

Review

# Disentangling the Belowground Web of Biotic Interactions in Temperate Coastal Grasslands: From Fundamental Knowledge to Novel Applications

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**Abstract:** Grasslands represent an essential part of terrestrial ecosystems. In particular, coastal grasslands are dominated by the influence of environmental factors resulting from sea–land interaction. Therefore, coastal grasslands are extremely heterogeneous both spatially and temporally. In this review, recent knowledge in the field of biotic interactions in coastal grassland soil is summarized. A detailed analysis of arbuscular mycorrhiza symbiosis, rhizobial symbiosis, plant–parasitic plant interactions, and plant–plant interactions is performed. The role of particular biotic interactions in the functioning of a coastal grassland ecosystem is characterized. Special emphasis is placed on future directions and development of practical applications for sustainable agriculture and environmental restoration. It is concluded that plant biotic interactions in soil are omnipresent and important constituents in different ecosystem services provided by coastal grasslands.

**Keywords:** arbuscular mycorrhiza; ecosystem services; coastal grasslands; parasitic plants; plant–plant interaction; resilience; rhizobial symbiosis; signal transfer



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## 1. Introduction

Grasslands form a large and essential part of terrestrial ecosystems in terms of occupied area as well as for both biodiversity maintenance and functional importance. Thirty years of progress in grassland ecosystem research has been reviewed recently, and it was revealed that grassland ecology and grassland ecosystem services were among the two most productive directions of research [1].

There is no doubt that grasslands are hotspots of plant diversity and important components of ecosystem service. In particular, carbon sequestration potential in grassland soils has been recently addressed and its global role has been emphasized [2]. Most importantly, interactions between plant and microbial diversity were recognized as the main driving force in carbon storage. Recently, there have been more attempts to make functional generalizations of grassland existence related to changes or gradients of environmental factors. For example, the belowground characteristics of plants—presence of clonal growth organs, vegetative buds, fine root spread—have been related to the degree of water availability in grasslands [3]. There has been an increasing awareness of the fact that precisely functional interactions involving plants and their diversity are important drivers of plant distribution and multiple ecosystem services in grasslands [4,5].

Among different grassland types, coastal grasslands are unique in that they are habitats where the influence of marine and terrestrial determining factors combine. On the other hand, both coastal areas and grasslands are important in their own right from the point of view of global ecosystem functioning. Conservation of coastal habitats in Europe has been an object of continuous scientific attention in the recent decades [6]. In a broader context, coastal habitats in general and coastal grasslands in particular play an important role in providing ecosystem services. Much attention has been focused on analysis of ecosystem

services in the context of grasslands [7]. However, coastal grasslands have often remained underrecognized in the analysis of European grasslands [8].

Biotic interactions in soil have been a relatively understudied aspect of functioning of coastal grasslands, but considerable evidence on adaptive importance of these interactions has accumulated from studies performed in other grassland types as well as in controlled conditions. For example, microbial symbioses with plants have been emphasized for their importance both in vegetation establishment and resilience [9]. Moreover, the contribution of biotic interactions to ecosystem services in general is an aspect that is not widely recognized. However, several aspects of changes in ecosystem services provided by coastal grasslands have been analyzed, including abandonment of grazing [10].

Within the framework of this review, an attempt will be undertaken to clarify whether there is a reason to believe that biotic interactions in the soil are determinants of the diversity and resilience of coastal grasslands and if these interactions can make a significant contribution to ecosystem services. In particular, answers will be sought for the following questions: (i) what types of biotic interactions with possible effects on vegetation composition, productivity, and resilience in coastal grasslands exist; (ii) why biotic interactions in coastal grasslands are important for ecosystem services; (iii) what future studies are necessary, and what are the perspective practical applications?

## 2. Heterogeneity of Environmental Conditions in Coastal Grasslands

In this section, it will be briefly analyzed how coastal grasslands differ from the other types of grasslands and why these differences are important for biotic interactions in soil. Except location in the immediate vicinity of the seashore and presence of grass and legume species, the definition of “coastal grasslands” might seem like an artificial construct, mostly because of the high heterogeneity of environmental factors leading to extreme diversity and fragmentation of coastal grassland habitats. Primarily, both spatial and temporal variability in soil edaphic conditions have been studied in coastal habitats, and they also clearly affect biotic interactions in the soil [11,12]. On the other hand, it is likely that it is the heterogeneity of soil conditions that accounts for the remarkable diversity in plant species that generally characterizes European temperate grasslands [13]. In addition, it has been suggested that grasslands with higher richness in plant species can buffer the negative effects of environmental heterogeneity on productivity [14].

Unlike other types of grasslands, coastal grasslands are dominated by the influence of environmental factors resulting from sea–land interaction. Analysis of these factors is beyond the scope of this review, but it is necessary to understand how the main types of coastal grasslands are formed due to differences in prevailing conditions. In general, substantial differences in water regime related to geomorphological and littoral processes determine the formation of two main types of coastal grasslands. Dune systems are formed on sand-accumulating active coasts, whereas grasslands form as a continuation of fixed dunes, and the most characteristic dominant environmental factor is drought. On less active non-accumulating shores, grasslands form as a continuation of salt marshes or may already be found in the beach area.

As a result, dominating environmental conditions in fixed-dune-associated and salt-marsh-associated coastal grasslands are fundamentally different. To a large extent, this applies to the soil moisture regime (drought vs. flooding) and potential exposure to salinity (occasional surface spray with seawater vs. periodic inflow of saltwater). In any case, coastal grasslands are subject to sharp fluctuations in environmental conditions over time and large spatial variations even over short distances, and in general form a highly dynamic and heterogeneous system. From the perspective of functional analysis of coastal grasslands, such differences explain the fact that conventionally dry (associated with dunes) and relatively wet (associated with beach or salt marshes) grasslands are considered separately.

A European-scale study has confirmed that dune perennial grasslands are significantly affected by local climatic conditions, resulting in differences in plant species composition

and distribution [15]. Mean annual temperature and mean annual precipitation appeared to be the main climate variables affecting floristic variability and community structure. Seven groups of grasslands in different geographical areas have been identified from north to south along an increasing temperature gradient, namely Baltic, North Sea, Atlantic, North Adriatic, Black Sea, South Atlantic, and Mediterranean–Atlantic. It appears that dry coastal grasslands associated with fixed dunes are more vulnerable to global climate change as rising temperature and changes in precipitation patterns can significantly affect species distribution, composition, and abundance [15]. For example, air-borne nitrogen deposition in stable dune grasslands results in a drastic decline in herbaceous species at the expense of dominance of fast-growing grass species [16].

There is not much research on the relationship between environmental heterogeneity in coastal habitats and plant taxonomic and functional diversity [17], but recent attention has at least focused on general aspects of environmental heterogeneity in terms of ecosystem services [18].

### 3. Diversity in Biological Interactions in Coastal Grasslands

Diversity in microbial interactions in coastal soils and important functional aspects for vegetation establishment and maintenance have been reviewed recently [19]. It is important to note that the main dichotomy between dune- and wetland-associated grasslands in the coastal zone is also reflected by major differences in microbial processes. While sea-water-affected wetland grasslands are characterized by high microbial activity and a high rate of mineralization of organic matter [20], microbial processes in dry grasslands are less active [21]. The complexity of the ongoing microbial processes and their dependence on the heterogeneity of conditions are characterized by ambiguous changes under the influence of complex environmental factors. For example, functional aspects of the nitrogen cycle in coastal habitats are especially affected by the influence of saltwater inflow. While flooding itself results in higher denitrification activity [20], an increase in salinity in freshwater-adapted wetlands leads to a decrease in denitrification rates [22]. However, in saltwater-adapted wetlands, the opposite effect may be observed, namely that intermediate salinity results in an increase in denitrification activity while freshwater intrusion results in almost complete loss of denitrification capacity [23]. These results point to the existence of special adaptation of a consortium of denitrifying microorganisms to a specific salinity level and indicate that hypersaline soils can be used as a source of such resistant strains for practical purposes.

It seems that decomposition of organic matter in coastal grasslands is similarly exposed to the effects of moisture regime and salinity. A community of saprotrophic fungi is a main decomposer of organic matter in grasslands, but bacterial decomposers participate mainly in degradation of relatively labile compounds [24]. Most importantly, microbial communities dominated by fungi shift to bacterial dominance as a result of increased salinity [25]. Many microorganisms involved in decomposition of organic matter produce biologically active substances with beneficial effects on plant growth as hormone-like substances or elicitors of defense responses [26]. There is no doubt that free-living microorganisms are important both for establishment of vegetation in coastal habitats as well as in adaptation of plants to heterogeneous conditions [27], but the main focus of the present review is on symbiotic interactions between plants and microorganisms and on plant–plant relationships, including the ones with parasitic plants.

