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Plant competition in mediterranean-type vegetation

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Abstract. Plant competition in communities subjected to stress and disturbance is an important ecological issue. We review studies on plant competition in mediterranean-type plant communities in order to discuss its effect on plant- and plant community structure, to determine the type of competition that takes place and the interaction between competition and effects of fire. Competition can intermittently effect all stages of the plant life cycle. Water and light seem to be the most frequent resources for which plants compete. Competition for nutrients also occurs and seems to be more intense when nutrient availability is high. Plant interference through allelopathy is also important. Competition may also occur after fire but it is not clear if it is less intense than in mature stands. As most of the studies have been carried out in California. More field experiments that combine the effect of competition and fire along with environmental gradients differing in water and nutrient levels should be conducted in other mediterranean regions in order to draw generalizations on the mechanisms of competition in plant communities.

Keywords: Allelopathy; Fire; Mediterranean community; Neighbour; Plant interference; Regeneration; Removal experiment; Resource competition.

Introduction

Fifteen years ago Connell (1983) and Schoener (1983) published extensive reviews about competition experiments in natural communities. Although there were differences of opinion as to the number of species that showed competition (Schoener 1985), both authors concluded that competition among plants is detectable, is strongly asymmetrical and shows spatial and temporal variation. Since then, several reviews updated, discussed and quantified field experiments on plant competition (Underwood 1986; Aarssen & Epp 1990; Goldberg 1990; Goldberg & Barton 1992). However, information on the role of competition in structuring specific natural communities is scarce, with the exception of Fowler's (1986) review on plant competition in arid and semi-arid communities which concluded that in deserts and in dry grasslands, competition for water limits plant survival and growth. She also mentioned the scarce information available to determine similarities and differences in plant-plant interactions among different biogeographic regions. Our aim is to review studies on plant competition in mediterranean plant communities.

Mediterranean regions occur in middle latitudes between parallels 30° to 40° north and south in five regions of the world, i.e. the Mediterranean Basin, California, central Chile, the Cape region in South-Africa and southwestern and southern Australia. Summer drought is the defining factor of the mediterranean climate (Köppen 1923). Annual rainfall ranges from 1500 mm in montane forest to below 90 mm in the most arid sites. The mean seasonal temperatures range from about 8 °C for the coldest month up to 25 °C for the hottest month. Annual mean temperatures range from about 11 °C to 17 °C (Beard 1983).

Mediterranean vegetation is dominated by evergreen sclerophyllous trees and shrubs (e.g. Specht 1969; Orshan 1983) with a herbaceous or shrubby understorey. From humid to semi-arid regions there is a gradient from vegetation with annual and perennial grasses and herbs (savanna understorey) to an evergreen and sclerophyllous vegetation (heathland understorey).

Mediterranean vegetation represents less than 5 % of the terrestrial ecosystems of the world. The high local species diversity and the wide distribution of mediterranean vegetation have attracted much attention. One of the most interesting aspects is that disjunct areas of land might share similar selective forces (Aschmann 1973; Cowling et al. 1996). Since the 1960s, emphasis has been biased towards abiotic effects on these communities, i.e. climatic regime, fire effects and resilience, water stress and soil nutrient deficiencies (Mooney & Conrad 1977; di Castri et al. 1981; Kruger et al. 1983; Dell et al. 1986; di Castri et al. 1988; di Castri 1991). However, the importance of plant-plant interactions mediating nutrient and water deficiencies has been neglected; competition is considered to be less important in shaping community structure than fire (Cowling 1987).

In all five mediterranean regions, the presence of dense, evergreen shrubland stands suggests that competition may be strong. Species packing is high, and usually there is a considerable canopy overlap of individual plants (Lamont et al. 1984). Furthermore, variable rainfall, summer drought and scarcity of some soil nutrients are three main characteristics of mediterranean ecosystems (Di Castri et al. 1988; Kruger et al. 1983). According to Grubb (1985) and Tilman (1987), limited soil resources would lead to intense competition, suggesting that in mediterranean communities competition for water and nutrients may be strong (Mooney & Dunn 1969). However, others argue that competition would be less intense with intense abiotic stress, specially in herbaceous vegetation (Grime 1973, 1977, 1979; Huston & Smith 1979). Thus, the review of studies on competition in mediterranean regions can contribute to elucidating the controversy over the intensity of competition in habitats subjected to abiotic stress.

On the other hand, mediterranean vegetation is frequently subjected to disturbance, mainly fire (Naveh 1974; Mooney & Conrad 1977). Post-fire succession may lead to less competition (Noble & Slatyer 1977) because it implies the reduction of plant density and a greater availability of resources at the individual plant level (water, nutrients, light and space). According to Grime (1977), competition would be less intense in the first stages of succession, due to lower density and size of plants, which would decrease resource demand. As succession advances, the increased individual size of plants results in competition among plants.

These various hypotheses are not contradictory if we assume that competition in a community may vary spatially and temporally (Wiens 1977; Connell 1983; Schoener 1983; Goldberg & Barton 1992) according to environmental gradients of resource availability and disturbance. Although competition may be strong in a mature, non-disturbed stand, it may decrease after a fire or other main disturbance (Sousa 1984). We document studies on competition after fire that might resolve this apparent dilemma for mediterranean vegetation.

