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Review

Direct plant–plant facilitation in coastal wetlands: A review

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ABSTRACT

Coastal wetlands provide important ecosystem services to humanity, but human activity and climate change are rapidly degrading these ecosystems. Thus the conservation and restoration of coastal wetlands becomes an urgent issue. Species facilitation among plants has regained attention of ecologists recently. Many studies in coastal wetlands have revealed direct plant–plant facilitation influencing community structure and ecosystem function, thus improving our understanding of community organization and giving new directions for the restoration of degraded coastal wetlands. Our paper examines studies of direct plant–plant facilitation in coastal wetlands with an emphasis on tests of the stress gradient hypothesis and influences of species facilitation on species zonation, species diversity patterns, phylogenetic diversity and ecosystem function. Investigating how plant–plant facilitation affects ecosystem function is an important future direction, which can provide basic knowledge applicable to the preservation and recovery of coastal wetlands in these times of rapid global change.

Coastal areas make up only 4% of the earth's surface, but more than 1/3 of the world's population resides in these areas. Coastal wetlands provide important ecosystem services to humanity, such as food, storm protection, shoreline protection and fishing nurseries (Gedan et al., 2009). However, human activity (e.g., agriculture and urban development) and climate change (e.g., rising sea level) diminish these areas and strongly disrupt coastal ecosystem functions (e.g., Comeaux et al., 2012). Restoration of disrupted coastal wetlands has been an urgent issue (Spencer and Harvey, 2012). Understanding when and how interactions among plants influence ecosystem functions (e.g., productivity, ecosystem stability) of coastal wetlands will provide basic knowledge for us to protect and recover these important ecosystems (Halpern et al., 2007). On the other hand, it is wildly known that coastal wetlands provide an ideal ecosystem to investigate the basic hypotheses of community ecology because of their simple plant community composition and long-length distinct and strong abiotic stress gradients from sea to inland. The influences of plant–plant interactions and their interactions with environmental stress on coastal wetland community organization have been well studied. Here, we review recent developments in the field of direct plant–plant interactions including: (1) the prevalence of direct plant–plant interactions in coastal wetland plant communities (e.g., salt marshes, cobble beaches, mangroves, and coastal forests); (2) mechanisms of direct plant–plant interactions in coastal wetlands and how to determine if plant–pant interactions are positive or negative; (3) how the strength of interspecies interactions vary across stress gradients and how these interactions influence species zonation and species diversity patterns along stress gradients; (4) the relationships between species interactions and species invasions. Then we propose a hypothesis of how species facilitation affects ecosystem function of coastal wetland.

1. Direct plant–plant facilitation in coastal wetlands

Direct plant–plant interactions include positive and negative interactions (i.e., species facilitation and competition). Plant–plant facilitation occurs when the presence of neighboring plants enhances survival, recruitment or growth of the target plant through modifying environmental conditions or providing associational defenses against herbivores. Almost a century ago, ecologists discovered that both species competition and facilitation were ubiquitous in natural plant communities. Subsequently, the influence of species competition on community organization has been thoroughly investigated; however, the importance of species facilitation has been largely neglected.

Recently, accumulating evidence suggests that species facilitation is essential in structuring plant communities, particularly in high stress environments (Bertness and Yeh, 1994; Bruno et al., 2003; Brooker et al., 2008). Both competition and facilitation among plants have been observed in coastal wetlands. For example,

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species showed a hierarchical structure in terms of competitive ability in a New England salt marsh. Species investigated, in order of competitiveness, were *Iva frutescens*, *Jucus gerardi*, *Spatina patens* and *Spartina alterniflora* (Pennings and Bertness, 2001). Competition among these species and species tolerance of environmental stress formed distinct plant zonation in the salt marsh. However, in the Spartina-Juncus zone of high salinity the salt tolerant but less competitive species, *S. Patens* ameliorated the abiotic stress of high salinity and facilitated colonization by the salt intolerant *J. Gerardi* (Bertness and Shumway, 1993).

Though most plant–plant facilitation experiments have focused on salt marshes, some have investigated cobble beaches or estuarine marshes and very few have investigated coastal forests or mangrove forests in particular (Huxham et al., 2010, Table 1). Moreover, most studies have assessed interspecific facilitation and largely disregarded intraspecific facilitation (i.e., positive density dependence). Negative density dependence, which can be caused by strong competition for resources, habitat overlap for individuals, increasing susceptibility to infection by pathogens or detection by consumers, is regarded as a key organization rule in traditional population dynamics. However, when the benefits of conspecific group living outweigh the effects of resource competition or other negative density dependence mechanisms, positive density dependence may occur, particularly in high stress environments (Goldenheim et al., 2008; Fajardo and Mclntire, 2011). This type of positive density dependence is very useful in restoration management of coastal wetlands (Halpern et al., 2007). We recommend researchers consider both interspecific and intraspecific facilitation and compare the relative role of inter- and intraspecific facilitation in shaping coastal wetland populations and communities to avoid underestimating the role of plant–plant facilitation.