Aside from mycorrhizal fungi, microbial endophytes represent another group of organisms forming intimate relationships with plants. In particular, fungal endophytes are considered to be important in adaptive responses, including abiotic stress tolerance [28]. However, in order not to complicate the picture and also considering the fact that endophytes are found in all parts of the plant, not only in the soil-bound roots, this aspect of the biotic interaction will not be further analyzed.

## 4. Mycorrhizal Symbiosis in Coastal Grasslands

### 4.1. Mycorrhizal vs. Non-Mycorrhizal Plants

For relevant information regarding classification of mycorrhizal associations, as well as characterization of functional aspects of mycorrhizal symbiosis, readers are invited to consult recent articles [29–31]. It needs to be mentioned, however, that, in grassland habitats, arbuscular mycorrhizal symbiosis is of primary importance, but there are also other types of mycorrhiza present, such as orchid mycorrhiza.

Most importantly, in order to understand the importance of mycorrhizal symbiosis, we should first determine whether mycorrhizal symbiosis is a widespread phenomenon in coastal grasslands. On the one hand, abundance, frequency, and anatomical diversity in mycorrhizal associations have been assessed in different coastal habitats, including grasslands [32]. On the other hand, a number of studies show the importance of mycorrhizae in the adaptation of plants to environmental factors, which are characteristic of coastal grasslands. For example, there is a considerable amount of research on the importance of mycorrhizal symbiosis in halophytes and its potential to increase salt tolerance in glyco-phytes. Interestingly, the first observations on mycorrhizal symbiosis in wild plants were from studies in coastal salt marshes and included several halophytic species [33].

One of the problems in assessing the functional importance of mycorrhizae in coastal grasslands is related to the limited universal nature of mycorrhizal symbiosis. This manifests as a low mycorrhizal intensity in different situations or even the appearance of non-mycorrhizal plant taxa. It needs to be emphasized that it is generally accepted that a relatively low degree of root mycorrhization does not automatically mean little functional importance, and, since the intensity of symbiosis is a highly variable quantity, it is easy to overlook the situation when individuals of a given plant species show significant signs of mycorrhization. Thus, even species described as non-mycorrhizal, such as *Triglochin maritima*, showed mycorrhizal structures in roots, such as vesicles and arbuscules, suggesting the presence of functionally active symbiosis but with relatively low intensity [32]. However, this species did not show any signs of mycorrhizal colonization in the previous studies [34], and genus *Triglochin* has been considered to be non-mycorrhizal [35]. Seasonal changes in mycorrhizal colonization showed that, in roots of *Triglochin maritima*, plants' intensity of mycorrhizal symbiosis increased from less than 5% in May to 25% in July, but the presence of arbuscules was very low in May and June but increased to 15% in July, reaching 25% in September [11]. Therefore, it can be hypothesized that the two dominant environmental factors are associated with the low intensity of mycorrhizal symbiosis on plants in relatively moist coastal grasslands, namely high salinity and soil flooding. These aspects will be analyzed further.

Given the fact that several plant families with significant halophyte occurrence (Asteraceae, Brassicaceae, Chenopodiaceae, Carophyllaceae) have been reported as essentially mostly non-mycorrhizal [35], the question of the general importance of mycorrhizal symbiosis in salt-affected habitats remains open.

### 4.2. Mycorrhizal Fungal Community Structure

Assessment of genetic diversity in arbuscular-mycorrhiza-forming fungal communities is an important aspect of microbial ecology. Because mycorrhizal fungi are associated with particular plant species and are subject to seasonality and environmental conditions, both the diversity and occurrence of mycorrhizal fungi are highly variable. Ecosystem-level comparison of different studies on the community structure has revealed that some Glomeromycota taxa are found globally, while others can be found only in certain ecosystems [36]. Ecological aspects of arbuscular mycorrhizal symbiosis in halophytic plant species have been reviewed, and it has been suggested that diversity in mycorrhiza-forming fungi seems to be more complex than usually assumed [37].

Only some studies so far have addressed community structure of mycorrhizal fungi in coastal grasslands. Using mycorrhizal roots of a single common plant species, *Hieracium pilosella*, high spatial diversity in fungal phylotypes was found in a sandy coastal grass-

land [38]. However, even a single root fragment from an individual plant contained almost all genetic variation found within the whole area. Most importantly, it was shown that there is a possibility that a single individual non-sporulating mycelium might cover an area at least 10 m in length. In another study, it was tested if the dominant mycorrhizal fungal strains found in roots of *Hieracium pilosella* can colonize individuals of other abundant plant species, *Hypochaeris radicata*, *Thymus serpyllum*, *Artemisia campestris*, and *Armeria maritima* [39]. As was expected, the dominating strains were found in root fragments of all five plant species but with spatial differences in intensity of occurrence. Therefore, it was concluded that presence of dominant fungal strain is an indication of presence of interconnecting mycelial mycorrhizal network in a coastal grassland.

The effect of changes in various environmental factors on the structure of mycorrhizal fungal communities in coastal grasslands has been studied very little. It should be assumed that the heterogeneity of dominant factors significantly affects this structure. Thus, changes in community structure of AM fungi have been assessed in respect to reclamation of saline coastal lands, and it was shown that vegetation succession following reclamation results in a decrease in overall fungal diversity and a shift from dominance of Acaulosporaceae and Gigasporaceae to Glomeraceae [40]. In salt-affected coastal plains, the community structure of arbuscular mycorrhizal fungi was strongly affected both by soil salinity and pH [41]. In a coastal dune ecosystem, diversity in mycorrhizal fungi was clearly segregated between the seaward (wind-disturbed) and landward (stabilized) slopes of dunes [42]. Therefore, it was concluded that zonal distribution of both abiotic and biotic (including host plant species) factors are determinants of the fungal community structure.

In addition, apart from genetical diversity, functional variability of mycorrhizal fungi seems to be important for the outcome of the effectiveness of the symbiotic relationship. Thus, it was shown that even communities of arbuscular mycorrhizal fungi with relatively low diversity may have significant functional heterogeneity [43]. Such characteristic features refer both to the nature of hyphal growth pattern and the intensity of mineral uptake, and they could also be important in maintaining the diversity in coastal grasslands, especially in mineral-poor soils, such as dune-associated grasslands.

#### 4.3. Mycorrhizal Symbiosis in Resource Acquisition

It is generally accepted that typical mycorrhizal plants provide fungal partners with sugars and vitamins, receiving in return water and minerals, mostly N, P, and K [44,45]. However, terrestrial orchid species have so-called mixotrophic type of nutrition and are dependent on the mycorrhizal partner at certain stages of development and receiving sugars and vitamins from it. Nutrition of mycoheterotrophic achlorophyllous plants occurs in the same way. Due to the potentially beneficial effect of the interaction on both partners, mycorrhizal symbiosis is designated as mutualistic and therefore essentially positive.

However, it must be remembered that mycorrhizal symbiosis is not always entirely mutualistic. While usually both partners benefit from the interaction, a continuum of mutualism–parasitism exists in nature [46]. The relationship can be shifted towards parasitism due to the genetic specificity of the particular plant–fungus interaction, or it can be induced by plant developmental stage or environmental factors. Some studies performed with grassland species in controlled conditions indicate that the nature of the mycorrhizal interaction may change differentially depending on the specific situation. Typical grassland species differentially responded to mycorrhizal colonization depending on their relative abundance: dominant species *Taraxacum officinale* and *Agrostis capillaris* were more negatively affected by parasitic-oriented strain of *Glomus intraradices*, but less abundant (subordinate) species *Prunella vulgaris* and *Achillea millefolium* were not negatively affected by the fungus [47]. Thus, plant hierarchy in grasslands can be significantly affected by the presence of particular taxa of mycorrhizal fungi. Moreover, mycorrhizal association of *Hieracium pilosella* was clearly beneficial, while it was parasitic for *Corynephorus canescens*, especially under species competition [48]. Both high available P concentration in soil and shade shifted mycorrhizal interaction from mutualistic to parasitic, showing that the costs

of C sent to symbiont exceeded the benefits from increased mineral nutrient availability in these conditions. In this respect, it would be important to determine how the saltwater inundation characteristic of wet coastal grasslands affects the mycorrhizal dependence of different plant species relative to the mutualism–parasitism continuum, especially given the differences in salinity tolerance of various plant species.