In this paper, we present a literature review on competition studies in mediterranean vegetation. Our main objectives are: (1) to confirm that competition occurs in mediterranean communities; (2) to describe its effect on plant performance and community structure; (3) to elucidate which kind of competition (*sensu* Connell 1990) we are dealing with; and (4) to discuss the interaction between competition and fire.

Methodology

Competition is defined as the negative interaction within or among species (Odum 1971). In the present study, competition is defined in the broadest sense (Connell 1990), including all limiting effects plants may have on each other, indirectly (resource exploitation) or directly (interference via physical contact or the release of toxic substances: allelopathy) that reduce or prevent plant growth and survival, and increase susceptibility to damage of neighbouring plants. Plant competition is usually asymmetric: one group of plants is strongly affected by the presence of another group but the reciprocal effect is weak or cannot be detected (Connell 1983). The main reason for this asymmetry is that larger plants obtain a disproportionate (for their relative size) share of the available resources (Weiner 1990). In this review, the term competitive ability will be used, unless otherwise noted, in the sense of either how strongly neighbours suppress other individuals – net competitive effect – or how they respond to the presence of individuals – net competitive response – (Goldberg 1990).

We did not limit the review to papers in a set of journals published during a certain period of time. In addition to a review of the Life Science Collection from the Current Contents Collection from 1988 to mid 1997, we also checked citations from these papers for older studies, and others published in books and local journals sometimes not listed in *Current Contents*. This method allowed us to include a wider range of literature than if we had limited the survey to only referenced publications. This review includes both field observations and experiments because both approaches are required for an adequate evaluation of the importance of competition (Roughgarden 1983). However, most observational studies can only suggest that competition occurs; only well-designed experiments can proof that there is competition (Aarsen & Epp 1990). Furthermore, in order to demonstrate that plants compete for a resource, the resource should be manipulated. If plants compete for a given resource, plants without neighbours and with higher resource levels will have higher performance than when only neighbours are removed or not added. We surveyed studies dealing with plant-plant interactions for one or more species or groups of species independently of the method used (App. 1).

Evidence of competition

Early studies on community structure attempted to infer the presence of competition based on field observations including changes of population structure through time, spacing and correlation analysis, and comparative analysis. Field observations in the Californian chaparral showed that shrub density decreases as a stand develops (Schlesinger & Gill 1978, 1980) and mortality is independent of shrub senescence (Zammit & Zedler 1992). Schlesinger and Gill (1980) found that *Ceanothus megacarpus* density decreased by 50 % during the first 6 yr after fire due to the death of small shrubs suggesting that competition was asymmetric: large individuals obtained a disproportionate amount of resources compared to small ones. Similarly, in Australia, *Banksia ericifolia* decreased in density when aged, in both a monospecific stand (Morris & Myerscough 1983) and a mixed stand (Zammit & Westoby 1987a).

However, self-thinning trajectories do not always follow the predicted trajectory of an increase of mean plant weight as density decreases according to the –3/2 law (Yoda et al. 1963). Morris & Myerscough (1983) found that in a monospecific stand of *B. ericifolia*, individuals had high mean plant weights for their density because accumulation of woody material was large. Stohlgren et al. (1984) found only two dead shrubs of *A. fasciculatum* amongst 69 individuals in a mature dense stand. Riggan et al. (1988) observed substantially less mortality in an old *C. crassifolius* than was predicted from growth rates and the –3/2 power model. The lack of classical self-thinning patterns may be because competition is not for light only, because there is an increasing death rate with age, or because populations are not even-aged and differences in establishment produced different adult mortality rates.

Traditionally, spacing analyses verify that populations change with time from clumped distributions among young into random ones, and random into regular or very dispersed individuals (Pielou 1960). In California, stands of young *Ceanothus megacarpus* were very dense and clumped when young, but densities decreased and the pattern became regular with time. However, many of the patterns investigated by community ecologists are complex effects of factors other than competition. Stohlgren et al. (1984) found an increase of clumping in lower densities suggesting spatial mosaics of resource availability. Patterns of seed dispersal and specific regeneration types could also modify or mask the spatial pattern supposed to exist if plants originate only from seeds and competition among seedlings takes place.

Despite the many correlation studies that demonstrate lower plant performance at higher plant densities, neighbourhood studies which suggest a negative correlation between target plant performance and neighbourhood performance have seldom been used because this method is difficult to apply in mixed stands (Table 1). Fuentes & Gutierrez (1981) reported a positive correlation between the sum of a canopy's ground projections and the distance of a target plant to its neighbour for several Chilean matorral species, suggesting that competition did take place. This relationship was common for both intraspecific and interspecific pairs. In South Africa, Bond et al. (1984) observed a positive correlation between the distance to nearest neighbour and the mean number of flower-heads in *Protea lorifolia*. Vilà et al. (1998) found a significant but weak negative relationship between biomass of *Erica multiflora* sprouts and a competition index which included proximity and size of the most dominant neighbour, *Rosmarinus officinalis*, in a 1.5 m radius around target plant suggesting that the presence of adult *R. officinalis* negatively affects the sprouting vigour of *E. multiflora*.

An important part of competition studies is based on comparisons of survival, reproduction, growth, etc. of a target species in areas where a potential competitor species is naturally absent with that of other areas where the potential competitor is coexisting (Table 1). Classical studies of this type compare the structure of the understorey vegetation with and without a woody overstorey (Sweeney 1956; Ashton 1976). This type of studies cannot eliminate the alternative hypothesis that the target species differ biologically in the two areas because environmental conditions other than the presence of the supposed competitor alter the performance of target plants (Underwood 1986).

