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Interactions between mediterranean shrub species eight years after experimental fire

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Abstract

This paper is part of a wider study in which different combinations of species were assayed for the revegetation of experimentally burnt heathlands. In this particular case, we determined whether there was any interaction between the dominant species, *Erica australis*, which recovered by vegetative resprouting, and the only successful woody species sown, *Cytisus* sp., eight years after fire and seven years after sowing. A detailed study was carried out on each square metre of cover and height of both species in three 160 m^2 plots. Total cover exceeded 100% in all subplots sown with *Cytisus*, whereas it did not reach 65% in the others, when both species coexist together. There was an inverse correlation between the covers of both species and a positive correlation between the height of *Erica australis* and the cover and the height of *Cytisus*. There was no significant difference in *Erica* cover in plots sown with *Cytisus* and plots not sown. There could be some competition for light, but both species are capable of coexisting with high canopy overlap, for at least some time. *Cytisus* is expanding from the seeded subplots, suggesting that the dense cover of *Erica australis* does not impede the establishment of *Cytisus*.

Introduction

Species that are typical of communities with frequent disturbances, as occurs in most Mediterranean ecosystems, regenerate by resprouting or from the soil seed bank (Naveh 1974; Keeley and Zedler 1978; Keeley 1986, 1992a, 1992b; Trabaud 1987). It is generally assumed that vegetative regeneration is an advantage in competition amongst species (Hanes 1981; Trabaud 1984, 1987; Bond and van Wilgen 1996; Pugnaire et al. 2000), since resprouters have a well-developed root system and only need to regenerate their aboveground parts. This advantage would make them successful in competition for light, nutrients and above and underground space, although it is more difficult for them to colonise new microsites. However, Kummerow et al. (1985) found that removal of *Adenostoma fasciculatum* sprouts in Southern California chaparral did not increase survival of the seeder *Ceanothus greggii* six months after fire.

In most of the Mediterranean basin, shrub communities have spread considerably due to ancient degradation of the forest and abandonment of pastures and cultivated fields. The result has been an increase in the risk of fires and loss of late-successional vegetation (Moreno et al. 1998; Luis-Calabuig et al. 2000; Reyes et al. 2000). Post-fire recovery in shrublands is usually quite rapid because of vegetative regrowth. However, repeated burning slows succession in these secondary stages and stops progression towards mature stages of forest (*Quercus pyrenaica* forest in the study area).

It has been pointed out that the effect of competition is minimal after a disturbance like fire, even though the same species compete when they have recovered to a certain size (Vilà and Terradas 1995). Generally, the problem of competition amongst species has been relatively neglected in fire-prone communities, even though it is of crucial importance for understanding function in these communities and for managing biodiversity (Bond and van Wilgen 1996). Although competition may also occur after fire, it is not clear if it is less intense than in mature stands (Vilà and Sardans 1999).

This paper is part of a wider study in which different combinations of herbaceous and woody species were assayed for the revegetation of experimentally burnt heathlands. Our aim was to find the most suitable combination of species to slow erosion on a short-term basis and favour succession towards forest over the long term (Fernandez-Abascal et al. 1998). Of the assayed species, only the shrub *Cytisus* sp. established well, and in a few years became dominant in the plots where it was sown. Our aim is to determine whether there is competition between the dominant species, *Erica australis*, which recovers by vegetative resprouting, and the only successful species sown, *Cytisus* sp. eight years after fire and seven years after sowing. Both species are highly branched evergreen shrubs (Tutin et al. 1964–1980) so competition, at least for space, would be expected.

In previous studies analyses have been carried on out the dynamics of growth in both species during the first years (Fernandez-Abascal et al. 1998; Marcos et al. 1999). *Erica australis* is characterised by its active resprouting capacity, which initially gives it an advantage in occupying space due to its well-developed root system, whilst other woody species had to start growing from seeds.