#### 4.4. Common Mycorrhizal Networks

The concept of common mycorrhizal networks (CMNs) has gained much scientific interest within recent decades [44,45,49–53]. However, due to obvious technical difficulties, experimental evidence for existence of CMNs in nature is still scant. Instead, studies of varying degrees of complexity are conducted in different model systems under controlled conditions.

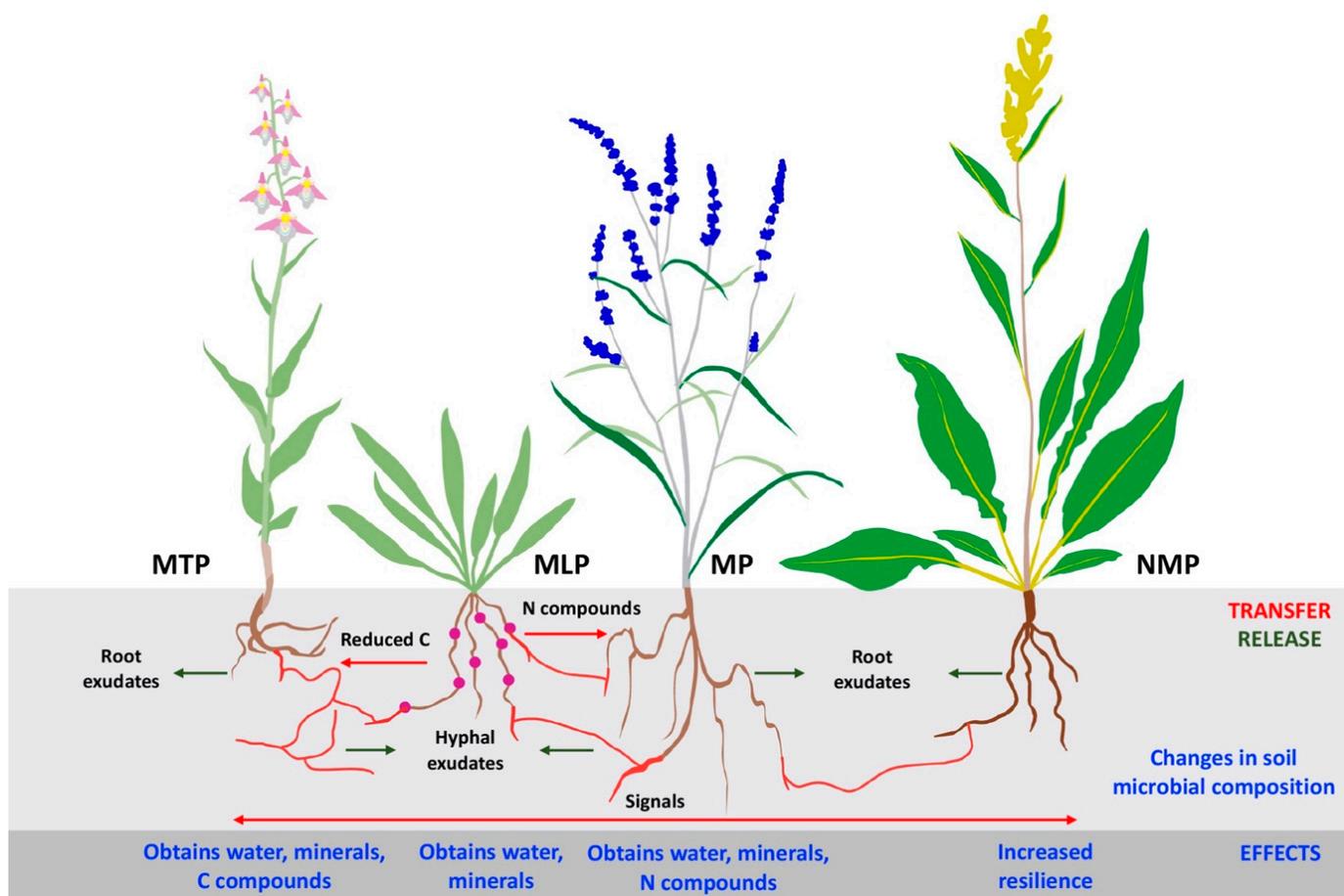
Historically, insights into mycorrhizal hyphal associations between multiple plants began with observations of the specific type of nutrition of achlorophyllous parasitic plants, mycoheterotrophy, where reduced carbon substances are received from a mycorrhizal partner, associated with an autotrophic plant [54]. Later, with the discovery of the presence of long-branched extraradical hyphae present in both ectomycorrhizal and arbuscular mycorrhizal associations, the understanding of the potential globality and functional importance of the mycorrhizal network expanded significantly.

The importance of non-mycorrhizal plants (non-host plants) in CMNs has been recently reviewed [55]. In particular, it was concluded that only fungal hyphae from already established mycorrhizal symbiosis can penetrate roots of non-host plants, without formation of any characteristic symbiotic structures. Usually, non-host plants are negatively affected by this type of interaction, and effects on systemic resistance are highly likely.

In contrast to unidirectional movement of mineral nutrients towards host plants, water transport in CMNs is bidirectional and changes during the day [45]. Similarly, it is proposed that movement in signaling substances by means of CMNs can occur in different directions [45]. Carbon cycling has been shown to occur in ectomycorrhizal CMNs but is still controversial in respect to AM networks [50,56]. Therefore, it seems that, apart from some specific situations (as in the case of mycoheterotrophic and mixotrophic associations), CMNs are less important as a mechanism for sharing mineral resources between symbiotic plants but rather act as means for information exchange between plants. Thus far, most evidence on the importance of mycorrhizal networks in plant communication is associated with studies on ectomycorrhiza-dominated ecosystems [51]. It has been proposed that stress-associated signals are transmitted more quickly through CMNs if compared to transfer of resources [56]. However, the chemical nature of the signals is far from clear. Initially, it was proposed that plant hormones salicylic acid and jasmonic acid are involved in the transfer of information through CMNs [57]. Recently, scientific information has begun to accumulate that small RNAs can be involved in important aspects of mycorrhizal symbiosis [58–60], but evidence for their role in signaling through CMNs is still lacking.

Moreover, recently, a term “hyposphere” was coined to describe a zone of soil around mycorrhizal hyphae where release of hyphal exudates results in establishment of specific abiotic and biotic conditions [61], forming similar differences from the bulk soil as in the case with the rhizosphere. Similar to exudates from plant roots, exudates from fungal hyphae also have an impact on bacterial diversity and abundance [61].

Continuum of specificity of mycorrhizal fungi is an important aspect to consider in respect to development and function of CMNs [52]. Overlap of host plant compatibility for a particular fungal strain is a critical characteristic for formation of functional CMNs, and, usually, this feature is found for dominant fungal taxa. Therefore, it is logical to assume that dynamics of plant communities are strongly dependent on functioning of CMNs, but empirical evidence for coastal grasslands is still not available. Potential mycorrhiza-related plant interactions in coastal grasslands are shown in Figure 1.



**Figure 1.** Mycorrhiza-related interactions in coastal grasslands. MTP, mixotrophic plant species; MLP, mycorrhizal legume plant species; MP, mycorrhizal plant species; NMP, non-mycorrhizal plant species. Mycorrhizal root fragments and mycorrhizal hyphae are shown in red.

#### 4.5. Mycorrhizal Symbiosis in Environmental Resilience

The issue of plant adaptation to heterogeneous environmental conditions is particularly important in grassland systems that are subject to sharp fluctuations in environmental conditions, such as coastal grasslands. The presence of mycorrhizal symbiosis in coastal plants has led to the idea of the importance of this type of symbiosis in plant adaptation. However, there has been a scientific debate on which partner of mycorrhizal symbiosis is more vulnerable to environmental constraints, plant host or fungal symbiont? Because there is a concept that mycorrhizal symbiosis is important for the plant to overcome environmental extremes, one might think that the fungal partner is the stronger side in this respect. There is no doubt that, similar to plant species specificity in tolerance to particular environmental factors, mycorrhizal fungal species and strains also differ in their ability to tolerate unfavorable conditions. Indeed, different mycorrhizal fungal species and strains show a wide range of tolerance to one of the dominant environmental constraints in coastal grasslands, soil salinity [62]. More specifically, spore germination was delayed in the presence of NaCl, and, in some cases, the spores did not germinate at all in saline conditions, but, in others, they reached a maximum germination in the presence of 300 mM salt. Similarly, the rate of hyphal extension of some fungal taxa was even stimulated in the presence of 150 mM NaCl, but, in general, salinity inhibited hyphal growth to a varying extent.