Keeley et al. (1981) reported that in chaparral the herb understorey that established from seeds in the first year after a fire was negatively related to the perennial plant cover, and that a dense cover of exotic annual grasses inhibited the recruitment of native annuals. Westman (1981) also described a negative relationship between the amount of dominant shrubs and the presence of herbs in the Californian coastal sage scrub in a chronosequence after fire. Herrera (1997) hypothesized that in southeastern Spain, clearing increased fecundity of *Lavandula stoechas* because there is competitive release. However, these studies do not demonstrate that competition is the driving force of plant suppression.

Table 1. Types of competition studies in mediterranean vegetation.

Type of study	Number of studies	%
Changes through time	17	21.8
Spacing analysis	1	1.3
Correlation analysis	12	15.4
Neighbourhood analysis	2	2.6
Comparisons	5	6.4
Laboratory experiments	6	7.7
Removal experiments	19	24.4
Additional experiments	8	10.3
Common garden experiments	5	6.4
Greenhouse experiments	3	3.8

Most comparative analyses concern ‘savanna-like’ communities, i.e. with an open tree layer dominated by *Quercus* and a herbaceous understorey, mainly grasses. In these communities, environmental differences have been detected beneath live trees and in the open (e.g. Parker & Muller 1982; Ovalle & Avendaño 1987). Beneath trees the radiation and temperature variation is lower than in the open while soil moisture and essential nutrients are more plentiful. There are marked differences in time and space (locally and regionally) on the effect of trees on plant recruitment. Germination and recruitment of the Californian *Q. douglasii* was negatively correlated with oak canopy cover in oak forest but positively correlated in a dense canopy savanna (Borchert et al. 1989). Similarly, the effect of the oak *Q. douglasii* canopy on herbaceous understorey varied along a rainfall gradient and depended on the species under consideration (McClaran & Bartolome 1989). Moreover, certain oaks have a positive effect and others a negative effect on herbaceous growth (Callaway et al. 1991) possibly due to varying soil depth, genetic and age variation of trees, tap-root injury or senescence, disturbance and herbivory. The herbaceous understorey also has a suppressing effect on regenerating trees which is known as the Gulliver effect (Bond & van Wilgen 1996).

Although most field observations confirm that competition takes place, manipulative experiments are necessary to prove it (Aarssen & Epp 1990). Different type of field experiments, especially well-designed removal experiments, have demonstrated that competition takes place in California (Christensen & Muller 1975a; Swank & Oechel 1991), in the Mediterranean Basin (i.e. Vilà et al. 1994; Vilà & Terradas 1995c; Thébaud et al. 1996) and in Australia (Hobbs & Atkins 1991).

Resource competition

Water

Mediterranean-type soils are very dry during the summer because of low rainfall and loss of water as a result of direct evapotranspiration from plant surfaces and percolation. Consequently, plant growth, reproduction and survival are reduced (Thomas & Davis 1989; Davis & Midgley 1990). According to Grime (1977) competition would be less important in habitats with soil water deficiency because plant growth would be limited by water stress rather than by competition.

Gordon et al. (1989) have studied the effect of annuals on oak seedlings in ‘savanna-like’ communities by planting single-species neighbourhoods of annuals around *Quercus douglasii* seedlings in outdoor boxes. This experiment demonstrated that several annuals negatively affected the seedling emergence and survival of this oak by depleting the soil water content. The effect of grasses (e.g. *Bromus diandrus*) was stronger than that of forbs (*Erodium botris*) because the tap-root system of grasses takes up significantly more water than the fibrous roots of forb species. Competition for water is also detected as a mechanism underlying a negative effect of grasses on shrub establishment. Additional experiments have demonstrated that in California, *Baccharis pilularis* shrubs cannot establish under annual grasses because shrub roots fail to reach soil moisture below the depth of the grass roots (Williams & Hobbs 1989).

Several other studies have not found a negative effect of herbs on seedlings growth (Kummerow et al. 1985; Moreno & Oechel 1988, 1991, 1992; Thomas & Davis 1989). Probably, the increasing use of water by herbs is balanced by decreasing evaporation from the soil surface because of cooler temperatures under herb canopies. The effect of seedlings on annuals has not been examined in these studies, but indirect evidence suggested little impact because seedlings without neighbours absorbed little soil water compared to annuals (Gordon et al. 1989).

Competition for water among woody species has been less studied than between grasses or herbs and woody species. Griffin (1973) compared the minimum water tension in selected stands with different densities of *Q. douglasii*, *Q. agrifolia* and *Q. lobata* in California and found that pre-dawn xylem sap tension increased during the summer season when the number of trees and saplings increased per area suggesting that there was competition for water. Competition for water may also be the mechanism of ‘jarrah’ shrub suppression in *Eucalyptus wandoo* stands in southwestern Australia (Lamont 1985).

Minerals

Nutrient deficiency is common in mediterranean soils (Kruger et al. 1983; Specht & Moll 1983). Fertilization experiments have shown that soil nutrient deficiency limits the growth of mediterranean species (McMaster et al. 1982; Witkowsky et al. 1990; Sardans 1997; De la Fuente et al. 1997). According to Grime (1973, 1979), the intensity of competition is low in habitats limited by nutrients. However, experimental results frequently support the opposite conclusion: in unproductive soils, competition for nutrients is intense (Newman 1973; Chapin & Shaver 1985; Tilman 1987; Wilson & Shay 1990; Wedin & Tilman 1993).