Material and methods

The study was conducted in an *Erica australis* shrub area in the province of León (NW Spain), M.T.U. coordinates: 30TUN282277. The slope is 10%, orientation N–NE and elevation 1063 m above sea level. The climate is subhumid Mediterranean, with a dry period in summer. Late succession vegetation should be *Quercus pyrenaica* forest, but most of the area is heathland, as a result of pasture being deserted in the 1960s with human migration from rural areas. The mean aboveground biomass was about 1700 g/m^2, with most of this biomass (1000 g/m^2) contributed by *Erica australis* (Fernandez-Abascal et al. 2002), with a mean cover 50% and a mean maximum height of 1 m.

Three 16 × 10 m plots were burned in July 1993 and revegetated in March 1994, using different species combinations, all of them natural to the area. Fifteen permanent subplots measuring 4 m^2 were established in each plot (4 treatments and a control replicated three times). These subplots were distributed according to the scheme in Figure 2. Treatments were randomly assigned to subplots. Seed quantity was estimated by weight in order to have 20,000 seeds, equally divided amongst the species assigned to each treatment, per square meter in each subplot sown.

1. Sowing of herbs (subplots H): *Lotus corniculatus* (40 g), *Agrostis capillaris* (2.4 g) and *Festuca rubra* (34 g).
2. Sowing of herbs and shrubs (subplots HS): *Lotus corniculatus* (20 g), *Agrostis capillaris* (1.2 g), *Festuca rubra* (16 g), *Cytisus* sp. (10 g), *Calluna vulgaris* (7 g) and *Erica australis* (24 g).
3. Sowing of herbs and plantation of oaks (subplots HO): *Lotus corniculatus* (20 g), *Agrostis capillaris* (1.2 g), *Festuca rubra* (16 g) and *Quercus pyrenaica* (4 oak seedlings, 2 months old).
4. Sowing of herbs and shrubs and plantation of oaks (subplots HSO): *Lotus corniculatus* (20 g), *Agrostis capillaris* (1.2 g), *Festuca rubra* (16 g), *Cytisus* sp. (10 g), *Calluna vulgaris* (7 g), *Erica australis* (24 g) and *Quercus pyrenaica* (4 oak seedlings, 2 months old).
5. Unsown control subplots with natural post-fire regeneration (subplots C).

A combination of *Cytisus scoparius* and *C. striatus* was used. Both species coexist in these areas, though they were not found in plot sampling conducted before the experimental fire. In the case of shrub and herb species, sowing was by scattering the seed (Fernandez-Abascal et al. 1998).

Initial results are reported elsewhere (Fernandez-Abascal et al. 1998; Marcos et al. 1999). In July 2001 we measured the cover and maximum height of both species in each one of the 160 m^2 of each plot.

Data were examined with analysis of variance to test for differences in the cover and height of *Erica australis* between subplots sown with *Cytisus* and subplots that had not been sown. Data were examined for normality and homocedasticity test (David et al. 1954; Cochan 1941). Regression analysis tested whether the cover and height of *Cytisus* varied with the cover and height of *Erica australis*. In this case data from quadrats in which either of the species did not appear were not taken into consideration.