Field studies of mycorrhizal symbiosis associated with halophytic plant species in highly saline habitats and often extremely variable moisture levels have usually revealed

the presence of functionally active mycorrhizal structures in their roots, however with variable colonization intensity. Examples of such studies are from Tabriz Plain in Iran [63], Central European salt marshes [34] (Hildebrandt et al. 2001), Sečovlje solar salterns in Slovenia [64], and saline soils in Hungary [65]. Seasonal trends in mycorrhizal colonization have been assessed for halophytes in Hungarian steppe habitats [66] and in saltwater-affected wet grassland [11]. The results of these studies suggest that intensity of root colonization is indeed negatively affected by increasing soil salinity, but number of fungal spores does not depend on the level of salinity. It also seems that environmental factors that have an impact on host plant physiology also affect fungal symbionts.

Both diversity and composition of mycorrhizal fungi only marginally differed between halophyte and non-halophyte species growing on salt-affected coastal plains [41]. In a typical halophyte species well-adapted to intermediate and high salinity, such as *Tripolium pannonicum* (syn. *Aster tripolium*), early stages of symbiotic interaction were more negatively affected by salinity in comparison to expansion of root colonization [67]. On the other hand, seasonal changes in intensity of mycorrhizal colonization in roots of several halophyte species growing in salt-affected grassland (*Aster tripolium*, *Glaux maritima*, *Plantago maritima*, *Trifolium fragiferum*, *Triglochin maritima*) showed negative dependence on fluctuations of soil salinity [11].

A number of entirely practically oriented studies on improvement in salinity tolerance in glycophytic crop species as a result of mycorrhizal fungi application are available, indicating that the use of salt-tolerant fungal strains has great practical potential. Such strains could be isolated from the rhizosphere of salt-affected coastal grassland soils. In particular, mycorrhizal inoculation increased plant growth under saline conditions for *Gossypium arboreum* [68], *Pennisetum glaucum* [69], *Zea mays* [70], *Triticum aestivum* [71], *Lactuca sativa* [72], *Lens culinaris* [73], and *Ocimum basilicum* [74]. In some studies, it has been stressed that the fungal strains used were isolated from saline habitats [70]. In one case, effect of two isolates of *Glomus mosseae*, either from non-saline or saline soil, were compared, and it was shown that, contrary to what was initially expected, the isolate from non-saline soil had a higher capacity to alleviate negative effects of salinity [68].

Similar experiments in controlled conditions have been performed also with some halophyte species. Thus, it was shown that mycorrhizal plants of grass species *Puccinellia distans* had better growth potential under saline conditions due to enhanced photosynthesis and improved ion homeostasis [75]. In addition, mycorrhizal symbiosis affected accumulation of osmotically active mineral elements, allowing to avoid uptake of Na [76]. In particular, for *Trifolium alexandrinum*, increased phosphorus uptake in mycorrhizal plants was associated with their better growth in saline conditions [77]. Nine psammophilic species native to coastal sand dunes and evidently adapted only to salt spray were tested for their ability to recover after repeated seawater treatment in controlled conditions when inoculated with mycorrhizal fungus *Glomus intraradices* [78]. The intensity of the survival-promoting effect of mycorrhizal colonization was a distinctly species-specific feature. On the positive side, mycorrhizal *Ammophila arenaria* plants showed less than 20% mortality after fourth application of 100% seawater concentration, while all non-mycorrhizal plants died after the third application of 100% seawater. From the worst side, mycorrhization of *Dorycinum pentaphyllum* plants only marginally improved their survival under diluted seawater treatment. However, both species showed similarly high mycorrhizal dependency and high intensity of root colonization by mycorrhizal fungus.

Soil flooding, either with fresh water or seawater, represents another common environmental factor in low-lying coastal grasslands. A number of practically oriented studies on flooding tolerance of mycorrhizal plants have been performed, including seedlings of *Citrus sinensis* [79], *Prunus persica* [80,81], *Pterocarpus officinalis* [82], and showing the overall beneficial effect of mycorrhization on flooding tolerance. Improved mineral nutrition, proline production, and suppression of ethanol production in roots during anoxic conditions were among the mechanisms responsible for growth improvement due to mycorrhizal symbiosis in flooded conditions. However, in a study with *Oryza sativa*, it was shown that, while

symbiosis activated the phosphorus uptake pathway in a fungal partner, it suppressed phosphorus uptake of the host plant [83]. As a result, mycorrhizal colonization decreased shoot phosphorus content in flooded conditions, and the effect of symbiosis was negative.

Closer to the topic of this review, two grass species (*Panicum hemitomon* and *Leersia hexandra*) native to nutrient-poor depressional wetlands in the southeastern USA coastal plain were used in a wetland mesocosm experiment to determine if controlled water regimes affect mycorrhizal colonization as well as if colonization affects plant growth [84]. It appears that intensity of mycorrhizal colonization decreases with increasing water levels even for species well adapted even to semi-aquatic conditions. However, mycorrhizal viability was not negatively affected, and symbiotic plants had higher phosphorus uptake even under flooded soil conditions in comparison to non-mycorrhizal plants. Mycorrhizal colonization of the same two grass species was assessed in field conditions along a hydrological gradient, and it was evident that the degree of root colonization decreased with water depth, but this did not affect number of mycorrhizal propagules in soil [85]. However, even plants growing in permanently flooded soil retained active mycorrhizal symbiosis in roots. Similarly, the number of hyphae and spores in soil with *Zea mays* plants was not affected by extended flooding in controlled conditions [86]. Other studies also supported the idea that flooding negatively influences root colonization with arbuscular mycorrhiza, but basic symbiotic functionality is not affected [67,87]. Similarly, in halophyte *Aster tripolium* plants, better tolerance of mycorrhizal plants to flooding was associated with improved osmotic balance and nitrogen uptake [88].

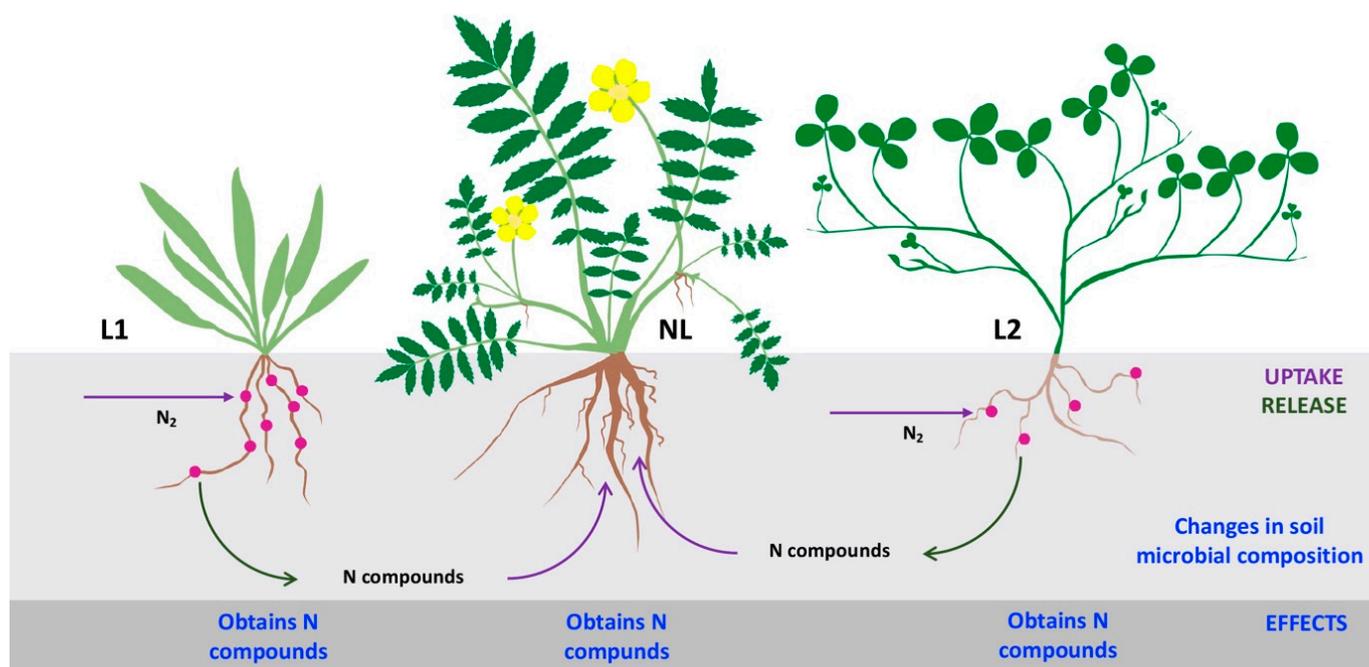
A field study along a tidal gradient in a mangrove swamp indicated that duration of flooding period mainly affected the community structure of arbuscular mycorrhizal fungi and resulted in increased intensity of mycorrhizal colonization [89]. When aquatic species *Polygonum hydropiper* and semiaquatic species *Panicum repens* grown under different hydrological regimes were compared in respect to mycorrhizal colonization and mycorrhizal community structure in natural conditions, it appeared that high flooding intensity led to a decrease in both mycorrhizal intensity and diversity level in both species [90]. However, moderate flooding resulted in an increase in mycorrhizal colonization and fungal species richness only in aquatic species *Polygonum hydropiper*. Recently, the role of arbuscular mycorrhizal symbiosis in wetland plants has been reviewed, and it was concluded that survival and development of these plants in native conditions is highly dependent on mycorrhizal colonization [91].