In chaparral the presence of shrubs reduced establishment, survival, total biomass and vegetative cover of understorey herbs when the soil was watered, suggesting that there is competition for nutrients (Swank & Oechel 1991). However, few studies have examined whether different levels of mineral availability induce different intensities of competition. Vilà & Terradas (1995) found that removal of neighbouring vegetation increased shoot growth and sprout recruitment of *Erica multiflora* in a Catalan 'garrigue' deficient in P. Addition of N-P-K fertilizer to the soil slightly intensified the negative effect of neighbours.

In a similar community, Sardans (1993) found that fertilization with P around *Pinus halepensis* saplings increased the strength of the negative effect of neighbours. In a common garden experiment, the negative effect of neighbours on *P. halepensis* and *Quercus ilex* ssp. *ballota* seedling growth was stronger in fertile rather than in infertile treatments depending on the soil type (Sardans 1997). In summary, neighbours can reduce plant yield under infertile conditions and competition can be more intense when soil nutrients are not limiting.

Light

In dense, well-developed stands competition for light determines the vertical structure of communities (Miller & Mooney 1974). Observational studies suggest that shaded overstorey trees or shrubs have a detrimental effect on understorey species. For example, the decrease of light levels due to evergreen oak *Quercus agrifolia* determined the species composition of the understorey (Parker & Muller 1982). McPherson & Muller (1967) suggested that competition for light is implied in the elimination of some shrub species in the chaparral. Rundel et al. (1987) found small shrubs thinned under shading of adult individuals and reported that in the shade of resprouting *Adenostoma fasciculatum* or other shrubs seedlings were etiolated and smaller than more exposed seedlings.

Experimental shading by meshes simulating canopy overlap have assessed that a decrease in irradiance has a negative effect on plant performance (McPherson & Muller 1967; Mahall & Schlesinger 1982; Sparks & Oechel 1993). In a Catalan machia, shading also decreased sprouting (Canadell 1995) but the effect was less intense than root competition (Vilà 1997).

However, field manipulations (Thomas & Davis 1989) did not demonstrate an apparent negative relationship between shade due to herb canopies and seedling mortality in the chaparral during succession after fire. Shading by dominant species can decrease water stress of understorey species and can increase water availability.

Facilitation

Some studies conducted in order to study competition have found the opposite effect. Positive interactions or facilitation (nurse effects) among plants have been reported especially between trees and understory vegetation (e.g. Parker & Muller 1982; Ovalle & Avendaño 1987; Callaway et al. 1991; Callaway & Davis 1998). Nurse effects are driven by direct amelioration of the microenvironment below the plant and, indirectly, by protection from herbivores, attraction of pollinators or beneficial changes in soil quality under canopies (Callaway 1995). For example, shaded microsites under herbs in the chaparral have lower maximum air temperatures than unshaded ones (Thomas & Davis 1989) and this could benefit seedling establishment of shrubs specially in arid areas (Callaway 1995).

There is evidence of a facilitation effect of adult plants on seedlings. In a Chilean woodland, Ovalle & Avendaño (1987) found that grasses were more productive under *Acacia caven* canopies than in open areas, due to an improved hydric balance. Similar positive effects have been detected in California. Seedlings of *Quercus agrifolia* were more frequently found under chaparral shrubs than in open areas where they were browsed more frequently than under the protection of shrub canopies. Some seedlings from planted acorns under several shrubs survived, whereas all seedlings in open areas had disappeared or dried out (Callaway & D'Antonio 1991). Acorns may be better protected against avian and mammalian predators under shrub canopies. Keeley (1992) reported that seedling establishment of several chaparral shrubs was enhanced under closed canopies and litter layers. Litter depth may protect from seed predation or increase the water holding capacity that may prevent the drying of seeds and thus reduce drought stress on seedlings. Similarly, Pugnaire et al. (1996a, b) found that the growth of herbs below the shrub *Retama sphaerocarpa* was better than in open areas in the most semi-arid regions of Spain (see also Haase et al. 1996, 1997). Facilitation may also occur among adult shrubs. The cover of *Adenostoma fasciculatum* is positively associated with *Ceanothus greggii* growth in fenced plots because it may provide protection from herbivory (Bullock 1991).

Allelopathy

The release of toxic substances by mature shrubs may inhibit plant germination, survival or growth as a direct negative effect of competition which may explain lower herb germination under mature shrubs than in gaps (Muller et al. 1968; McPherson & Muller 1967,1969;

Christensen & Muller 1975a). It is believed that dormancy in many refractory seeds may be enforced by exogenous inhibitors leached from the shrub foliage during rain. Following a fire, the negative effect of these shrub-derived toxins would be eliminated.

Leachates from plant parts have a negative effect on plants grown in bioassays (McPherson et al. 1971). Christensen & Muller (1975b) demonstrated that aqueous *Adenostoma fasciculatum* leaf- and canopy extracts that contained phenolic acids (Kaminsky 1981) suppressed germination and growth of herbs in chaparral. In Californian savannas, root leachates of *Quercus douglasii* seedlings, composed mainly of hydrophobic components, reduced the biomass of *Bromus diandrus* (Callaway et al. 1991). Foliage exudates of several Australian mediterranean trees reduced seed germination of *Avena fatua* (Hobbs & Atkins 1991). Leaf exudates of *Cistus ladanifer* that contained phenolic compounds inhibited germination of the least abundant species in the community (Chaves & Escudero 1997).

