and thus we have kept the record on *A. hortensis* [43]. According to the current nomenclature of Index Fungorum, *P. minor* is not considered a distinct species from *P. arborescens*. However, following [47], who have deepened the taxonomic status of *Peronospora* species on *Atriplex*, we have kept the record as *P. minor*.

Against this background, we report *P. atriplicis-hortensis* on *A. hortensis* [43]; *P. littoralis* on *A. littoralis* [43,47]; *P. minor* on *A. patula* [43,47,49–53]; and *P. atriplicis-hastatae* on *A. prostrata* [43,47].

The *Atriplex*/*Peronospora* binomial has a long history of records. The species described on *Atriplex* seem to be extremely specialized and exclusive of one host species, further confirming the narrow species concept in downy mildews. Molecular phylogenetics is a powerful tool to infer the evolutionary history and relation of different species and is fundamental for understanding the taxonomy, host range, and specificity of closely related organisms. These findings are essential for disentangling the host–pathogen interactions and the complexity of host range in downy mildews. In the optic of agricultural use of this halophyte, these works are a breakthrough in developing accurate diagnosis and pest control protocols.

Another important pathogen frequently associated with *Atriplex* spp. is *Ascochyta caulina* (*Pleosporales*). van der Aa and van Kesteren [44] examined several specimens collected all over Europe and grouped different species names under the synonym *A. caulina*. However, these authors stated that the isolates showed different conidial shapes depending on the host organ: conidia found on leaves and associated with leaf spots were bigger than those found on stems. Moreover, leaf conidia were hyaline to yellowish green and often 1-septate, occasionally 2- and 3-septate, while those on the stem were yellowish to pale brown and only 1-septate. Thus, due to their different phenotypes, the authors claimed that they may be different species. *A. caulina* is the causal agent of leaf spot and stem necrosis, and it was reported on stem and leaves of *A. prostrata* (indicated as *A. hastata*), stem and leaves of *A. hortensis*, and leaves of *A. littoralis* and *A. patula* [44]. In artificial inoculation trials, the application of *A. caulina* conidia successfully resulted in leaf necrosis on *A. patula* and *A. prostrata* within one week [151].

Later, Andrianova and Minter [46] described another fungal pathogen, *Stagonospora atriplicis*, as a leaf spot agent on *A. hortensis*, *A. littoralis*, *A. patula*, and *A. prostrata*. They described the disease as the presence of numerous, irregular, and small spots starting from central or basal leaves on the stem, mainly occurring during the summer. According to Andrianova and Minter [46], the name *S. atriplicis* and its synonyms (*Septoria atriplicis* and *Phyllosticta atriplicis*) have been misunderstood in many studies and are listed among other synonyms of *A. caulina* [44,152]. The authors stated that differences based on the conidial shape (multi-septate, holoblastically produced from annellated conidiogenous cells in *S. atriplicis*; 1-septate, enteroblastically produced from phialides in *A. caulina*) are key features in differentiating the two species. Interestingly, by analyzing two isolates (CBS 246.79 and CBS 344.78) of *A. caulina* from *A. prostrata* (reported as *A. hastata*), de Guyter et al. [153], through molecular phylogeny based on the analysis of actin sequence data, proposed a final identification of *Pleospora calvoescens* for the *A. caulina* isolate CBS 246.79 and *Pleospora chenopodii* for the isolate CBS 344.78. However, in a recent taxonomic revision based on a multi-gene phylogenetic analysis, both isolates were designated as *Neocamarosporium chenopodii* (anamorph *A. caulina*) [154]. Since both *A. caulina* and *S. atriplicis* are still accepted

taxa, we have kept the original names provided by the authors. In addition, some authors noted *Ascochyta atriplicis* as another leaf spot agent on *A. prostrata* [54,62].

Other pathogenic species known to cause leaf spots on *Atriplex* are *Passalora spegazzinii* (*Mycosphaerellales*) on *A. hortensis* [45] and *A. patula* [55,59], and *Passalora dubia* (*Mycosphaerellales*) on *A. patula* [54–58].

Among the fungi belonging to the phylum Basidiomycota, *Uromyces peckianus* (*Pucciniales*) is described on *A. patula* in Canada as the agent of rust [45]. The author, by annotating an index of plant diseases, referred to a study by Fraser [61], where aecia of *U. peckianus* were collected and successfully inoculated on *A. patula* plants. Finally, *A. nummularia* was found to be susceptible to shoot blight caused by *Diaporthe incospicua* (*Diaporthales*), which is the only disease annotated on this species. [48].

#### 4.2. *Beta vulgaris* subsp. *maritima*

*Beta vulgaris* subsp. *maritima* (Amaranthaceae, sea beet) is the only species considered in the genus *Beta*, for which we retrieved five fungus–host associations. Overall, all the pathogens belong to different orders and cause foliar diseases, although with a different array of symptoms. The most frequently reported species is the rust agent *Uromyces betae* (*Pucciniales*). This biotroph was described twice on *B. vulgaris* subsp. *maritima* by the Norwegian botanist and mycologist Halvor B. Gjørnum in the Madeira archipelago, Portugal [65,66].

Moreover, like cultivated varieties of *B. vulgaris*, sea beet is susceptible to beet downy mildew (BDM) caused by *Peronospora schachtii*. BDM is a widespread disease, and it is commonly found on beet [47]. Gustavsson [53] described *P. schachtii* on this species in Spain and Portugal.

Another important pathogen is *Cercospora beticola* (*Mycosphaerellales*), a leaf spot agent. Despite being a very common pathogen of beet, we retrieved only one record [63]. *Cercospora* leaf spot is considered one of the most devastating foliar diseases on this crop. Dark and grey spots on leaves and petioles characterize this disease, which, at an advanced stage, can cause the collapse of the whole leaf [155].