It is difficult to generalize a potential role of mycorrhiza in respect to plant adaptation to soil moisture regime in coastal grasslands due to extreme variability in this factor across different coastal grassland habitats. However, it is evident that soil moisture regime is a significant determinant of both mycorrhizal community structure as well as intensity of symbiosis and its functional properties [92]. On the other hand, there is no doubt that mycorrhizal symbiosis modulates morphological and biochemical adaptations of drought-stressed plants, as summarized in the recent reviews [93,94]. As mycorrhizal colonization usually results in formation of induced systemic resistance of host plants [95], further studies of specific responses to drought in mycorrhizal vs. non-mycorrhizal coastal grassland plants are needed.

## 5. Rhizobial Symbiosis in Coastal Grasslands

Legume plant species (Fabaceae) are of special importance both in natural as well as agroecosystems due to symbiosis with N<sub>2</sub>-fixing bacteria. Rhizobial symbiosis in wild legume plants provides an important contribution to the nitrogen cycle on Earth, being a part of the biological nitrogen fixation process. From an ecological point of view, shortage in plant-available nitrogen is one of the factors limiting plant growth in heterogeneous habitats, such as coastal dunes and dune grasslands [96], and both plant community structure and productivity are affected by symbiotic rhizobia in these habitats [97]. Additionally, rhizobia-legume symbiosis is the major type of N acquisition into soil of arid ecosystems [98]. From the perspective of sustainable agriculture, inclusion of legumes in crop sequences

allows additional fixed nitrogen to accumulate in the soil, increasing plant-available N pool and in general benefiting non-legumes cultivated in subsequent years and allowing to decrease application of N-based chemical fertilizers [99]. This allows for efficient use of low-input agricultural systems. In addition, factors not related to N are also important for soil sustainability, possibly related to nodule-emitted hydrogen, with further effects on soil microbial diversity [100]. It is also becoming clear that tolerance of legume crop species to adverse environmental conditions can be positively affected by rhizobial symbiosis [101]. This aspect is especially important due to global climate change and its negative impact on agricultural productivity. Possible rhizobial-symbiosis-related interactions in coastal grasslands are shown in Figure 2.



**Figure 2.** Rhizobial-symbiosis-related interactions in coastal grasslands. L1, L2, symbiotic legume plant species; NL, non-legume species.

Rhizobial bacteria (Pseudomonadota:  $\alpha$ -proteobacteria and  $\beta$ -proteobacteria) are Gram-negative soil bacteria. As facultative symbionts, rhizobia are freely living in soil (resident rhizobia) but are able to benefit from forming symbiosis with legume species as N<sub>2</sub> fixation occurs only in symbiotic rhizobia. Competition among soil-resident rhizobia for nodule formation can lead to formation of completely or partially inefficient N<sub>2</sub> fixation as rhizobial strains with high competitive ability might have low N<sub>2</sub> fixation efficiency. Therefore, it is always necessary to distinguish between nodulation specificity (an ability to infect a legume to form a nodule) and effectiveness of N<sub>2</sub> fixation (an ability of formed nodules to fix N<sub>2</sub>). Nodulation specificity seems to be associated with modulation of plant immunity as a result of developing interaction between the partners [102]. By this mechanism, hosts can restrict nodulation by even potentially efficient symbionts, resulting in nodule formation with inefficient symbionts leading to parasitic type of interaction [103].

It appears that nodulation specificity and intensity are determined mainly by a host plant [104]. Host plants are able to select microorganisms from bulk soils both at the taxonomic and functional level [105]. Some rhizobia have very high host specificity, such as the ones forming nodules only on *Cicer arietinum*, having highly conserved genes involved in both nodulation and N<sub>2</sub> fixation [106]. Some legume hosts (such as *Glycine max* and *Sophora flavescens*) have very low specificity for rhizobia, being nodulated by various rhizobial species possessing diverse symbiosis-associated genes [107]. In addition, soil factors (edaphic factors) can further modulate the outcome of the established symbiosis and

also can have an effect on nodule microbiome, such as, for example, in the case of soil pH and *Trifolium* species [108]. Moreover, the importance of plant community effects cannot be ruled out [109]. On the other hand, metabolically more versatile rhizobial strains, being capable to use a wide range of energy-providing substrates, are usually more competitive in contrast to metabolic specialist strains [110]. For *Trifolium* and other legume genera, strains with effective N<sub>2</sub> fixation have been shown to be more competitive for nodule occupancy [111,112].

Critical soil conditions (such as low soil moisture, salinization, soil waterlogging, etc.), whose likelihood of occurrence continues to increase due to global climate changes and overall anthropogenic pressure, are likely to negatively affect symbiotic N<sub>2</sub> fixation in legume crops [101]. Many rhizobial strains native to local soils or commercially produced rhizobial products have low efficiency or even low viability in unfavorable conditions; therefore, they will not provide efficient contribution to the soil N pool necessary for sustainable agricultural production or to increase soil fertility. Isolation of resilient rhizobial strains will allow to develop new bacterial products suitable for problematic soils and highly heterogeneous environmental conditions. Use of local bacterial isolates adapted to particular (local) environmental and soil conditions is especially desirable for this purpose. Such an approach can possibly prevent so called ‘rhizobial competition problem’, when rhizobial strains effective in controlled conditions fail to be successful in field conditions, being outcompeted by highly nodulating but inefficient indigenous soil bacteria better adapted to local conditions [113,114].

In the ecological context of ecosystem functioning, there is a reason to believe that rhizobial symbiosis in coastal grasslands acts as an important determinant factor in interactions both between plant species as well as between plant species and their environment. While principal empirical evidence exists for the critical role of rhizobial symbiosis in determining both plant productivity and community structure in dune-associated coastal grassland derived from microcosm studies [97], similar information is sparse for salt-affected wetland grassland systems. However, separate studies have shown the ability of rhizobial symbiosis to promote growth of legume plants under salinity conditions. Thus, dual inoculation with mycorrhizal fungi and rhizobium stimulated growth and improved mineral nutrition of salt-stressed *Lathyrus sativus* plants [115]. Moreover, extreme tolerance of grassland species *Lotus tenuis* to drought, waterlogging, and salinity has been associated with its ability to form early associations both with rhizobia as well as arbuscular mycorrhizal fungi [116].

Recently, two experiments in controlled conditions have been performed with two coastal legume species, *Trifolium fragiferum* from salt-affected wet grassland [117] and *Anthyllis maritima* from dry dune grassland [118]. Rhizobial symbiosis was a significant factor, which determined the nature of the interaction between *Trifolium fragiferum* and *Trifolium repens* [117]. In particular, plant growth was affected by interaction between the origin of bacterial isolate, NaCl treatment, and species coexistence. It was also concluded that, in conditions when one legume species has established symbiosis with more efficient N<sub>2</sub>-fixing bacteria in comparison to that of other species, the species with less efficient symbiosis can benefit from this interaction. This mechanism is similar to that described for interaction between symbiotic legume species and non-legume species [119]. For *Anthyllis maritima*, rhizobial symbiosis differentially affected growth and physiological performance of plants through interaction of salinity and burial with sand [118]. Symbiotic conditions positively affected photosynthesis-related traits, but the effect was negative for growth and tissue integrity indices.