Plant exudates can also have an indirect effect on the surrounding environment and reduce neighbouring plant germination or growth, independent of toxicity. Some chaparral species produce substances which accumulate on the soil surface and make the soil less wettable (DeBano et al. 1967). The reduction of some herbs under oak trees could be a consequence of root exudates that inhibited the growth of nitrifying bacteria (Wilson & Rice 1968) which would decrease N-availability at the plant level. Some chemical compounds produced in the process of litter decomposition are inhibitory for both heterotrophic and autotrophic bacteria and fungi (Chou & Muller 1972) and thus, rates of mineralization may be reduced. Kaminsky (1981) presented evidence that phytotoxins of microbial origin collected from soil beneath *A. fasciculatum* canopies were capable of inhibiting germination of seeds and growth of herbs. However, the nature of the association between specific soil microbes and specific species remains unclear.

Nevertheless, the importance of allelopathy in natural communities has been much debated because some experiments have been considered as unrealistic (Whittaker & Feeny 1971; Rice 1974). Leachates have a high osmotic concentration that may prevent germination of seeds independent of their chemical composition (Anderson & Loucks 1966). In several studies where the role of allelopathy in determining inhibition or reduction of neighbours' growth is assessed, low light levels (Christensen & Muller 1975a) and foraging of animals (Bartholomew 1970) may explain the negative effect of shrub canopies on herb establishments. Furthermore, herb germination is not always suppressed by shrubs. Swank & Oechel (1991) did not find that herbs germinated less under mature *A. fasciculatum* shrubs than in gaps as found by Sweeney (1956) and Kaminsky (1981).

In summary, although plant leachates may have a direct or indirect negative effect on plant neighbours, their occurrence is difficult to demonstrate and their effect may not be consistent. Hobbs (1984) showed that leachates from several *Ericaceae* can have a stimulating, inhibiting or null effect on the species itself or on other species, and Li & Romane (1997) described a clear case of 'auto-allelopathy' in *Quercus ilex* in southern France.

Competition and fire

Fire is the most significant disturbance in Mediterranean-type ecosystems and its study has received much attention during the last decades. Two main regeneration strategies have been proposed during stand recovery after fire: seeders and resprouters (Wells 1969; Naveh 1974; Keeley 1977; Keeley & Zedler 1978). Seeders are killed after fire and reappear by seedling recruitment, while resprouters regrow vegetatively after fire by underground structures, mainly from basal sprouts. A greater and faster regeneration of resprouters as compared to reseeders suggested that long-lived species with the ability to survive after fire should have an overwhelming advantage in competition (Keeley & Zedler 1978). To our knowledge, only one study has tested this hypothesis and the results were not supportive. Kummerow et al. (1985) found that removal of *Adenostoma fasciculatum* sprouts did not increase survival of the seeder *Ceanothus greggii* 6 months after fire.

Most studies have found a weak effect of competition after fire. In montane chaparral, shrub removal did not affect seedling density in most functional groups (Tyler 1995). In maritime chaparral, shrub removal did not affect seedling emergence, but did improve survivorship of annual herbs (Tyler 1996). In a Catalan shrubland, Vilà & Terradas (1995b) did not find a significant effect of several neighbours on resprouting *Erica multiflora* after fire.

Differences in regeneration after fire can explain the coexistence of species at the adult age. Lottery models, i.e. non-equilibrium models, have been developed to explain coexistence by competition during establishment in highly disturbed communities (Chesson & Warner 1981). In mediterranean-type vegetation, competition among recruits would be for space which would be allocated randomly. This theory explains that even if segregation does not occur among mature plants, it may occur at the regeneration stage allowing species to coexist. For example, Lamont & Bergl (1991) found that the three co-occurring adult *Banksia hookeniana*, *B. attenuata* and *B. menziesii* in a sand-dune habitat in western Australia had the same water potential, similar phenology, non-significant different shoot dimensions, and intermingled roots with equal root architecture and extension. However, these co-occurring *Banksia* spp. showed different regeneration characteristics i.e. seed release from unburned cones, post-dispersal predation or field germination (Cowling & Lamont 1987).

Disturbance reduces or eliminates plant cover and increases availability of resources (Sousa 1984). After fire there is an increase of soil resources (Fox & Fox 1987; Tyler & D'Antonio 1995). Nevertheless, few studies have been conducted considering the interaction between the increase in resources and the intensity of competition after fire. In coastal chaparral, Tyler & D'Antonio (1995) found that *Ceanothus impressus* seedling survival and growth was associated with an increase in the distance of near neighbours while predawn xylem pressure potentials tended to be greater when neighbours were further away, suggesting that they were competing for water. In a Catalan shrubland, Sardans (1997) found that fertilization with phosphorus (P) increased *Pinus halepensis* seedling biomass after neighbour removal, suggesting that plants were competing for P after fire.