Powdery mildew caused by *Leveillula taurica* (*Erysiphales*) is another foliar disease recorded on sea beet in Italy and Corsica (France) [64]. The genus *Leveillula* comprises obligate parasites with a broad range of hosts, described on approximately one thousand different plant species, especially members of Solanaceae [156]. Morphologically, *Leveillula* species are very close to each other, and this has led to confusion in the species definition. It was proved that *L. taurica* s. lat. is a species-complex and not a monophyletic group [123]. Heluta and Minter [157] advocated that the isolates of *L. taurica* s. lat. described by Amano [64] on sea beet are probably *L. cylindrospora*. *Leveillula* powdery mildew is commonly spread in Central and West Asia and in the Mediterranean area [158]. Typical symptoms are observed on the lower side of affected leaves, which are characterized by abundant and white sporulation, whereas, on the upper side, the infection can result in chlorotic spots that eventually coalesce leading to leaf shredding.

Finally, sea beet is reported as a host of *Septoria betae* (*Mycosphaerellales*) in Australia [60].

#### 4.3. *Cakile maritima*

*Cakile maritima* (Brassicaceae, sea rocket), the sole species considered in the genus *Cakile*, is an annual, succulent herb that thrives in sand dune habitats [159]. On this halophyte, five different orders have been noted (*Albuginales*, *Erysiphales*, *Mycosphaerellales*, *Peronosporales*, and *Pleosporales*) for a total of eight different species.

In general, *C. maritima* is highly susceptible to *Alternaria* spp. infections, as four different species are described on this host (*A. arborescens*, *A. alternata*, *A. brassicicola*, and *A. mali*). The *Alternaria* spp.–*C. maritima* pathosystems have been extensively investigated [67–70]. The best-known and most widely investigated species associated with this halophyte is *Alternaria brassicicola* (*Pleosporales*) which causes black necrotic lesions on many parts of the

host. On the surface of infected tissues, the pathogen produces spores that are airborne or dispersed by water splash [70]. *Alternaria brassicicola* has been successfully demonstrated for vertical transmission of the disease from one generation of *C. maritima* to another, as it was frequently isolated from seeds and fruit coats [67]. Seed dispersal seems to play a key role in the spread of this pathogen [70]. This pathogenic species has also been isolated from flowers, although attacks on fruits have been shown to provide a higher fraction of pathogen inoculum on seeds. Sampling of *C. maritima* fruits yielded 30% of infected seeds, while up to 60% of seedlings were found to be infected when germinating from attacked fruits [67]. Moreover, plant age and geographical location strongly influence the incidence of the disease. The fraction of infected plants is the highest in adult plants and gradually decreases in young plants and seedlings. In addition, the disease incidence was found to be higher when moving from the sea toward the beaches and the surrounding areas. Thus, a positive relationship between the distance from the sea and disease incidence has been demonstrated [70]. Another pathogenic *Alternaria* species that was frequently recovered from the Australian population of *C. maritima* is *A. alternata* [67]. Nevertheless, this species accounts only for a small fraction of the infected plants, thus resulting in a lower incidence of the disease compared with *A. brassicicola*. In glasshouse inoculation trials, *A. brassicicola* was able to infect both adult plants and seedlings, whereas *A. alternata* was not able to develop any symptoms in seedlings. Moreover, when both species were inoculated on fruits, the fraction of seeds infected by *A. brassicicola* was significantly higher than those infected by *A. alternata*. Therefore, *A. brassicicola* displayed higher colonization fitness and was able to exclude *A. alternata* [67]. The aggressiveness of *A. brassicicola* towards its host is so high that disease incidence can reach 100% by the end of the growing season. Although initial disease spread mainly relies on infected overwintering adults or plant debris, since *Alternaria* is a polycyclic pathogen, outbreaks can reach critical levels during the growing season. The occurrence and distribution of the diseases are deeply dependent on the behavior of pathogenic species. The polycyclic nature of the pathogen characterizes the epidemiology of the disease with several extinction and colonization events [70]. Furthermore, the Australian population of *A. brassicicola* infecting *C. maritima* is genetically highly variable. From five different populations of *C. maritima*, 222 isolates were found representing 202 unique genotypes, and this high level of variability may suggest the occurrence of a sexual recombination process in *A. brassicicola* [160].

On the other hand, the Tunisian population of *Alternaria* infecting *C. maritima* is different. Field surveys of symptomatic plants revealed that the species most frequently associated with black lesions was *A. alternata*, followed by *A. arborescens* and *A. mali*, whereas no *A. brassicicola* isolates were found [68]. All the tested isolates were proved to be pathogenic after artificial inoculation trials by application of a conidia suspension on leaves [68]; the isolates tested for pathogenicity resulted mycotoxigenic.

Mycotoxins are secondary metabolites produced by several fungal species and represent a threat to food security as exposure can cause health complications. The main mycotoxins produced by *Alternaria* species are: alternariol (AOH); alternariol monomethyl ether (AME); altuene (ALT), which belong to the group of dibenzopyrone derivatives; alterotoxins (ATXs); and tenuazonic acid (TeA). Some fungal species can even produce host-specific mycotoxins [161]. The *Alternaria* species pathogenic on *C. maritima* were positive for AOH, AME, ALT, and TeA biosynthesis with a different spectrum of production [68].

In artificial inoculation trials in saline conditions, the presence of salt (200 mM NaCl) was associated with a lower susceptibility to *A. alternata* infection [69]. This is the sole study where a pathosystem involving a halophytic species was investigated in the presence of salt. Interestingly, when both saline and biotic stress were applied, plants exhibited a higher growth rate and photosynthesis compared to single-stress application. The key to the alleviation of salt stress over fungal attack might reside in the intrinsic ability of halophytes to tolerate salinity and hence, after exposure to the stress, the defense mechanisms implemented by the plants (e.g., improved scavenging of reactive oxygen species) might act towards other stresses [69]. On the other hand, the susceptibility to

salinity of fungal and fungal-like species must be considered as some species can tolerate this stress better than others (see Section 6 for a discussion of salt stress in fungal and fungal-like organisms).

