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# Positive plant interactions in the Iberian Southeast: Mechanisms, environmental gradients, and ecosystem function

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ABSTRACT

Semi-arid ecosystems are privileged sites to address the effects of plant interactions on community structure and dynamics because environmental conditions are demanding and may change quickly, altering in significant ways the balance between positive and negative effects among neighboring plants. Plant interaction processes have been well documented in the semi-arid region of Southeast Spain over the last 15 years. In this article we review the growing body of research on plant–plant interactions available from this area, highlighting its importance in increasing our knowledge on this field of study. This review has been organized in five sections, i) facilitation mechanisms; ii) the nurse effect; iii) the balance of interactions and environmental, ontogenic, temporal, and spatial gradients; iv) the effects of facilitation on biodiversity; and, v) facilitation and ecosystem functioning. Mechanisms of facilitation in these systems are relatively well known, but not completely explored. In these environments competition, mainly for water, is intense between neighbors and switches in intensity from belowground to aboveground as productivity increases. By contrast, facilitation may decrease quickly with increasing productivity, although the balance between facilitation and competition is not fully understood, and is further complicated because shifts can also be driven by factors such as life history or physiology of interacting species. Positive interactions are critical for maintaining biodiversity in some ecosystems in SE Spain, but their role as a driver of ecosystem functioning is less clear. Research on plant–plant interactions in this region has been highly influential and has contributed to our overall understanding of plant community dynamics. Despite the important progress achieved during the last 15 years, there is still substantial scope for exploring the effects of plant interactions at the ecosystem level, and their role as modulators of disturbances such as the current global environmental change.



## 1. Introduction

Arid and semi-arid ecosystems are characterized by scarce and highly variable resources (water and nutrients) in space and time, and by overall harsh climatic conditions. In these environments, dominant perennial plants cause changes in micro-climate and soil properties leading to the formation of so-called "fertile islands" under plant canopies. These particular microsites are spots of high biological activity that concentrate an important part of the local flora and fauna (Gutiérrez et al., 1993; Maestre and Cortina, 2005; Pugnaire et al., 1996b; Pugnaire and Lázaro, 2000; Vetaas, 1992). In fertile islands facilitation, or the net positive effect of one plant species on another, predominates but interactions between species are complex. Survival and growth of plants in such patches may be mediated by improved micro-climate (Moro et al., 1997a, 1997b; Valiente-Banuet and Ezcurra, 1991), higher water availability (Dawson, 1993) or soil nutrient content (Armas et al., 2008; Pugnaire et al., 1996a; Reynolds et al., 1999) caused by perennial species, while light deprivation and mechanical and chemical effects of litter (Holmgren et al., 1997; Moro et al., 1997a) may have negative effects. Overall, facilitation plays a prominent role in plant community dynamics in arid environments (Flores and Jurado, 2003; McAuliffe, 1988; Pugnaire et al., 1996a).

During the last two decades there has been an unprecedented surge in interest on facilitative interactions worldwide, which has prompted important advances in our knowledge of the factors shaping composition, structure, and functioning of plant communities (see Brooker et al., 2008 and Callaway, 2007 for recent reviews). In this review we address how plants facilitate growth of others in semi-arid environments of SE Spain, the mechanisms

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underlying facilitation processes, the variability of these processes influenced by resource gradients, and their consequences at the community and ecosystem level, highlighting the contribution of positive interactions to the general ecological theory. We used evidence based on observational experiments as well as on field manipulations and glasshouse experiments, including spatial pattern analysis, physiological measurements, and isotopic determinations (Fig. 1). These topics are organized in five sections, which encompass the bulk of research carried out in the last 15 years on plant–plant interactions in SE Spain. We also discuss the contribution and implications of this research to our understanding of community ecology in arid and semi-arid Mediterranean ecosystems. Other topics, relevant to plant interactions, such as biological soil crusts, trophic interactions, or ecosystem restoration, are treated elsewhere in this issue (Cortina et al., 2011; González-Megías et al., 2011; Maestre et al., 2011), and thus will not be discussed here.

The south-eastern corner of Spain is characterized by a warm, dry Mediterranean climate. The proximity of the sea and the relative low elevation causes lack of frost and mean annual temperatures in the 16–19 °C range. Extreme summer temperatures are common and daytime maximum of 45 °C have been recorded in some years, while soil surface may reach 80 °C. Mean annual rainfall in this region is low, with higher precipitation in autumn (linked to heavy storms and torrential phenomena) and early spring. There is also marked inter-annual rainfall variability (Lázaro et al., 2001). Mean annual rainfall is below 350–400 mm but precipitations lower than 200 mm are registered locally in some coastal areas (e.g., Cabo de Gata). Conversely, precipitation in mountains is often above 400 mm. It is, however, important to note the existence of hidden precipitations (by fog condensation) and the fact that high air humidity in coastal areas may cause an important decrease of evapotranspiration (Domingo et al., 2011). The low rainfall in this area is a direct consequence of its geographical isolation, originated by a chain of mountains over 2000 m in elevation (the Betic Ranges) that surround the region to the west and north. These mountains prevent the arrival of Atlantic fronts that sweep the rest of Spain, and make this the driest zone in Europe. Such singular environmental conditions limit plant growth and the establishment of forests, which are restricted to the top of mountains, and microsites with high humidity and deep soil profiles. These forests are dominated by holm oak (*Quercus ilex*) and xeric coniferous species such as Aleppo pine (*Pinus halepensis* Mill.) and several species of juniper (*Juniperus oxycedrus* L. and *J. phoenicea* L.).