Fire and competition contribute to shape small-scale community patterns (Bond & van Wilgen 1996). Fire interacts indirectly with competition by increasing the susceptibility to flame damage in dense vegetation. Ne'eman et al. (1992) reported that high fire intensity under *Pinus halepensis* reduced post-burn recruitment of both herb and shrub species near pine skeletons. Higher seed mortality under dense vegetation may be common due to the high temperatures reached and the inhibitory effect of ashes on seed germination. Consequently, reduction in seedling density would decrease competition. Fire may also decrease the aggregation of species in burned patches. After fire, seeds of the serotinous *Bankia* spp. aggregate in unburned litter patches generating clumps of seedlings. Seedling mortality by self-thinning in litter patches is higher than in burned patches where less seedlings are established (Enright & Lamont 1989).

Overall, although it is assumed that there is an increase of resources after fire, resource competition occurs especially among crowded seedlings. More field experiments are needed to investigate if the intensity of competition is lower after fire than in mature stands. Furthermore, fire-competition feedbacks such as the effect of crowding in the fire regime deserve further attention.

Concluding remarks and future directions

There is a clear evidence that both interference competition (allelopathy) and resource competition affect plant size, cover, growth, survivorship, germination and flowering in mediterranean communities. However, most studies do not assess the abiotic resources underlying competition. Watering and shading experiments support competition of plants for water and light. Plant growth and reproduction are also limited by nutrients. However, there is scarce information on which specific minerals plants compete for. Furthermore, no study has investigated if competition for water is more important than competition for nutrients.

Species may compete with some species but not with others and with certain particular species at some times or places but not at others (Connell 1983). For example, oak seed germination and seedling recruitment is not inhibited by mature oak canopies (Borchert et al. 1989) or mature chaparral shrubs (Callaway & D'Antonio 1991) but is dramatically affected by grasses (Schultz et al. 1955). Likewise, a species responds to competition differently depending on its regeneration and life history stage (Fowler 1986), especially in woody plants. However, there are no conclusive results on whether competition is stronger in mature stands than in regenerating stands after fire nor the nature of competition in both stages.

It is also assumed that plant competition is asymmetric (Connell 1983; Weiner 1990). However, few studies have conducted reciprocal treatments to generalize if asymmetry is common between pairs of species in mediterranean vegetation (Went et al. 1952; Fuentes & Gutierrez 1981).

Communities in mediterranean regions are especially interesting because one can investigate the interaction of competition with environmental stress and disturbance. Future studies addressing the following questions may provide the greatest contribution to understanding the role of competition in mediterranean-type vegetation.

1. *What is the importance of competition compared to other biotic factors?* Most competition studies have not included the role of other ecological constraints in determining community structure (but see Swank & Oechel 1991; Tyler 1995, 1996). For example, herbivory is responsible for many demographic vegetation changes, especially after fire (Mills 1986). Competition may interact with herbivory by decreasing herbivore pressure in crowded vegetation compared to open areas (Vilà & Lloret 1997) or by changing competitive superiority between species pairs (Mills 1986). More emphasis should be put on investigating competition-herbivory feedbacks in mediterranean-type vegetation.

Table 2. Number of studies supporting and proving different types of competition in mediterranean vegetation. See text for study differences between support and prove of competition.

Type of competition	Support	Prove
Abiotic resources	11	12
Soil resources	-	6
Water	7	7
Nutrients	3	-
Phosphorus	-	1
Light	11	4
Allelopathy	6	4
Susceptibility to herbivory	1	-

2. *Which soil nutrient do plants mainly compete for?* Several studies have proved that plants compete for soil resources especially water (Table 2). However, field experiments that combine neighbour manipulation with soil fertilization with N, P and other minerals are necessary in order to find the particular nutrient plants mainly compete for.

3. *Does competition switch to facilitation when there is an increase in abiotic stress?* Plant-plant interactions can be negative or positive depending on environmental stress (Greenlee & Callaway 1996; Callaway & Davis 1998). Most studies conducted in mediterranean regions have only lasted from 1 to 2.5 yr (Fig. 1) and this period of time is too short to detect temporal changes in competition intensity. Given that mediterranean regions have high interannual raining variability (Kruger et al. 1983), these regions are excellent scenarios to study temporal variability in the intensity of competition.

4. *Is competition after fire driven by the same resources as in mature stands?* As stated before, mediterranean fire-prone communities are poor in nutrients. However, fire releases large amounts of nutrients into the soil (Kruger et al. 1983). Nevertheless, such studies are not conclusive to determine whether resource competition is more intense after fire than in mature stands. Competition studies within resource gradients and with a chronosequence of fire frequency would give more insight into the importance of resource competition in plant succession after fire.

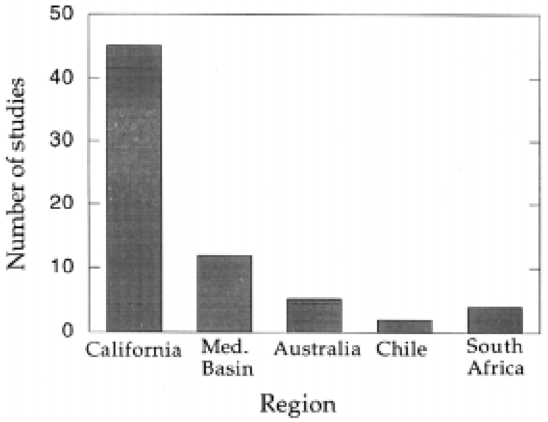

Fig. 1. Number of competition studies conducted in mediterranean regions of the world.