Furthermore, the phylum Oomycota comprises other important pathogens described on *C. maritima*. Occurrences of *Albugo candida* (*Albuginales*) on sea rocket were reported in Egypt [73], Wales [50], Spain, and Portugal [74]. *A. candida* is a biotrophic plant pathogen widely known as the causal agent of white rust or white blister on Brassicaceae, with an impressive range of hosts. The disease is characterized by the formation of white blisters (or sori) on the infected tissues, usually leaves, representing the zoosporangia bearing zoospores, which are dispersed either by air or water splash [162]. It should be noted that *A. candida* was proposed to be a species-complex with at least two different clades [163,164]; however, no specimens of *A. candida* on *C. maritima* were investigated. *Hyaloperonospora parasitica* (*Peronosporales*) is another member of the phylum Oomycota, which was found to cause downy mildew on *C. maritima* in Egypt and therein reported as *Peronospora parasitica* [71]. This species was accommodated into the novel genus *Hyaloperonospora* by Constantinescu and Fatehi [165].

Other pathogenic species occasionally described on *C. maritima* are the ring spot agent *Mycosphaerella brassicicola* (*Mycosphaerellales*) [72], and the powdery mildew agent *Erysiphe cruciferarum* (*Erysiphales*) [64].

#### 4.4. *Crithmum maritimum*

*Crithmum maritimum* (Apiaceae) is a perennial herb that thrives on the Mediterranean coasts. It is a facultative halophyte that is gaining a lot of interest in recent years for both nutrition and medicinal use, due to its high content of essential oils [166,167].

*Leveillula* powdery mildew is the only disease noted on this species, and the causal agents are *L. lanuginosa* and *L. taurica*. Powdery mildew caused by *L. taurica* was recorded in France [64,76] and Israel [75]. The same authors also reported the presence of *L. lanuginosa* as a powdery mildew agent on *C. maritimum* [75].

#### 4.5. *Eryngium maritimum*

*Eryngium maritimum* (Apiaceae, sea holly or sea eryngo) is a perennial species of flowering plants native to most European coastlines whose leaves and roots can be used as a food source. On this halophyte, four different fungal orders are recorded (*Diaporthales*, *Entylomatales*, *Helotiales*, and *Mycosphaerellales*). Each order includes only one species, with *Entylomatales* (comprising the sole species *Entyloma eryngii-maritimi*) being unique to this species [79].

The genus *Entyloma* (phylum Basidiomycota) counts more than 160 species, responsible for leaf smut. This disease is characterized by the presence of spots, which represent sori bearing teliospores. *Eryngium* spp. are particularly susceptible to *Entyloma* leaf smut, and the fungal species are highly host-specific [79,168]. Four host-specific species of *Entyloma* were described by Savchenko et al. [79], including *E. eryngii-maritimii*. This novel species was established by analyzing specimens collected on *E. maritimum* in France and Wales. A few distinctive features of *E. eryngii-maritimii* make this species easily distinguishable from the others: the production of small-size spores (the smallest within the genus) and greenish gray sori.

*Diaporthe angelicae* (*Diaporthales*) is noted as the causal agent of stem necrosis on *E. maritimum* [80–82]. This species is a common pathogen described in the family Apiaceae [169]. In both the above-mentioned publications, the fungus was reported with a different name, i.e., as *Diaporthopsis angelicae* by Ellis and Ellis [80], and as *Diaporthe nigrella* by Unamuno [81], which are now both considered synonyms of *D. angelicae* [169,170].

Finally, two leaf spot agents are described on this halophyte: *Cylindrosporium eryngii* (*Helotiales*) [77], which was first described by Ellis and Kellerman [171] as a leaf spot agent on *Eryngium yuccifolium* Michx., and *Pseudocercospora eryngii* (*Mycosphaerellales*) [54,78] reported as *Septoria eryngii* (now considered a synonym).

#### 4.6. *Lepidium* spp.

In the genus *Lepidium* (Brassicaceae), four different species have been considered: *L. latifolium* (broadleaved pepperweed), *L. perfoliatum* (clasping pepperweed), *L. ruderales* (stinking pepperweed), and *L. subulatum*. Fourteen different pathogenic species, accounting for nine different orders (*Albuginales*, *Diaporthales*, *Erysiphales*, *Glomerellales*, *Mycosphaerellales*, *Peronosporales*, *Pleosporales*, *Pucciniales*, and *Urocystidiales*) were retrieved. This genus includes several species that have a worldwide distribution and generally are weeds [172]. However, some species, such as *L. latifolium*, have edible leaves with a high content of nutraceutical compounds [173,174].

Overall, all four plant species are susceptible to downy mildew. On *L. subulatum*, *Perofascia lepidii* is described as the causal agent of the disease [53]; it is reported as *Peronospora lepidii*, subsequently accommodated into the *Perofascia* genus by Constantinescu and Fatehi [166], the sole pathogen described on this species. *P. lepidii* is also described on *L. latifolium* [83] and *L. ruderales* [51,83]. On the latter species, *Hyaloperonospora parasitica* is another downy mildew agent [51], whereas on *L. perfoliatum*, *Hyaloperonospora lepidii-perfoliati* is reported as the causal agent of this disease [43].

Powdery mildew is another common disease of *Lepidium* spp; this disease is described in three of the *Lepidium* species considered, and the main causal agent is *Erysiphe cruciferarum*. This plant pathogen was found on *L. latifolium* [54,62,64,76,86,87] *L. perfoliatum* [64,76] and *L. ruderales* [54,64,76,93]. Powdery mildew caused by *E. cruciferarum* commonly occurs on many Brassicaceae crops and is characterized by the presence of a powdery whitish coat on the upper side of infected leaves, representing conidiophores bearing conidia which are air-dispersed [175]. *Leveillula taurica* is reported as another powdery mildew agent on *L. latifolium* [64].