Salinity tolerance vs. susceptibility of symbiotic nitrogen fixation in legume species has been reviewed, with an emphasis on practical use of legumes in saline agriculture [120]. In particular, the list of salt-tolerant nitrogen-fixing plant species was included, showing that more than 40 legume species have an important potential in this respect. Within the present review, 11 legume species characteristic for coastal grasslands of the Baltic Sea have been identified (Table 1). Clover species (*Trifolium*) from coastal grasslands are especially

promising targets for assessing both genetical and functional diversity in rhizobial symbiosis. *T. fragiferum* is one of the most resistant clover species with high potential for practical use. While not economically used in Europe, it is exploited in the USA, Australia, and New Zealand as a resilient component of temperate perennial grasslands. The species has shown great tolerance against different unfavorable environmental and anthropogenic factors, and it can be classified as a crop wild relative, with a potential for use in breeding of tolerant forage crops. Recently, physiological and genetic diversity in *T. fragiferum* accessions from Latvia were comprehensively characterized and it was shown that geographically isolated wild populations of *T. fragiferum* from the Baltic Sea region are important as a source of abiotic-stress-tolerance related genes [121,122]. Especially interesting is the fact that, in Northern Europe, the species is naturally associated with coastal habitats. *T. fragiferum* micropopulations are geographically isolated and can be found in sites with relatively high soil salinity [123], and their salinity tolerance has been confirmed in controlled conditions [124]. Most importantly, dependence of *T. fragiferum* plants belonging to different accessions on their native symbiotic rhizobia was experimentally characterized [125]. Particular host plant–rhizobia combinations showed significant differences in plant growth stimulation and N acquisition, pointing to existence of genetic variation in N<sub>2</sub>-fixing ability within the bacterial population in the Baltic Sea region. As several of the studied *T. fragiferum* accessions are especially tolerant to saline and waterlogging conditions, it is highly possible that their associated native rhizobia have pronounced tolerance to these conditions. While rhizobial diversity in other clover species, such as *Trifolium repens* or *Trifolium pratense*, has been relatively well characterized (for example, [126]), there are no previous functional studies involving rhizobial isolates from *T. fragiferum* plants. Therefore, further characterization and selection of salt- and soil-waterlogging-tolerant rhizobial strains from root nodules of *T. fragiferum* plants in the Baltic Sea region is a promising direction of future studies.

**Table 1.** Legume plant species from coastal grasslands.

Species	Presence in Coastal Habitats <sup>1</sup>	Salinity Tolerance <sup>1</sup>	Presence in eHALOPH Database (Life Form) <sup>2</sup>
<i>Anthyllis vulneraria</i> subsp. <i>maritima</i> (Hagen) Corb. (syn. <i>Anthyllis maritima</i> Schweigg. ex K.G.Hagen)	0	1	–
<i>Lathyrus palustris</i> L.	3	3	hydrohalophyte
<i>Lotus maritimus</i> L.	6	3	–
<i>Lotus tenuis</i> Waldst. and Kit. ex Willd.	7	4	hydrohalophyte
<i>Melilotus albus</i> Medik.	1	2	annual
<i>Melilotus altissimus</i> Thuill.	1	3	–
<i>Melilotus dentatus</i> (Waldts. and Kit.) Pers.	4	4	annual
<i>Ononis spinosa</i> L.	4	2	–
<i>Trifolium fragiferum</i> L.	7	3	herbaceous perennial
<i>Trifolium pratense</i> L.	1	2	–
<i>Trifolium repens</i> L.	1	2	–

<sup>1</sup> Tyler et al. [127]; <sup>2</sup> eHALOPH database (V4.65, <https://ehaloph.uc.pt>, accessed on 15 May 2023).

## 6. Plant–Parasitic Plant Interactions in Coastal Grasslands

Several groups of plants have evolved parasitic lifestyles and are benefiting from direct interaction with common plant species acting as their hosts [128]. In contrast to mycoheterotrophic parasites, obtaining resources from host plants indirectly through their symbiotic mycorrhizal partners, haustorial parasites feed directly on host tissues through modified root homologous structure, haustorium [128]. Differences in the degree of dependence of the parasite on the host plant determine their further classification, which is associated with significant functional differences. Parasites requiring attachment to their hosts for completing the life cycle are known as obligate, while facultative parasites are being able to reproduce without attachment. In relation to photosynthesis, parasitic plants are either hemiparasites (being able to photosynthesize) or holoparasites (lacking

photosynthesis). Regarding the place of attachment of the haustoria to host plant, root versus stem parasites have been recognized. However, it was recently discussed that, since some hemiparasitic *Cuscuta* species possessing chlorophyll derive 99% of organic carbon from their hosts, the type of functional connection (either to xylem or phloem) is more important for classification regardless of photosynthetic ability [129]. Therefore, an alternative classification system of parasitic plants has been proposed based on particular functional characteristics in the life cycle: euphytoid parasites, mistletoes, parasitic vines, obligate root parasites, and endoparasites [129].

Interactions between parasitic plants and their hosts have gained recent scientific interest mainly for several practical reasons. First, several parasitic plants are economically important weeds to crops, such as species of *Orobanche* and *Striga* [130]. Second, hemiparasitic plants of genus *Rhinanthus* and some other genera are recognized as ecosystem engineers, significantly affecting species diversity and abundance in grassland habitats [131]. However, the relationship between parasitic plants and their hosts could also have a wider meaning, both in a fundamentally biological sense and in ensuring resilience of ecosystems.

Orobanchaceae is the largest parasitic plant family, with over 2100 species [128]. Facultative hemiparasitic plants (or euphytoid parasites according to the recent system of classification) of the genus *Rhinanthus* are photosynthetically active and at least partially autotrophic but benefit from haustorial contact with host plants as means for uptake of xylem water together with inorganic nutrients and organic substances. Species of the genus are widely distributed in grassland habitats. While having only xylem connectivity, even *Rhinanthus* spp. are able to obtain a significant part of carbohydrates from their host plants [132]. *Rhinanthus* spp. have low host specificity and can use several plant species as hosts simultaneously [133]. However, plant species differ in their ability to resist parasitic interactions, which could be dependent on host gene silencing [134]. Aside from the effects of a parasite on host plants, host plant functional characteristics seem to be important determinants of the relationship as the morphology of both *R. minor* and *R. angustifolius* plants is shown to be affected by the host species [135,136].

Recently, a role of *Rhinanthus* species in grassland biodiversity at multiple trophic levels has been reviewed [137]. It was found that the most common effect is decrease in abundance and/or biomass of grass species, but the effect on plant species diversity is either neutral or positive. As grasses are better hosts for *Rhinanthus* species, an increase in density of *Rhinanthus* plants usually linearly decreases both biomass of grasses as well as cumulative cover of legumes [138]. Due to differences in plant susceptibility to parasitic plants, competitive ability of hosts is decreased while that of non-host species concomitantly increases [139]. Therefore, different species of *Rhinanthus* have been used for restoration of grasslands in Europe [140]. Other hemiparasitic plant species, such as *Pedicularis canadensis* and *Comandra umbellata*, can be used for grassland restoration in different parts of the world [141].

Thus far, communications between parasitic plants and their hosts have been analyzed mostly from the perspective of bidirectional exchange of chemical factors during establishment of the relationship [142]. Existence of other effects of parasitic plant–host plant interactions beyond resource transfer are highly possible. A relatively early review discussed the possibility that transfer of mRNAs from host plant to parasite can affect the fate of their interaction [143]. In other parasite–host interactions besides *Rhinanthus* spp., exchange of proteins and RNAs is a factor contributing to the development of the interactions and their outcome. Thus, during interaction between *Cuscuta* spp. and their hosts, it was found that mRNAs move bidirectionally [144,145]. Most importantly, host-derived mRNAs are translated to protein in the parasite [146]. In addition, novel parasite-derived miRNAs target host plant mRNAs [147].

The idea that parasitic plants, similar to these of *Rhinanthus* spp., parasitizing multiple hosts simultaneously, might act as founders of common root networks similar to these made by mycorrhizal hyphae has been expressed recently [148]. In contrast to *Cuscuta* spp. plant parasites [149], these types of relationships have not been explored in *Rhinanthus*–host plant

associations, and no information is available on three-way interactions between a parasite and two host plants belonging to different species. It can be proposed that, in addition to resources, there is an intensive exchange of signals, including small RNAs, between the parasitic *Rhinanthus* spp. and its host, which can influence their response to the action of other environmental factors. *Rhinanthus* species are commonly found also in coastal habitats [150], where periodic flooding with seawater is one of the crucial determining abiotic factors for species coexistence. It can be hypothesized that both species diversity and resilience in plant associations where hemiparasitic plants are present are positively affected through exchange of signals by means of a parasite–host network. In particular, salinity tolerance of non-halophytic plant species can be boosted by presence of halophytic plant species.