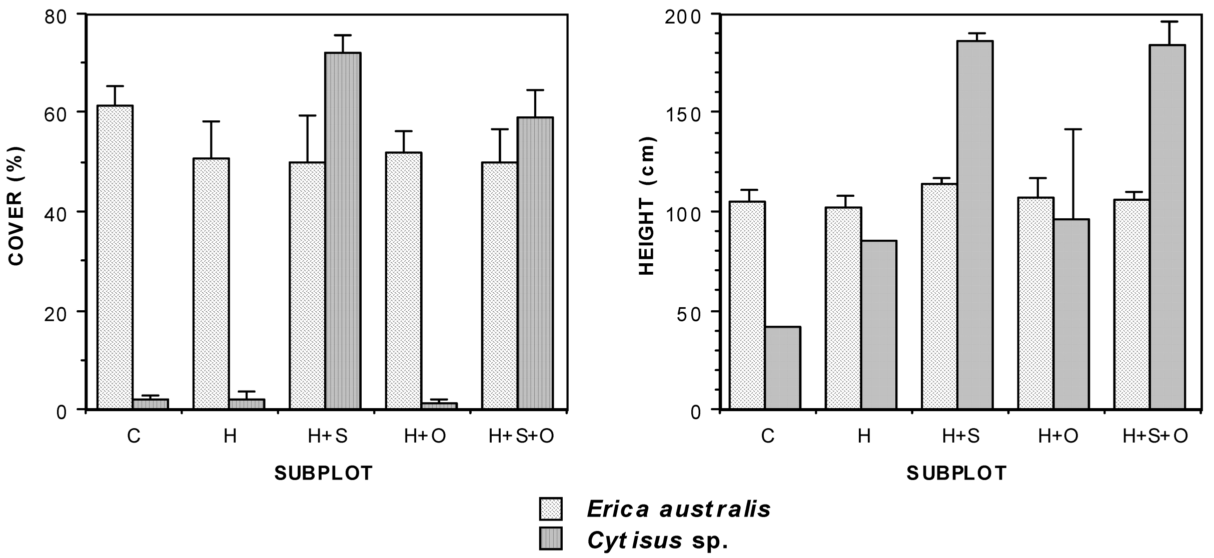

Figure 1. Mean and standard error of *Erica australis* and *Cytisus* spp. cover and height in the subplots of the three plots, eight years after experimental burning and seven years after sowing.

Results

Erica australis, the dominant species before experimental burning, recovered by vegetative resprouting and eight years later had mean covers between 50% and 62% (Figure 1). No significant differences were detected ($p = 0.72$) when comparing *Erica* cover in subplots sown and unsown with *Cytisus*. *Cytisus* cover was clearly larger in the sown subplots, the average being between 59% and 72%, whilst in the non sown ones it did not exceed 5%. Total cover (both species) was > 100% in all subplots sown with *Cytisus*, but did not reach 65% in the others, and the differences were statistically significant ($p < 0.001$).

The mean maximum height per square metre in the sown subplots was greater in *Cytisus* (above 1.8 m) than in *Erica* (with mean values between 1.0 and 1.2 m). Again, there were no significant differences in the height of the latter species, whether the former was present or not.

Erica australis was present in all the quadrats of plot 1, in 158 of plot 2, and 136 of plot 3 (Figure 2). *Cytisus* colonised areas were it was not sown, but it colonised a considerably smaller area than did *Erica*, occupying 71 m^2 in plot 1, 84 in plot 2 and 69 in plot 3. The spatial distribution of *Cytisus* was clearly clumped, but so was that of *Erica australis* (significant differences from random dispersion, $p < 0.001$) in the three plots. In the 126 m^2 where both species occured, total cover was > 100% in 102 quadrats and > 150% in 15.

Regression between the covers of *Erica australis* and *Cytisus* revealed no significant tendencies when the 480 quadrats were considered (160 $m^2 \times 3$ plots). If the quadrats in which one of the two species did not appear are excluded from these analyses, there was a highly significant negative relationship ($p < 0.001$) between the species (Figure 3).

There was a significant and positive relationship between the height of the species ($p < 0.001$), with *Cytisus* plants reaching a height > 2 m in 40 quadrats, and some even surpassing 3 m. There was also a positive relationship ($p < 0.05$) between the height of *Erica australis* and the cover of *Cytisus*. However, the comparison between the cover of *Erica australis* and the height of *Cytisus* shows no relationship.

Discussion

The high density of individuals in Mediterranean evergreen shrubland suggests that competition may be strong. Experiments, however, are needed to confirm this hypothesis (Vilà and Sardans 1999). Although experiment was not initially focused on competition, it plays a potential role during succession. The aim of sowing *Cytisus*, a leguminous shrub usually associated with better soil quality than *Erica australis*, was to encourage succession towards a forest community