In addition, the white rust agent *Albugo candida* is reported on *L. latifolium* [74,89], and *L. ruderales* [54]. This disease is widespread in Europe and, through artificial inoculations, Koike et al. [89] showed that the *A. candida* isolate they found was highly host-specific. Indeed, while the first symptoms of white blister appeared on *L. latifolium* within 14 days, no disease was noted on other economically important crops such as rocket, mustard, cauliflower, and broccoli. Therefore, Koike et al. [89] concluded that the isolate does not belong to any of the previously described races of the pathogen. Another evidence of the high host specificity of the white rust agents *Albugo* spp. is provided by Rector et al. [90]. These authors characterized a pathogenic isolate of *A. lepidii* that was able to infect *L. latifolium* while not causing any symptoms on rocket, cauliflower, broccoli, pak choi, and radish. The isolate has been proposed as a bioherbicide to control the spread of broadleaved pepperweed. Bioherbicides are herbicidal agents, derived from living organisms or natural sources, specifically targeted to control and regulate the growth of weeds in agricultural and ecological environments [176].

Within the phylum Basidiomycota, we report the leaf smut agent *Urocystis coralloides* (*Urocystidiales*) on *L. perfoliatum* and *L. ruderales* [91] and two rusts (*Pucciniales*), *Uredo isiacae* on *L. latifolium* [88] and *Puccinia aristidae*, on *L. perfoliatum* [59].

*Lepidium perfoliatum* is also reported as a host of *Verticillium dahliae* (*Glomerellales*) [92], while on *L. latifolium* leaf spot agents such as *Alternaria brassicae* [84] and *Cercospora bizozेरiana* (*Mycosphaerellales*) [85], and the canker and dieback agent *Cytospora ribis* (*Diaporthales*) [82] are described.

#### 4.7. *Portulaca oleracea*

*Portulaca oleracea* (Portulacaceae) is the one with the most associated records. We retrieved the highest number (nine) of different fungal and fungal-like orders recorded on this species (*Albuginales*, *Botryosphaeriales*, *Cantharellales*, *Glomerellales*, *Helotiales*, *Microascales*, *Pleosporales*, *Peronosporales* and *Thelephorales*) resulting in 16 different pathogenic species. The orders *Botryosphaeriales*, *Microascales* (phylum Ascomycota), *Cantharellales*, and *Thelephorales* (phylum Basidiomycota) are unique to this species.



This abundance of records can be attributed to the widespread recognition of *P. oleracea* as a major noxious weed for various important crops [177]. Nonetheless, this species has succulent stems and leaves with a high content of omega-3 fatty acids and can be consumed moderately as an alternative source of this important fatty acid [178].

The most detailed and well-documented disease on *P. oleracea* is the white rust caused by *Wilsoniana portulacae* (*Albuginales*). By analyzing different specimens through scanning electron microscopy, light microscopy, and ITS phylogeny, the genus *Wilsoniana*, together with the genus *Pustula*, was proposed as a new combination apart from the genus *Albugo*, within the order *Albuginales* and subclass *Albuginomycetidae* [179]. White rust of *P. oleracea* has been widely documented [51,74,77,98,103,112–117]. Leaves are the main organs where the infection occurs, although some characteristic symptoms can be occasionally observed on stems. A typical symptom on the upper side of leaves is the presence of white blister-like pustules, which correspond to irregular yellowish chlorotic areas on the lower side. White pustules can be seen on stems as well, but more rarely. If systemic infection occurs, plants display swelled stems and reduced leaf size, which eventually drops [114,115,117]. In addition, it has been shown that, in species of the *Albuginaceae* family, the development of pustules directly involves the enzymatic lysis of host cell walls, rather than a mechanical process [116]. Lytic enzymes detach the mesophyll from the epidermis, which is then disrupted by the primary sporangia enabling the dispersal of spores from the secondary sporangia [116].

*Dichotomophthora lutea* is known as a foliar pathogen causing leaf spot. de Hoog and van Oorschot [101] introduced this new species, previously included in the genus *Dactylaria*, by morphologically analyzing specimens collected from various plant species, including *P. oleracea*. The identity of the *Dichotomophthora* species was later confirmed by molecular phylogeny [102]. The multi-locus molecular phylogeny suggested that the genus *Dichotomophthora* belongs to the order *Pleosporales* and is closely related to the genus *Curvularia* [102]. On *P. oleracea*, *D. lutea* causes spots that are oval to irregular in shape and pale brown with dark borders [100]. Since 2015, leaf spot outbreaks have been reported in Iran, where this plant is commonly cultivated. The pathogenicity of isolates was confirmed by artificial inoculation trials on 2-month-old purslane plants [102]. Other foliar pathogens occasionally described on *P. oleracea*, are *Phyllosticta portulacae* (*Botryosphaeriales*) [103] and *Stemphylium vesicarium* [99].

Another member of the genus *Dichotomophthora*, *D. portulacae* (*Pleosporales*), is frequently associated with stem necrosis on *P. oleracea*. This fungus was first described by Mehrlich and Fitzpatrick [106] in Hawaii (USA) on stems and leaves. The occurrence of this disease was recently recorded in Iraq [107]. A detailed description of symptoms is provided by Klisiewicz et al. [109]. The disease is characterized by dark lesions and constrictions on the main stem and occasionally on lateral branches; from the main stem, lesions can progress and hit the root system, with damaged tissues showing an abundance of sclerotia. The disease is particularly severe in young plants and seedlings. In artificial inoculation trials, the leaves of 4-week-old plants showed necrotic spots within 24 h. The disease progressed to the main stem and branches and eventually resulted in dieback, which was promoted by high air humidity; affected leaves displayed a yellow color and eventually fell off the plants. Klisiewicz et al. [109] found 35 isolates of *D. portulacae* in California (USA). In addition, Mitchell [108] designated black stem rot as the main symptom of *D. portulacae* on *P. oleracea* in Texas (USA). In Turkey, *D. portulacae* was associated with crown rot and root rot on cultivated purslane [105]. Here, in artificial inoculation trials, damping-off of 3-week-old seedlings was evident within eight days after inoculation.