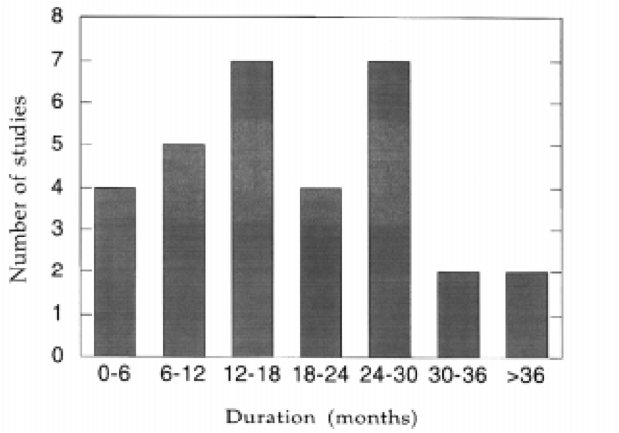

Fig. 2. Duration of competition studies in mediterranean regions of the world.

5. *Are there differences among different mediterranean regions?* Not all mediterranean areas have been explored with the same intensity (Fig. 2). Most of the experiments have been conducted in California. The scarcity of studies conducted in other mediterranean regions, especially in South Africa and Chile, makes it difficult to generalize on the role of competition in mediterranean communities across the world. Since different regions vary in disturbance regime and soil fertility (Kruger et al. 1983), they may also vary in the importance of competition in structuring plant communities. More field observations and experiments should be conducted in mediterranean regions other than California.

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App. 1. Characteristics of studies on plant competition in mediterranean vegetation.

Life form, stage^1	Area^2	Effects^3	Type of comp.^{4}	Type of study^5	Reference
Shrub/shrub	CA	– seed set	light	Shading	Alpert et al. (1985)
Tree/grass	CA	– gr. *	ab. res. ?	Co (36 mo)	Bartolome (1986)
Tree/tree sdl.	CA	–, + germ. *	light ?	Ct	Bochert et al. (1989)
Shrub/shrub	CA	+ height, dens. *	herb. prot. ?	Ct	Bullock (1991)
Shrub/tree sdl.	CA	+ surv. *	water ?	Ct, Ae (26 mo)	Callaway & D'Antonio (1991)
Tree/grass, forb	CA	–, + gr. *	nut., all. ?	Ct	Callaway et al. (1991)
Shrub/tree sdl.	CA	0 surv.	light	Ae (24 mo)	Callaway (1992)
Shrub/shrub	MB	+ shoot gr.		Re (13 mo)	Canadell (1995)
Shrub/grass	CA	– dens., gr. *	all. ?	Le	Chou & Muller (1972)
Shrub/shrub sdl.	CA	– surv., germ., gr.	light, all. ?	Re (3 mo)	Christensen & Muller (1975 a, b)
Shrub/shrub	SA	– diversity *		Ct	Cowling & Gxaba (1990)
Grass/shrub	CA	– surv., gr.	ab. res.	Cge, Ge	Da Silva & Bartolome (1984)
Shrub/shrub	SA	+ xylem*	water ?	Ct	Davis & Midgley (1990)
Grass/grass	CA	– surv., gr.	ab. res.	Ae (24 mo)	Dyer & Rice (1997)
Shrub/shrub	CH	– canopy size *	ab. res. ?	Na	Fuentes & Gutierrez (1981)
Ann. grass, forb/tree sdl.	CA	– germ., gr. & surv.	water	Cge (7 mo)	Gordon & Rice (1993)
Ann. grass, forb/ tree sdl.	CA	– root gr., gr.	water	Cge (8 mo)	Gordon et al. (1989)
Grass/tree sdl.	CA	– germ., surv.	ab. res., all.	Ae (1 yr)	Griffin (1971)
Shrub spr./shrub spr.	MB	– germ., recr.	light, water ?	Co	Herrera (1997)
Shrub/ann. grass, ann./per.	AU	– surv.	ab. res., all.	Ct, Re (32 mo)	Hobbs & Atkins (1991)
Shrub/grass	CA	– germ., gr.	all.	Le, Ae (20 mo)	Kaminsky (1981)
Shrub sdl./shrub sdl.	CA	– surv.		Ct	Keeley & Zedler (1978)
Shrub/grass, grass/grass	CA	– cover *	ab. res. ?	Ct	Keeley et al. (1981)
Tree sdl., sapling	CA	+ recr. *	ab. res. ?	Ct	Keeley (1992)
Shrub spr./shrub sdl., herb	CA	0 gr.	ab. res. ?	Re (23 mo)	Kummerow et al. (1985)
Shrub sdl./shrub sdl.	AU	– surv.	ab. res.	Ae (9 mo)	Lamont et al. (1989)
Tree/shrub sdl.	AU	– surv. *	water	Le, Ca	Lamont (1985)
Tree/grass	CA	–, + cover, gr. *	ab. res. ?	Co	McClaran & Bartolome (1989)
Shrub/shrub	CA	– gr., dens. *	light ?	Ct	McPherson & Muller (1967)
Shrub/shrub	CA	– surv., gr.	light, all. ?	Ge, Le, Co	McPherson & Muller (1969)
Shrub/grass	CA	– gr.	all.	Le	McPherson et al. (1971)
Shrub/shrub	SA	– dens. *	ab. res. ?	Ca	Midgley &Watson (1992)
Shrub/shrub	CA	– surv. *	water ?	Ct	Montygierd-Loyba & Keeley (1987)
Shrub/shrub	AU	– surv. *	ab. res. ?	Ca	Morris & Myecough (1983)
Shrub/shrub, grass	CA	– cover, dens. *	all. ?	Ca, Le	Muller et al. (1968)
Tree/grass	CA	– gr.	light, nut. ?	Re (72 mo)	Murphy & Crampton (1964)
Tree/grass	CH	+ gr.	ab. res.	Ct, Re	Ovalle & Avendaño (1987)
Tree/grass, forb	CA	–, + dens., gr. *	light, nut. ?	Co	Parker & Muller (1982)
Grass/grass	MB	–, 0 germ., gr.	water	Ge	Peco & Espinares (1994)
Shrub/shrub	SA	– surv., gr.	soil res.	Cge	Richards et al. (1995)
Shrub/shrub	CA	– surv., dens. *	light ?	Ca	Riggan et al. (1988)
Shrub/shrub sdl.	CA	– surv., gr. *	light ?	Ct (12 mo)	Rundel et al. (1987)
eighbours/tree	MB	– gr.	nut.	Re (12 mo)	Sardans (1997)
Tree sdl./tree sdl.	MB	– gr.	P	Cge (24 mo)	Sardans (1997)
Shrub/shrub	CA	– shrub dens. *	water, light ?	Ct	Schlesinger & Gill (1978)
Shrub/shrub	CA	– shrub dens. *	water, light ?	Ct	Schlesinger & Gill (1980)
Grass/shrub sdl.	CA	– surv., gr.	ab. res.	Ae (5 mo)	Schultz et al. (1955)
Shrub/grass	CA	– cover, dens., fl. *	ab. res., all. ?	Ca	Shmida & Whittaker (1981)
Grass/grass	CA	– dens., gr.	water ?	Ca, Re (6 mo)	Schultz & Biswell (1952)
Shrub/shrub	CA	– shrub dens. *	ab. res. ?	Ct	Stohlgren et al. (1984)
Shrub/herb, grass	CA	– germ., surv., cover	soil res.	Re (12 mo)	Swank & Oechel (1991)