## 2. Main facilitation mechanisms

In arid and semi-arid environments in SE Spain facilitation involves mainly shade, increased water or nutrient availability, improvement of microclimatic conditions as well as protection from herbivores. These mechanisms are discussed below.

### 2.1. Shade

Shade provided by the canopy of large plants may protect seedlings and other plants from temperature extremes, reducing thermal stress and water loss through transpiration, thereby protecting seedlings from photoinhibition (Moro et al., 1997a, b). Shading may impose a cost on photosynthesis, but most species from arid environments have photosynthetic optima under the prevailing radiation in such environments (Gómez-Aparicio et al., 2006; Valladares and Niinemets, 2008; Valladares and Pugnaire, 1999) and many benefit from the decrease in radiation provided by perennial plant canopies. With soil surface reaching over 70°C under full sunlight, any plant or object casting a shade has beneficial effects on other plants (Armas and Pugnaire, 2005; Moro et al., 1997b; Pugnaire et al., 1996a), and establishment of many species is mainly restricted to shady places. Shade benefits are at the core of

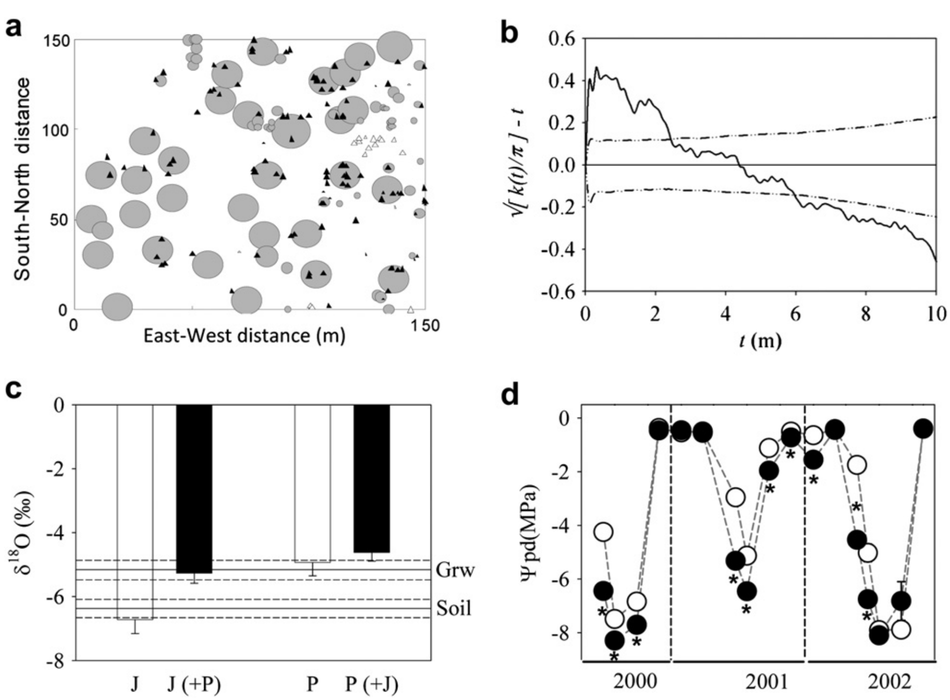


**Fig. 1.** Evidence on plant interactions in SE Spain was based on observational experiments as well as on field manipulations and glasshouse experiments, including spatial pattern analysis, physiological measurements, and isotopic determinations. Examples are the mapping of *Ziziphus lotus* and *Asparagus albus* in a coastal sand dune (a); spatial point pattern analysis of juvenile *Stipa* tussocks vs. *Cistus* shrubs (b); isotopic comparison of $^{18}O$ in sap of *J. phoenicea* (J) and *P. lentiscus* (P) living isolated (clear bars) or with the other species (solid bars) compared to soil and ground water (Grw) (c); and pre-dawn water potential of *J. phoenicea* growing with (solid dots) and without (clear dots) *P. lentiscus* (* significant differences at $P < 0.05$). Original data from a) Tirado and Pugnaire (2005); b and d) Armas and Pugnaire (2005, 2009); and c) Armas et al. (2010).