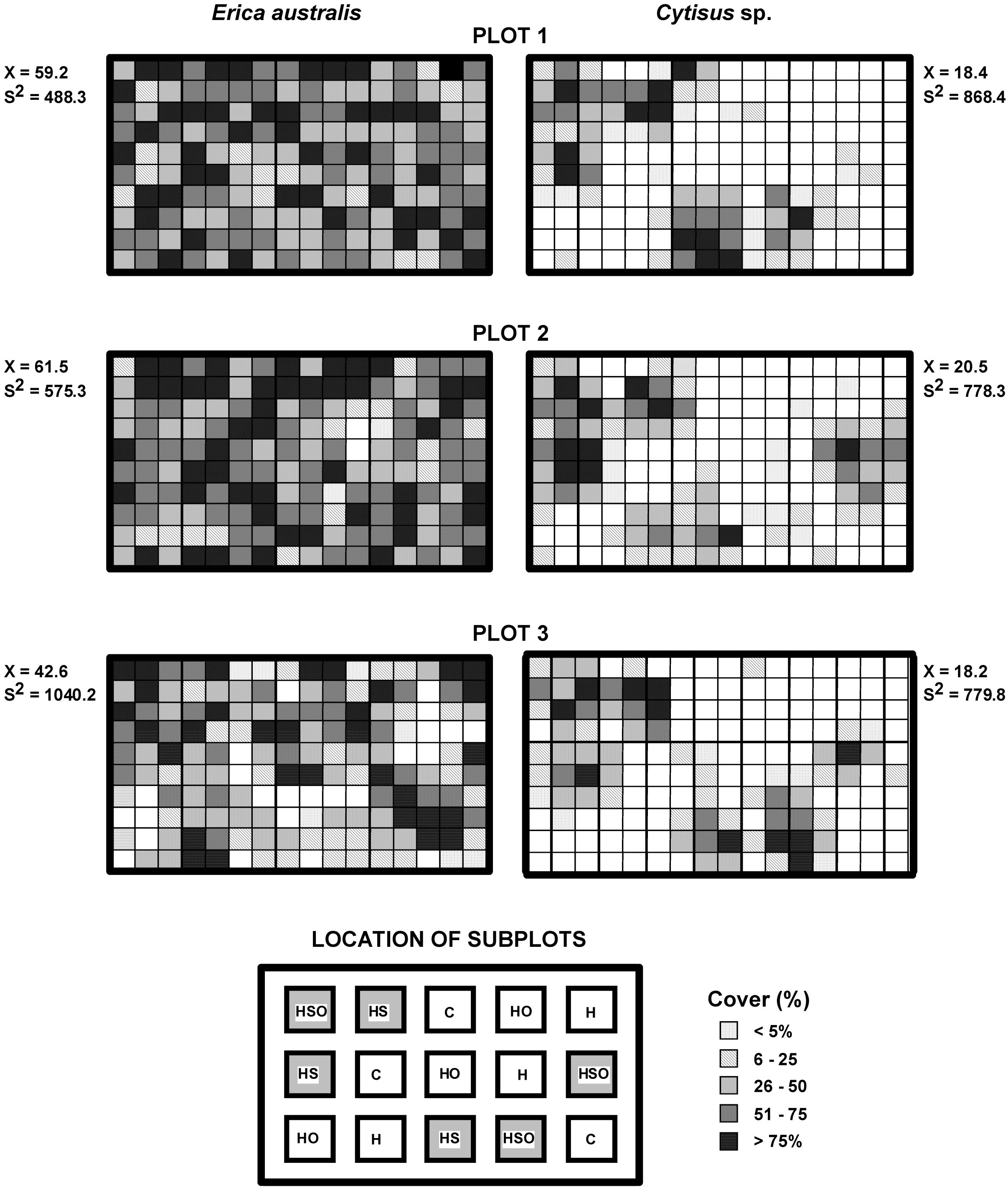

Figure 2. Cover (%) per square metre of *Erica australis* and *Cytisus* sp. in the sampling carried out in the summer 2001, eight years after experimental fire and seven years after sowing. Mean (X) and variance (S^2) for each species and plot are included. A sketch of location of the subplots in each plot is also included. In plot 2, row 3, subplot H was replaced by subplot HSO by mistake during sowing (the order in this plot, row 3, was: HO = herbs + oaks, HSO = herbs + shrubs + oaks, HS = herbs + shrubs, H = herbs, C = control)