Numerous previous studies have shown the importance of miRNAs in post-transcriptional regulation of plant responses and tolerance to salinity both in halophytes [151,152] and glycophytes [153–155], and were reviewed recently [156,157]. In general, it was concluded that one of the most important miRNA target groups are transcription factors, in turn having control functions over salinity responses. Therefore, it is highly likely that, in conditions of salt-affected habitats, including coastal grasslands, transfer of miRNAs by parasitic plant–host network affects salinity tolerance of individual plants involved in it.

Several parasitic plant species have been described as able to make associations with halophytic plant species, including obligate holoparasite *Cynomorium coccineum* [158,159], *Cuscuta salina* [160], and *Cuscuta campestris* [161]. Interestingly, transmission of Na and Cl ions from host plant to mistletoe parasite *Plicosepalus acaciae* under increased salinity has been shown, and it was concluded that the parasite can be classified as euhalophyte [162]. In this respect, no information is available on putative salinity tolerance and ion accumulation potential of *Rhinanthus* spp., but it can be expected that *Rhinanthus serotinus* accessions found in salt-affected grasslands will have considerable salinity tolerance, at least when parasitizing on halophytic hosts.

In temperate coastal grassland plant communities, several hemiparasitic plant species of family Orobanchaceae are relatively common (Table 2, Figure 3). There is no information available if obligate plant species can be found in coastal grasslands, but these are frequently found in coastal salt marshes [160,163,164]. Interestingly, potential hemiparasitic plant species from coastal grasslands appear to be non-mycorrhizal (Table 2). Only plants from genus *Pedicularis* have been reported as facultatively mycorrhizal [35]. Potential plant–parasitic plant interactions in coastal grasslands are shown in Figure 4.

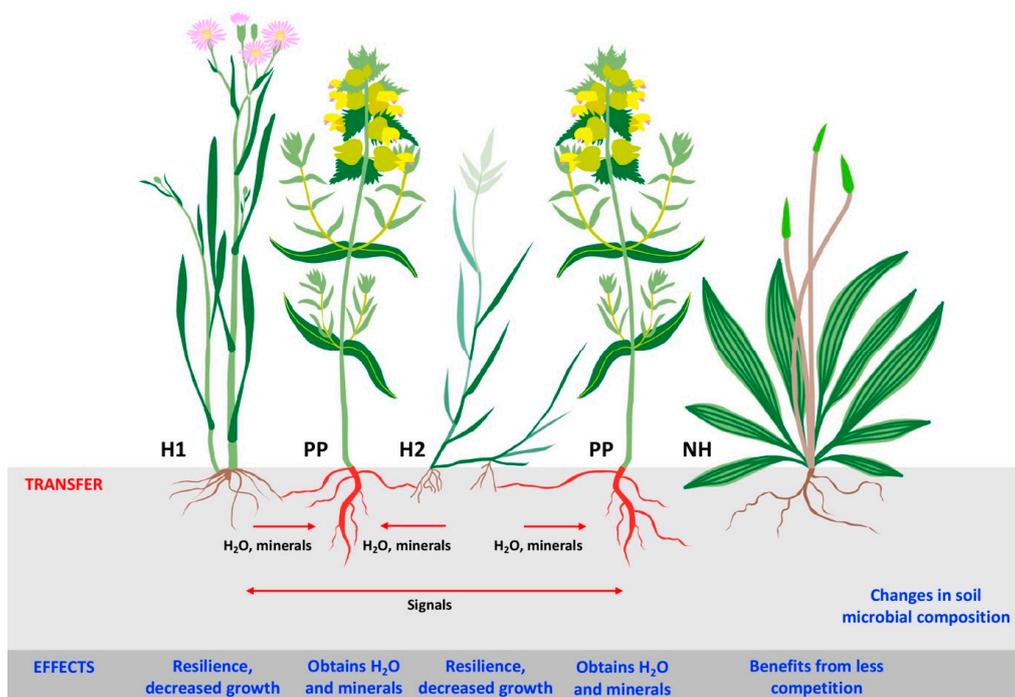
**Table 2.** Hemiparasitic plant species of family Orobanchaceae from coastal grasslands.

Species	Presence in Coastal Habitats <sup>1</sup>	Salinity Tolerance <sup>1</sup>	Presence in Coastal Habitats <sup>1</sup>	Mycorrhizal Status <sup>2</sup>
<i>Euphrasia nemorosa</i> (Pers.) Wettst.	1	2	–	NM
<i>Euphrasia stricta</i> J.P.Wolff ex J.F.Lehm.	1	2	–	NM
<i>Melampyrum arvense</i> L.	0	1	–	NM
<i>Odontites litoralis</i> Fr.	10	4	parasite	NM
<i>Odontites vernus</i> (Bellardi) Dumort.	3	2	–	NM
<i>Odontites vulgaris</i> Moench	2	2	–	NM
<i>Pedicularis palustris</i> L.	3	2	–	NM-AM
<i>Rhinanthus minor</i> L.	1	2	–	NM
<i>Rhinanthus serotinus</i> (Schön) Oborny (syn. <i>R. angustifolius</i> C.C.Gmel.)	1	2	–	NM

NM, non-mycorrhizal; AM, arbuscular mycorrhiza. <sup>1</sup> Tyler et al. [127]; <sup>2</sup> Soudzilovskaia et al., 2020 [35].



**Figure 3.** Hemiparasitic plant species found in coastal grasslands. (A) *Rhinanthus serotinus* together with *Agrostis stolonifera*, *Centaurea jacea*, *Phragmites australis*, *Trifolium fragiferum*, *Trifolium pratense* in salt-affected wet coastal grassland on island of Kihnu, Estonia. (B) *Melampyrum pratense* in coastal grassland on island of Saaremaa, Estonia. (C) *Odontites vulgaris* together with *Agrostis stolonifera*, *Centaurea jacea*, *Phragmites australis*, *Trifolium fragiferum*, *Trifolium pratense* in salt-affected wet coastal grassland on island of Kihnu, Estonia. (D) *Euphrasia nemorosa* in coastal dune grassland on Pape, Latvia.



**Figure 4.** Parasitic-plant-related interactions in coastal grasslands. PP, parasitic plant species; H1, H2, different host plant species; NH, non-host plant species.

## 7. Plant–Plant Interactions in Coastal Grasslands

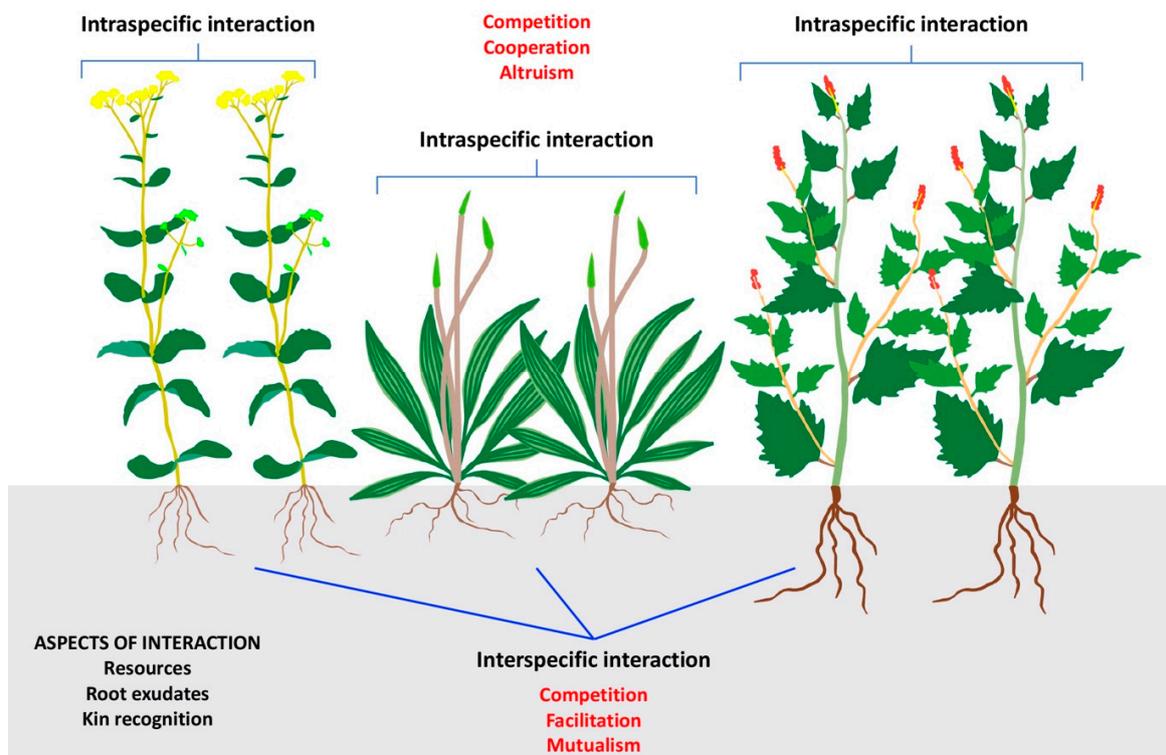
The problem of interactions between plants and their role in ecosystem functioning is not a very often studied problem. However, it has been assessed both experimentally as well as using synthetic approaches. In general, both competition (leading to detrimental effects) and facilitation (leading to beneficial effects) are considered as the main general principles of species interactions [165,166]. In respect to competition for resources, nutrients, water, and light are considered to have main importance [167]. Interaction between plants beyond resource acquisition can result from release of chemical substances into the environment as a result of a process known as allelopathy [168]. The definition of allelopathy includes direct effects of compounds released by one plant (or plant remains in soil) on other plants, but it is clearly evident that indirect effects are most common, such as the effect of root exudates on soil microbial diversity. A recent meta-analysis on allelopathic effects on plants has revealed that coexistence of taxonomically related species as well as dominance of single species can be facilitated by means of allelopathy [169]. Moreover, root-emitted volatile organic compounds are important clues in plant–plant interactions and can significantly affect plant defense responses [170]. A potential role of allelopathy in grasslands has been reviewed relatively recently [171,172], and it is evident that allelopathic effects in coastal grasslands cannot be ignored. On top of that, kin recognition acts as a mechanism controlling both plant communication and defense [173,174], but this aspect will not be further analyzed because there are not many studies specifically using coastal-grassland-related model systems.