2. Mechanisms of plant–plant facilitation in coastal wetlands

The major mechanism for species facilitation among plants in coastal wetlands is the reduction of abiotic or biotic stress (Fig. 1). Biotic stresses, such as herbivory, could be reduced by neighboring plants decreasing the probability of encounters between target plants and animal consumers, thus defending target plants from animal consumption (Alberti et al., 2008; Daleo and Iribarne, 2009). Abiotic stresses often reduced through plant–plant facilitation include high salinity, flooding, and nutrient limitation stress.

Salinity stress may be reduced through the presence of neighboring plants shading their surrounding soil, thus decreasing water evaporation rate and preventing salt accumulation in the soil. Alternatively, neighboring plants could absorb salt from the soil and store it in their tissues or excrete it from their salt glands, thus reducing the salinity of their ambient environment (Bertness et al., 1992). An additional mechanism could be increased proline production in target plant cells enabled by nitrogen supplementation from neighboring plants (Levine et al., 1998). Flooding stress may also be reduced by neighboring plants. Flood-tolerant plants could ameliorate anoxic substrate conditions by enhancing soil oxygen levels through rhizosphere oxidation. Alternatively neighboring plants could lift the soil to decrease waterlogging (Fogel et al., 2004). Limiting nutrient stress could be decreased through plant–plant facilitation when neighboring plants enrich the soil with nutrients (Levine et al., 1998). Facilitating tolerance of other biotic and abiotic stresses such as sea waves, pollination or dispersal stress has also been proposed as mechanisms of species interaction (Table 1). However, the cumulative effects of co-occurring environmental stresses, particularly abiotic and biotic stresses on species interactions, which may play an important role in community assembly are still poorly understood (Bulleri et al., 2011).

3. Experimental approaches to studying plant–plant facilitation

In contrast to studies on other ecosystems (e.g., semiarid grasslands or alpine plant communities) which have employed removal experiments to investigate plant–plant facilitation (e.g., Choler et al., 2001), studies in coastal wetland employed transplant experiments. Removal experiments involve the elimination of all neighboring plants around the target individual. Target plant performance is then compared between removal and control treatments. In transplant experiments, patches of conspecific individuals are transplanted into another plant zone (with or without neighboring plants). Then plant performance is compared between transplant and control treatments. Both experimental approaches are popular methods for detecting of plant–plant facilitation, and both have their own advantages and disadvantages.

Removal experiments are suitable for species with a scattered distribution, but can only be operated on widely spread species. Moreover, it is impossible to detect species-specific interactions in removal experiments. On the other hand, transplant experiments can only be conducted on densely populated species and are inappropriate for species with a scattered population distribution population (except when cultivating seedlings). Approaches such as spatial point process, Hierarchical Bayesian analysis which was designed to investigate community-level (larger than only one or a few pairs of species in the community) consequences of species interactions (Raventos et al., 2010; Wang et al., 2011) are rarely used in coastal wetland studies. Additionally, many studies on species facilitation are too short term to achieve equilibrium in species interactions, thus longer observations are necessary.

4. Tests of the stress gradient hypothesis in coastal wetlands

The stress gradient hypothesis (SGH) was put forward by Bertness and Callaway (1994) at a time when ecologists did not appreciate the role of facilitation in communities. The SGH was

Table 1
Direct plant–plant facilitation in different coastal wetlands.

Ecosystem	Benefactor	Beneficiary	Mechanism	Study sites	Literature
Salt marsh	*Spartina patens*; *Distichlis spicata*	*Juncus gerardi*	Lowering salinity	Southern New England salt marsh, USA	Bertness and Shumway (1993)
Salt marsh	*Triglochin maritina*	*Plantago maritinma*; *Limonium nashii*	Decreasing waterlogging and salinity	Northern New England salt marsh	Fogel et al. (2004)
Estuarine marsh	*Sarcocornia perennis.*	*Spartina densiflora*	Reducing herbivory by crabs	Mar Chiquita coastal lagoon and the Bahia Blanca estuary, Argentina	Alberti et al. (2008)
Cobble beach	*Spartina alterniflora*	*Suaeda linearis*	Buffering sea waves	Rhode Island, USA	Irving and Bertness (2009)
Cobble beach	*Suaeda linearis*	*Suaeda linearis*	Reducing evaporative stress	New England shore, USA	Goldenheim et al. (2008)
Coastal forest	*Cladium jamaicense*	*Pinus taeda*; *Pinus serotina*	Lowering salinity	Swanquarter National Wildlife Refuge, USA	Poulter et al. (2009)
Mangroves	*Avicennia marina*	*Ceriops tagal*	Reducing salinity	Gazi bay, Kenya	Huxham et al. (2010)