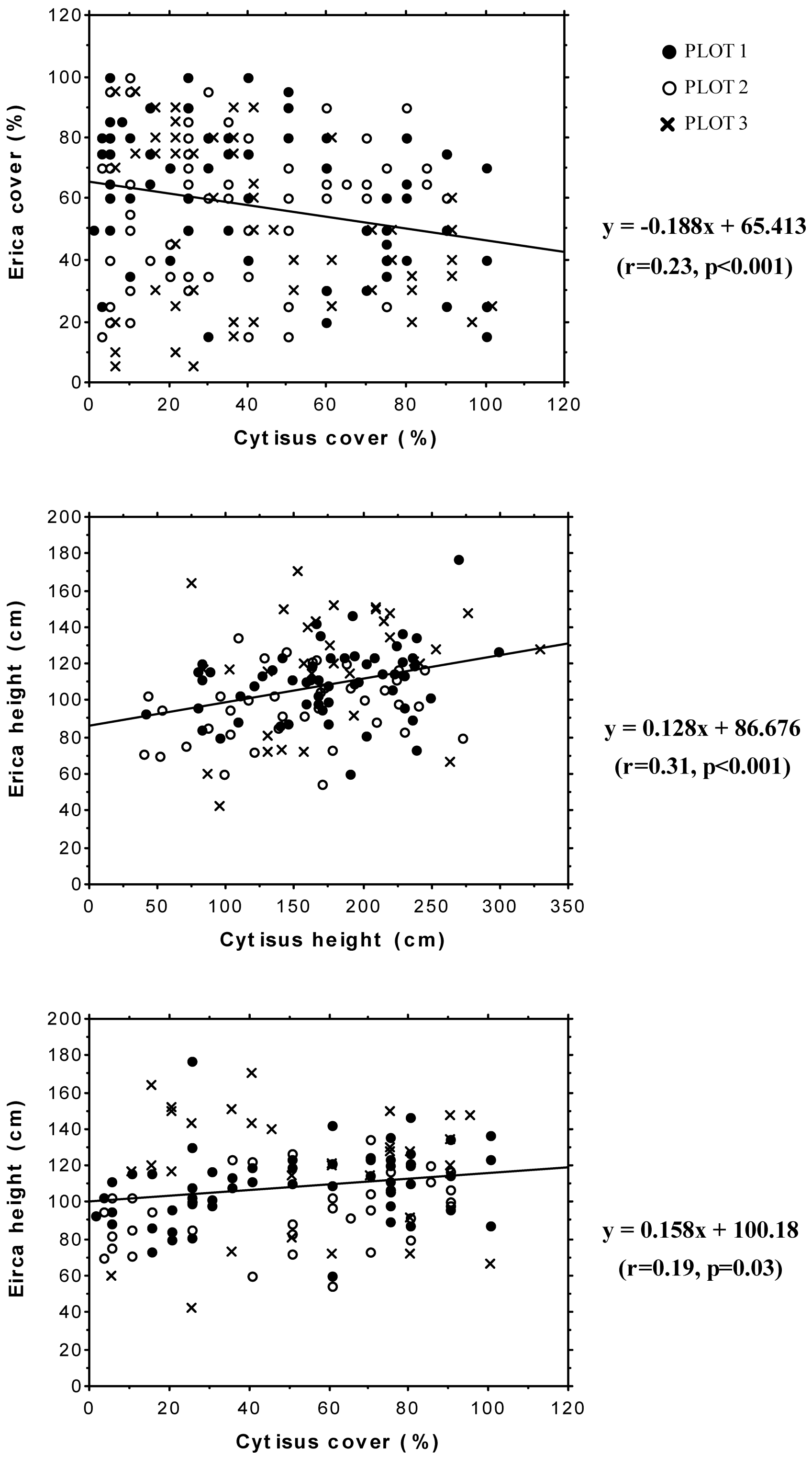

Figure 3. Regression analysis on *Cytisus* sp. and *Erica australis* cover, *Cytisus* sp. and *Erica australis* height and *Cytisus* sp. cover and *Erica australis* height.

(Fernandez-Abascal et al. 1998; Marcos et al. 1999). We expected that *Erica australis*, if not eliminated, might be displaced as dominant species over time.