*Curvularia portulacae* (*Pleosporales*) is described as another pathogenic fungus causing stem rot on purslane. The disease was described by Rader [110], who proposed a new species, namely *Helminthosporium portulacae* that was subsequently accommodated into the genus *Curvularia* Boedijn [180]. Rader [110] described the presence of water-soaked lesions along the stem which coalesce and cover the whole plant organ; abundance of conidia on stems and leaves was also reported.

Furthermore, three different species of *Colletotrichum* (Glomerellales) are reported: *C. spinaciae* [95], *C. fructicola*, and *C. gloeosporioides* [94]. Purslane is described as a host of *C. fructicola* by the European Food Safety Authority as well [181]. Since the Simmonds [94] specimen has not been further studied, there is little chance that is a record of *C. gloeosporioides* sensu stricto, while it is probably a *C. gloeosporioides* species complex. In any case, this fungal genus is responsible for anthracnose, a disease characterized by the presence of sunken, dark brown lesions representing fruiting bodies (known as acervuli) bearing conidia. This disease mainly hits leaves and fruits; however, no information about the pathosystems is provided in the examined literature.

Notably, *P. oleracea* is particularly susceptible to rot agents. Other pathogens causing rots on various tissues occasionally documented on purslane are *Berkeleyomyces basicola* (*Microascales*) causing black root rot [96], reported as *Thielaviopsis basicola*, and accommodated into the genus *Berkeleyomyces* by Nel et al. [182]; *Globisporangium intermedium* and *G. irregulare* (*Peronosporales*) causing root dieback [104]; *Sclerotinia sclerotiorum* (*Helotiales*) causing crown rot [98]; and *Rhizoctonia solani* (*Cantharellales*) [97] and *Sclerotium rolfsii* (*Thelephorales*) [94], both causing basal stem rot.

*Portulaca oleracea* is indicated as a host of *Verticillium dahliae* (*Glomerellales*) [92]. Inoculated purslane plants displayed mild symptoms such as stunting, reduced plant height and root development, lower pigment content in the stem, and brown discoloration of the tap root. The author stated that no clear *Verticillium* symptoms, like wilt or chlorosis, were visible. It is known that purslane can represent a source of inoculum for some important pathogens without being damaged. Important pathogens like *Phytophthora capsici* [183], *Globisporangium sylvaticum*, and *G. ultimum* [184] were associated with roots of *P. oleracea*. In both studies, artificial inoculation trials failed to cause any visible symptoms. These case studies provide important insights into pathogenicity and virulence. Pathogenicity is defined as the ability of a pathogen to cause disease on a particular host and is regarded as a qualitative trait. It mainly depends on the ability of the pathogen to invade and colonize the host. Virulence is the extent of damage caused to the host; thus it is a quantitative property [185]. The above-mentioned studies concerned species that were pathogenic (i.e., able to colonize the host tissues) but caused no or mild symptoms (i.e., no or weakly virulent). In this scenario, pathogenic organisms can successfully establish and survive within a particular host, potentially acting as a means of spreading to other crops.

#### 4.8. *Salicornia* spp.

In this review, three different species within the genus *Salicornia* (*Amaranthaceae*) have been considered: *S. perennans* (glasswort), *S. perennis* (perennial glasswort), and *S. ramosissima* (twiggy glasswort). Despite its success as a halophytic crop, only a few documents were retrieved, accounting for two pathogenic species, belonging to as many orders. *Salicornia* spp. can be exploited for human consumption as a source of pharmaceutical compounds, for biodiesel production, for the remediation of saline soils, and for the treatment of saline effluents from aquaculture [186,187]. This genus includes branched plants with succulent and articulated stems [7].

*Uromyces salicorniae* (*Pucciniales*) is a rust agent affecting all three *Salicornia* species [121]. On *S. perennans*, this rust was reported several times [54,77,119–121]. In addition, on *S. perennans* (reported with its synonym *S. europaea*), a strain of *Phytophthora inundata* was isolated in the Netherlands from leaves showing dark lesions [118].

#### 4.9. *Salsola* spp.

The genus *Salsola* (*Amaranthaceae*) comprises several halophytic annual herbs, characterized by spinous leaves which thrive in arid and semi-arid regions [188]. *S. kali* (common saltwort) and *S. tragus* (Russian thistle) are the two species considered in this review. Nine pathogenic species, residing in five orders (*Diaporthales*, *Erysiphales*, *Glomerellales*, *Hypocreales*, and *Pucciniales*), were found. Although considered noxious weeds, both *S. kali* and *S. tragus* can be agronomically exploited, especially as forage for cattle and sheep [189]. Most

of the studies describing the occurrence of plant pathogens on such species have explored the potential of causal agents to be employed as bioherbicides [130–132,190]. For instance, the potentiality of the anthracnose agent *Colletotrichum salsolae* (*Glomerellales*) has been widely investigated for the control of *S. tragus* [130,131]. The pathogen was first described by Schwarczinger et al. [128] in Hungary as *C. gloeosporioides*, isolated from leaves and stems showing the typical symptoms of anthracnose, i.e., chlorotic spots with acervuli developing on the center of the lesions. Pathogenicity was confirmed through artificial inoculations, which led to the death of inoculated plants within two weeks [128]. The disease was also reported in Greece [129] and Russia [130]. Berner et al. [191] designated the pathogenic strain of *Colletotrichum* as *C. gloeosporioides* f. sp. *salsolae*. Later, the resolution of the *C. gloeosporioides* species complex led to the establishment of the novel and highly host-specific species *C. salsolae* [192]. The application of *C. salsolae* as a biocontrol agent against Russian thistle was tested in open fields in Greece and Russia [131]. The authors monitored the development of the disease over two years and concluded that the treatment of infested fields with *C. salsolae* could eliminate the weed. In addition, they found a strong relationship between disease incidence and rainfall, suggesting that the pathogen mainly spreads through rain splash and high moisture conditions promote the disease.

The stem canker agent *Diaporthe eres* (*Diaporthales*) was also assessed as a mycoherbicide [132]. It was isolated in Russia from dark necrotic lesions at the base of the stem of symptomatic *S. tragus* plants. In artificial inoculation trials, spraying of conidia suspension onto leaves and stems led to a disease incidence of 100% at 70 days after inoculation [132].