App. 1 (*cont.*)

Life form, stage[1]	Area[2]	Effects[3]	Type of comp.[4]	Type of study[5]	Reference
Sdl./herb	CA	– surv. *		Ct	Sweeney (1956)
Neighbours/ann.	MB	– surv. gr., repr.	water, nut.	Re, Ae	Thébaud et al. (1996)
Shrub sdl./shrub sdl.	CA	–, + surv.	water, light	Ct, Re (12 mo)	Thomas & Davis (1989)
Shrub sdl., grass/shrub sdl.	CA	– surv., gr. *	water ?	Ca	Tyler & D’Antonio (1995)
Shrub sdl., spr./shrub sdl., spr.	CA	0 dens., regr.	ab. res.	Re (12 mo)	Tyler (1995)
Shrub/sdl.	CA	–, 0 germ., - surv.		Re (11 mo)	Tyler (1996)
Neighbours/shrub	MB	– shoot gr., fl.	soil res.	Re (18 mo)	Vilà & Terradas (1995a)
Neighbours/shrub	MB	– sprouting		Re (27 mo)	Vilà & Terradas (1995b)
Neighbours/shrub	MB	– sprouting, fl.		Re (30 mo)	Vilà &Terradas (1995c, 1998)
Neighbours/shrub	MB	– sprouting		Re (7.5 mo)	Vilà et al. (1994)
Neighbours/shrub	MB	– sprouting, fl.	light, soil res.	Re (22 mo)	Vilà (1997)
Shrub/shrub	MB	– sprouting		Re (13 mo), Na	Vilà et al. (1998)
Shrub/shrub, shrub/grass	CA	– germ., recr.	ab. res.	Re, Ca (24 mo)	Went et al. (1952)
Shrub/grass	CA	– surv., dens. *	ab. res. ?	Ca	Westman (1981)
Grass/shrub	CA	–, 0 surv., dens.	water	Ae (6 mo)	Williams & Hobbs (1989)
Shrub/shrub	AU	–, 0 surv., dens. *	ab. res. ?	Ca	Zammit & Westoby (1987a)
Shrub/shrub	CA	– surv., dens. *	ab. res. ?	Ca	Zammit & Zedler (1992)

[1] Plant life form, stage effect/plant life form, stage response; ann = annual; per = perennial; sdl. = seedling; spr. = sprout;

[2] AU = Australia, CA = California, CH = Chile, MB = Mediterranean Basin, SA = South Africa;

[3] – = negative effect; + = positive effect; 0 = null effect; dens. = density, fl. = flowering, germ. = germination; gr. = growth; recr. = recruitment; repr. = reproduction, surv. = survival; xylem = xylem pressure potential; * = competition may occur, but has not been proven;

[4] ab. res. = abiotic resource; all. = allelopathy; herb. prot. = herbivory protection, nut. = nutrient, res. = resource. ? = the type of competition is suggested but not proven;

[5] Ae = additional experiment; Ca = correlational analysis; Cge = common garden experiment; Co = comparisons (mainly open *vs.* under canopy); Ct = changes through time; Ge = greenhouse experiment; Le = laboratory experiment; Na = neighbourbood analysis; Re = removal experiment; Sa = spacing analysis. In parentheses: duration of the study in months.