It has been hypothesized that positive Interactions between plant species are more common in less favorable environmental conditions, while competition prevails under conditions approaching optimum [175,176]. There is some reason to believe that, similarly, interspecies competition will decrease under more heterogeneous conditions compared to less heterogeneous ones. Usually, only competition between individuals belonging to different species is assessed experimentally, but it is evident that both intraspecific and interspecific interaction need to be considered [177]. Detailed analysis of conceptual approaches in respect to facilitation, including differences between interspecific and intraspecific relationships, has been performed [178]. An additional problem is related to differences between pairwise vs. multi-species designs in species competition experiments, clearly indicating that plant interactions in complex plant communities show both additive and non-additive effects [179]. Diversity in plant–plant interactions in coastal grasslands is shown in Figure 5.

Grasslands in general have been studied in terms of plant–plant relationships. In particular, competition between grassland species has been assessed in respect to drought and heavy rainfall [180] and soil moisture gradient in alpine grasslands [181]. Information on plant–plant interactions in coastal grasslands is rather limited. More data are available for associated coastal habitats, salt marshes, and sand dunes. In salt-affected habitats, as in coastal salt marshes, plant competition is an important mechanism, which determines the distribution of species along the salinity gradient depending on the salt tolerance of the plants [182]. While the majority of typical halophyte species are able to grow and reproduce efficiently in non-saline conditions, they are not able to compete successfully with less-salt-tolerant species in low-salinity conditions. Therefore, species distribution in habitats with pronounced salinity gradients reflects their relative salinity tolerance. However, non-tidal salt marshes and salt-affected wet coastal grasslands are characterized by large spatial and temporal variation in soil salinity, not allowing for establishment of clear vegetation patterns [11,183]. Usually, in such habitats, individuals of halophyte species grow next to individuals of less-salt-tolerant species, suggesting that there are other types of interactions between these species besides competition.

Facilitation has been assessed in coastal communities, as in the case of established *Honckenya peploides* plants forming favorable conditions for germination and emergence of trapped seeds of *Leymus mollis* [184]. In addition, an increase in the intensity of sand accre-

tion for dune-adapted plant species, while it reduced plant biomass, promoted facilitation between them [185].



**Figure 5.** Diversity in plant–plant interactions in coastal grasslands.

Plant–plant interactions in coastal dunes have been reviewed, and it was concluded that understanding of this type of interactions is especially important for conservation and restoration [186]. There is no doubt that the mutual influence of different plant species at the functional level is also an important aspect for understanding the operation and resilience of the coastal grassland ecosystem in general.

Plant–plant interactions with possible importance in coastal grasslands are summarized in Figure 5. In addition, all types of biotic interactions in soil analyzed in this review evidently affect plant–plant interactions, including mycorrhizal [187] and rhizobial symbiosis [117,118]. Interactions between parasitic plants and their hosts include also effects on non-host species and need to be taken into the account when total plant interactions in a habitat are considered.

It is clear that one of the results of plant–plant interaction is the appearance of species associations. However, the formation and existence of these associations are usually examined only from the side of changes in environmental factors, but functional interactions are seldom analyzed. Only relatively recently, the conceptual basis of molecular aspects of plant–plant interactions has started to take shape [188]. This section is not mandatory but may be added if there are patents resulting from the work reported in this manuscript.

## 8. Conclusions and Perspectives

The performed analysis of information clearly shows that plant biotic interactions in soil are omnipresent and important constituents in different ecosystem services provided by coastal grasslands. Not only are supporting and regulating services strongly dependent on these interactions as affecting primary production, nutrient cycling, invasion resistance, etc., but provisioning services can also greatly benefit, for example, from discovery of resistant symbiotic microorganisms that could be used in provision of agricultural resilience. It is no less important that coastal grasslands can serve as a source of empirical knowledge about

the impact of environmental heterogeneity on ecosystem functioning and the importance of plant interactions in it.

It seems that the coexistence of species in grassland habitats as well as environmental resilience of these plant assemblages are more directly affected by biotic interactions in soil than previously thought. Interactive effects of mycorrhiza and rhizobial symbiosis of legume plants have been assessed, showing that plants benefit more from dual interactions [189]. However, many potentially mycorrhizal legume plants can act as hosts of hemiparasitic plants. A study of such three-way interactions would be particularly challenging for salt-affected coastal grassland plants.

Based on analysis of biotic interactions in soil of coastal grasslands, several lines of research seem to be especially promising, both for the design of experimental systems as well as choice regarding model plant species. Such general possible research directions could include the following: role of clonal plants in environmental resilience of coastal grasslands, as recently analyzed in respect to the role of clonal growth in halophyte resistance to heterogenous salinity conditions [190]; transfer of hormonal signals and small RNAs between individual organisms by mycorrhizal and parasitic plant networks and their regulative effect on plant growth and responses to environmental constraints, especially, salinity and flooding; role of processes of epigenetic memory as mechanisms for fine-tuning plant adaptation to relatively short-term but persistent changes in environmental conditions in coastal grassland habitats; functional role of symbiotic interactions in adaptation to highly heterogeneous availability of plant nutrients in coastal grasslands; and many others.

At the level of mechanisms of interaction between plants and their symbiotic microorganisms, as well as between parasitic plants and their hosts, inoculation experiments in highly controlled conditions can be successfully applied. Simplified experimental systems, such as aseptically cultivated seedlings or root cultures, seem to be particularly promising as they enable eliminating undesirable effects of soil-related factors [191–195]. The exchange of chemical and molecular signals between the involved partners and the functional results can be monitored by means of various molecular biology approaches. High-throughput sequencing can be used to efficiently sequence transcriptome and small RNA libraries. Comparison of sequence data from different variants of experimentally manipulated plant–symbiont as well as host plant–parasitic plant combinations will allow for identification of differentially expressed genes as well as for possible movement of RNA molecules between interacting partner organisms. Combined with modern methods of data analysis, such as statistical network analysis [196,197], such studies will provide an opportunity to critically evaluate the importance of plant biological interactions in functioning of ecosystems and the services they provide, including these of coastal grasslands.

From the point of view of practical innovations and developments, based on an understanding of biotic relationships in coastal grasslands, resilient symbiotic microorganisms, both arbuscular mycorrhizal fungi and rhizobial bacteria, need to be isolated and identified. Detailed genetical and functional characterization of the isolated fungal and bacterial strains could lead to development of new plant fertilizers and growth stimulants for the promotion of sustainable agriculture or urban greening measures, especially useful in marginal or degraded lands.

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