Furthermore, the rust agent *Uromyces salsolae* is under examination as a potential bioherbicide for the control of *S. tragus* [190]. Interestingly, the same species is reported as a rust agent on *S. kali* [126,127].

On *S. kali*, two additional members of *Pucciniales* were noted: *Uromyces chenopodii* [66,98,125] and *Puccinia aristidae* [124]. This species was also indicated as a host of two powdery mildew agents, *Leveillula cylindrospora* [123] and *L. taurica* [64], *V. dahliae* [92], and *Dactylonectria macrodidyma* (*Hypocreales*) [122].

#### 4.10. *Soda inermis*

*Soda inermis* (=Syn.: *Salsola soda*, *Amaranthaceae*, Monk's beard) is an annual shrub widely spread in the Mediterranean Region. This crop can tolerate high levels of salinity and displays a marked ability to accumulate sodium from the soil [193,194]. Although this crop is highly consumed and cultivated in commercial greenhouses in Mediterranean countries, there are only a few reports about diseases caused by pathogens. We retrieved two records on this halophyte: *Leveillula cylindrospora* (*Erysiphales*) as a powdery mildew agent [76] and *Uromyces salsolae* (*Pucciniales*) as a rust agent [133].

#### 4.11. *Suaeda* spp.

The genus *Suaeda* (*Amaranthaceae*) comprises several halophytic species, which can be either annual or perennial. In this study, two species have been considered: *S. maritima* (sea-blite) and *S. vera* (shrubby sea-blite) for which we retrieved only one association. Both species have edible leaves; *S. maritima* is particularly rich in proteins, minerals, and vitamins [195], while *S. vera* seeds can be employed as a source of edible oil [196]. On both species, the rust *Uromyces chenopodii* (*Pucciniales*) is the only fungal pathogen reported in the literature, with several records [66,77,103,120,134–136].

### 5. Host Range of Pathogens of the Mediterranean Halophytes

A plant disease is the result of the interaction between a susceptible host plant, one or more virulent pathogens, and the environment. The plant–pathogen interaction is a complex process involving pathogen- and plant-derived molecules and represents a dynamic situation in which a co-evolutionary arms race takes place. As one side advances, strong selective pressure arises on the other to increase or modify its specific response [197].

Plant–pathogen characteristics evolve and vary both in space and time and are strongly associated with differences in the level of losses caused by the disease [197]. Therefore, host–pathogen interactions are usually the outcome of evolutionistic mechanisms by which the two components of the system evolve synergistically, and this is emphasized in the case of highly specific pathogens. Nonetheless, besides those exclusive to one host species, there are many cases of pathogenic species with a broad range of hosts, both at genus and species levels. Pathogenic species reported on two or more different halophytic plant hosts are summarized in Table 3.

**Table 3.** Host range of pathogenic species. Only pathogenic species reported on two or more different Mediterranean halophytic host species have been considered.

Pathogenic Species	Host Family	Host Species
<i>Albugo candida</i>	Brassicaceae	<i>Cakile maritima</i> <i>Lepidium latifolium</i> <i>Lepidium ruderales</i>
<i>Ascochyta caulina</i>	Amaranthaceae	<i>Atriplex hortensis</i> <i>Atriplex littoralis</i> <i>Atriplex patula</i> <i>Atriplex prostrata</i>
<i>Erysiphe cruciferarum</i>	Brassicaceae	<i>Cakile maritima</i> <i>Lepidium latifolium</i> <i>Lepidium ruderales</i> <i>Lepidium perfoliatum</i>
<i>Hyaloperonospora parasitica</i>	Brassicaceae	<i>Cakile maritima</i> <i>Lepidium ruderales</i>
<i>Leveillula cylindrospora</i>	Amaranthaceae	<i>Salsola kali</i> <i>Soda inermis</i>
<i>Leveillula taurica</i>	Amaranthaceae Brassicaceae Apiaceae	<i>Beta vulgaris</i> subsp. <i>maritima</i> <i>Salsola kali</i> <i>Lepidium latifolium</i> <i>Crithmum maritimum</i>
<i>Passalora spegazzinii</i>	Amaranthaceae	<i>Atriplex patula</i> <i>Atriplex hortensis</i>
<i>Perofascia lepidii</i>	Brassicaceae	<i>Lepidium latifolium</i> <i>Lepidium ruderales</i> <i>Lepidium subulatum</i>
<i>Puccinia aristidae</i>	Amaranthaceae Brassicaceae	<i>Salsola kali</i> <i>Lepidium perfoliatum</i>
<i>Stagonospora atriplicis</i>	Amaranthaceae	<i>Atriplex hortensis</i> <i>Atriplex littoralis</i> <i>Atriplex patula</i> <i>Atriplex prostrata</i>
<i>Urocystis coralloides</i>	Brassicaceae	<i>Lepidium perfoliatum</i> <i>Lepidium ruderales</i>
<i>Uromyces chenopodii</i>	Amaranthaceae	<i>Salsola kali</i> <i>Suaeda maritima</i> <i>Suaeda vera</i>
<i>Uromyces salicorniae</i>	Amaranthaceae	<i>Salicornia perennans</i> <i>Salicornia perennis</i> <i>Salicornia ramosissima</i>

Table 3. Cont.

Pathogenic Species	Host Family	Host Species
<i>Uromyces salsolae</i>	Amaranthaceae	<i>Salsola tragus</i> <i>Salsola kali</i> <i>Sida inermis</i>
<i>Verticillium dahliae</i>	Amaranthaceae Brassicaceae Portulacaceae	<i>Salsola kali</i> <i>Lepidium perfoliatum</i> <i>Portulaca oleracea</i>

At host genus level, *L. taurica* is the most heterogeneous species as it is documented on four different host genera, residing in three different families. *L. taurica* powdery mildew was reported to affect members of the family Amaranthaceae, in the host plants *B. vulgaris* subsp. *maritima* and *S. kali* [64]; Apiaceae, in *C. maritimum* [64,75,76]; and Brassicaceae, in *L. latifolium* [64]. Similarly, the wilt pathogen *V. dahliae* was described on species of three different families, corresponding to as many plant host genera. Occurrences of this pathogen were reported on *L. perfoliatum*, *P. oleracea*, and *S. kali* [92].