After fire, *Cytisus* spp. can recover by both vegetative resprouting and seeds (Fernández-Santos and Gómez-Gutierrez 1994; Fernández-Santos et al. 1999) that are stimulated by higher temperatures during fire (Tárrega et al. 1992; Reyes and Boedo 2001). Isolated plants of this species appear in stretches of *Quercus pyrenaica* forest, close to the study area, but not in the stretches of unburnt heathlands or in those subjected to burning by shepherds. This is clearly due to the fact that there is no seed bank on the soil (Valbuena et al. 2000) since *Cytisus* seeds sown after experimental fire grew well, though somewhat slower than the natural recovery of *Erica australis* by resprouting (Marcos et al. 1999). *Cytisus* is therefore capable of germinating and growing despite the initial advantage of the resprouter (*Erica australis*). *Cytisus* spp. are typical of the understorey, and therefore have no problem germinating in the shade, which also could favour their growth. Reyes et al. (2000) found that *Cytisus striatus* has greater germination rates in the dark than with photoperiod.

Eight years after fire, *Erica australis* cover and height had recovered, coinciding with results obtained by Calvo et al. (2002). *Cytisus*, which behaves like a seeder, had < 5% cover during the first year, but reached a mean of 70% in the fourth year (Marcos et al. 1999), a similar value to that found after seven years. Initial rapid growth slowed, perhaps as a result of competition. Vilà and Sardans (1999) state that there is less competition after a fire because plant density decreases and more resources are available; as succession advances and the individuals increase in size, there is greater competition amongst plants. Fernández-Santos and Gómez-Gutierrez (1994) reported intraspecific competition in *Cytisus balansae*, with a decrease in population density between the fourth and sixth year after fire.

In the studied area, plants of both species have grown sufficiently for interaction to occur, though it is not very apparent. The cover of *Cytisus* is the same as or greater than *Erica australis* in the sown subplots. There are no obvious differences in the cover of the latter species in the subplots despite the fact that in some quadrats with high density of both species overall covers surpassed 150%. This overlap of species aboveground probably also occurs belowground (Casper and Jackson 1997) because the roots are very branched and with lignotubers to enable resprouting (Fernández-Santos and Gómez-Gutierrez 1994; Fernández-Santos et al. 1999; Moreno et al. 1999; Cruz and Moreno 2001).

Also, the spatial occupation by *Cytisus* of each plot is far from complete, though its expansion around the seeded subplots can be seen. This is probably explained by vegetative growth and seeds dispersal by autochory, causing new stems or seedlings to appear near the parent plant. In 1999 *Cytisus* occupied 75 m^2 in plot 2 (Marcos et al. 1999), but 84 m^2 in 2001, suggesting that the dense cover of *Erica australis* does not impede the establishment of *Cytisus*.

Although it is not possible to detect the effect of *Cytisus* on the height and cover characteristics of *Erica australis* when comparing the sown and unsown subplots by analysis of variance, regression analysis revealed an inverse correlation between the cover of the species. On the other hand, the direct correlation between the height of the two species could indicate possible competition for light (Pugnaire et al. 2000). Also, the greater the cover of *Cytisus* the higher *Erica australis* grows. Greater growth in *Cytisus* could favour an increase in the height of *Erica* at the expense of a reduction in its cover whilst trying to avoid the shade.

In the studies carried out on fire-prone communities, there has been a tendency to ignore interactions between species because they were believed irrelevant in predicting successional change (Bond and van Wilgen 1996). Frequent disturbances, which periodically cause a reduction in phytomass and subsequent competition, would allow species coexistence. However, it is not clear whether competitive exclusion and progress towards a more mature stage would occur in the absence of these disturbances. Keeley (1992a, 1992b), in a study on chaparral sites unburned for 120 years, found a vigorous shrub population and although colonisation by tree seedlings could be observed, successional replacement of the chaparral was not imminent.

In our study, the species are capable of coexisting with high canopy overlap, for at least some time. Further, the colonisation of new microsites by *Cytisus* shows that there is a tendency for shrub overlap to increase.

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