The rust *P. aristidae* is the only member of this group of pathogens that was described on hosts belonging to two different families, corresponding to as many host genera, namely Amaranthaceae, in *S. kali* [124], and Brassicaceae, in *L. perfoliatum* [59]. Interestingly, besides two records on Brassicaceae [59,88] (Table 2), all the other members of the order *Pucciniales* were revealed solely on species in the family Amaranthaceae.

Other pathogens with two or more host species are exclusively described on members of the same family, e.g., *A. candida*, *E. cruciferarum*, *H. parasitica*, *L. cylindrospora*, *U. chenopodii*, and *U. salsolae*, whereas others are limited to one host genus, namely *A. caulina*, *P. lepidii*, *P. spgazzinii*, *S. atriplicis*, *U. coralloides*, and *U. salicorniae* (Table 3). Interestingly, the pathogenic species found on *Atriplex* spp. are not shared among any other host taken under consideration. This is also the case for *Salicornia* spp., albeit very few records were retrieved for this halophyte and thus it is more likely to be due to insufficient information.

Finally, it is worth noting that, in this study, many of the listed pathogenic species (e.g., *A. alternata*, *G. irregulare*, *R. solani*, and *S. sclerotiorum*) are only reported once despite having an extremely broad host range. This is further proof of evidence on how research on this topic should be encouraged to widen the current knowledge about the range of hosts and distribution of these economically important pathogens.

## 6. How Fungi and Fungal-like Organisms Deal with Osmotic Stress

Like plants, microorganisms inhabiting saline ecosystems must adapt to live in such extreme environments. Osmotic stress response, either hypo- or hyperosmotic, varies among the kingdoms and fungal and fungal-like organisms are not an exception. Salinity can negatively or positively affect plant pathogens.

In the first case, which is the most common, high salt concentrations reduce the production of mycelia and conidial formation because of negative osmotic potential along with toxic and nutritional effects [198]. The growth of wilt fungi, *V. dahliae* and *Verticillium albo-atrum*, on potato dextrose agar (PDA) or Dox media declined with the increase in NaCl concentration [199,200]. Bhai et al. [201] also made similar findings in *Phytophthora capsici*. In *Fusarium oxysporum* the synthesis of gibberellic acid (GA) and indole acetic acid (IAA) showed a drastic decline when NaCl concentration was higher than 1% [202].

On the other hand, salinity can promote the growth of some plant pathogens, which is reflected in enhanced pathogen activity through increased enzymatic and cellular metabolic activities. There are some reports on the positive effects of salinity on plant pathogens. *Cercospora* leaf spot was favored by soil salinity [203] and a significant increase in mycelium growth of *Fusarium solani* by sea salt and NaCl was also observed by Firdous and Shahzad [204]. Chlamydospores of *F. oxysporum* f.sp. *vasinfectum* exhibited better growth and greater virulence on cotton in a saline medium [205]. *Sclerotium rolfsii* produced

more xylanase and galactanase with increased salt concentrations [206]. The NaCl concentration required to reduce the growth of *Pythium aphanidermatum* isolates by 50% ranged from 23 to 62 dS m<sup>-1</sup> ( $\approx$ 13.5–36.2 g L<sup>-1</sup>), with an average of 46 dS m<sup>-1</sup> ( $\approx$ 26.9 g L<sup>-1</sup>) [207]. Russo et al. [208] observed the growth of *Globisporangium irregulare* even at 32 g L<sup>-1</sup> of NaCl, which is almost the salt concentration of seawater. In general, the growth of plant pathogens under NaCl conditions leads to increased virulence and may result in adaptation to salinity over time causing the appearance of halophytic strains.

To the best of our knowledge, only a few studies have examined the physiological response of Oomycota to osmotic stress, but sensing mechanisms are not addressed.

A central role in osmoregulation was attributed to proline as a compatible solute in *Phytophthora nicotianae* [209]. High concentrations of proline were detected in sporulating hyphae, with the content being much lower in vegetative hyphae and germlings and almost null in zoospores. Incipient zoospores accumulate proline as long as they are in the sporangium lumen (a hyperosmotic environment) and release this solute as soon as they are discharged from the sporangium into a hypoosmotic environment [209]. Moreover, in *Phytophthora cinnamomi*, the switch from a hypoosmotic condition to a hyperosmotic condition resulted in an increase in proline content in hyphae [210]. Recently, Lacalendola et al. [211] have demonstrated the ability of encysted zoospores of *Achlya bisexualis* to regulate cell turgor in hyperosmotic conditions by evaluating their biomechanical responses.

On the other hand, the mechanisms of osmotic stress sensing and response are well documented in Fungi. The most detailed mechanisms of sensing are those described in yeasts and major insights are provided by the halosensitive *Saccharomyces cerevisiae* and the halotolerant black yeast *Hortaea werneckii*. This heavily melanized yeast thrives in hypersaline habitats, making it a model organism for osmotic stress, particularly salt stress, in fungi [212]. In *S. cerevisiae*, salt adaptation is mediated by the osmosensor proteins Sho1p and the histidine-kinase Sln1p [213]. In *H. werneckii*, a central role has been attributed to the homolog putative osmosensor protein HwSho1p [214] and the histidine-kinase (HK)-like osmosensor HwHK7p (*S. cerevisiae* Sln1p homolog) [215]. After sensing, cells respond to hyperosmotic changes by activating the high osmolarity glycerol (HOG) pathway, a mitogen-activated protein kinase (MAPK) pathway. The activation of the osmosensors triggers a kinase cascade, which consists of three MAPKs (MAPKKK, MAPKK, MAPK) activated by sequential phosphorylations. The last MAPK activated is Hog1p. Thus, once Hog1p is phosphorylated, it migrates into the nucleus where it triggers several genes involved in osmotic stress response [215].

In filamentous fungi, sensing and response to osmotic stress are different. In *Aspergillus nidulans*, for instance, ShoAp (Sho1p homolog) may not be involved in the activation of HogAp (Hog1p homolog) MAPK and, hence, in osmotic stress response [216]. This is due to the lack of a Pro-rich domain in the downstream MAPKK, and the activation of the HOG pathway depends on the two-component signaling (TcsBp) histidine kinase [216]. Similar findings were identified in *Fusarium graminearum* mutants lacking both *FgSHO1* and *FgSLN1*, which did not show greater sensitivity to osmotic stress compared to the wild type [217]. The same authors reported a central role for *FgSHO1* in conidiation, virulence, and deoxynivalenol biosynthesis. Similarly, in *V. dahliae*, *VdSHO1* mutants were not sensitive to osmotic stress but lost the ability for host penetration and melanin biosynthesis [218]. Conversely, in *Magnaporthe oryzae*, the causal agent of rice blast, mutants lacking *MoSLN1* showed a greater susceptibility to osmotic and oxidative stress together with a loss of pathogenicity [219]. The central role of Hog1p in osmotic stress response has been confirmed in several plant pathogenic fungi such as *F. graminearum* [220], *A. alternata* [221], *V. dahliae* [222], and *Botrytis cinerea* [223].

Regardless of differences in sensing and signaling, physiological and biochemical responses to osmotic stress are shared to a certain extent among the fungal kingdom. The main mechanisms include ion homeostasis, biosynthesis of compatible solutes, and modifications of plasma membrane fluidity. Turgor adjustment requires the maintenance of balanced ion concentration, which is achieved primarily through active transport. In addition,

Na<sup>+</sup> ions are toxic to cells, even at low concentrations. The extremely halotolerant *H. werneckii* adopts a “Na<sup>+</sup> exclusion” strategy as it can maintain very low intracellular levels of both Na<sup>+</sup> and K<sup>+</sup> ions [224]. This strategy is accomplished by active transport of Na<sup>+</sup> outside the cell, mainly through Na<sup>+</sup>/H<sup>+</sup> antiporter and Na<sup>+</sup>-exporting P-type ATPases [225,226]. Cell turgor is also maintained through the biosynthesis of compatible solutes, in particular, glycerol. In *S. cerevisiae*, glycerol biosynthetic gene *GPD1* is the main target of phosphorylated Hog1p [214]. In *H. werneckii*, two homologs of *GPD1* were identified, *HwGPD1A* and *HwGPD1B*, which are both induced by salt stress [227]. Glycerol is mainly accumulated in the exponential phase of growth, together with erythritol, arabitol, and mannitol, which instead are synthesized principally during the stationary phase [228]. The crucial role of glycerol in osmotic stress response is supported by its integration in all the above-mentioned mechanisms. For instance, *S. cerevisiae* can uptake glycerol through the H<sup>+</sup>/glycerol symporter Stl1p [229]. Genes encoding for this symporter were also found in *M. oryzae* [230]. Furthermore, due to its chemical properties, glycerol is easily leaked from the plasma membrane, forcing cells to adopt strategies to keep proper fluidity while avoiding excessive leaking. To do this, *H. werneckii* embeds melanin into the cell wall, increasing its ability to retain this compatible solute [231]. The main modifications in plasma membrane composition are a higher unsaturation level of the lipidic bilayer and the promotion of phosphatidylcholine and phosphatidylethanolamine biosynthesis [232]. Contrary to what was found in *H. werneckii*, salt-exposed *S. cerevisiae* cells increase the sterol-to-lipid ratio in the membrane [233].

## 7. Conclusions

In the examined bibliography on major Mediterranean halophytes, only a few studies have investigated host–pathogen associations in cultivated plants (apart from artificial inoculation trials), and, in most documents, host plants were collected in the wild, as part of checklists, or they represented hosts for type specimens of pathogenic species. Most of the pathogenic species have been isolated from above-ground organs, especially leaves. In particular, in genera *Atriplex*, *Beta*, *Cakile*, *Crithmum*, *Salicornia*, *Soda*, and *Suaeda*, only foliar diseases were recorded.

It is probable that several other pathogens have been neglected, as plants can be exposed to different pathogens when they grow in the wild or are cultivated. Apart from *Salicornia* spp. and *S. inermis*, the consumption of other halophytic species is mainly linked to ethnobotanical traditions, and this explains the limited bibliography on the topic. However, if we intend to turn these species into market-oriented crops, to eliminate the risks of foraging, the responsibility of production must lie with experienced growers. Hence, growing protocols must be implemented, including pest and disease management. This aspect is highlighted by those cases in which highly specific pathogens have been isolated (for example, the pathosystems *Peronospora* spp./*Atriplex* spp. and *A. candida*/*Lepidium* spp.), which are not related to major crop pathogens. They are genus- or even species-specific pathogens that can represent a reservoir of new diseases to which greater attention should be paid. In the optic of agricultural exploitation of these species, it is fundamental to assess the occurrence of pathogens to develop accurate control strategies. On the other hand, halophytes can be secondary hosts for pathogenic species and represent a significant source of inoculum for important pathogens of important crops. Moreover, some species can promote the spread of pathogens through the dissemination of infected organs (e.g., infected seeds as in *Alternaria* sp./*C. maritima*). In this regard, the pathosystem *A. alternata*/*C. maritima* is of pivotal importance, as it is the only host/pathogen binomial investigated in salinity conditions. In the study, the presence of salt was associated with reduced susceptibility of the host toward the pathogen. The role of salt in disease development is a key aspect that needs to be deepened as this abiotic factor can affect the virulence and the production of secondary metabolites in plant pathogenic species. Therefore, boosting research on plant diseases of halophytic plants is crucial to identifying novel diseases and better understanding the spread of pathogenic species.

Finally, if halophytic plants are intended for consumption, it is essential to evaluate the risks associated with the presence of mycotoxigenic species.

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