

Woody species tolerance to expansion of the perennial tussock grass *Ampelodesmos mauritanica* after fire

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Abstract. In Mediterranean shrublands, post-fire accumulation of above-ground biomass of resprouters is faster than that of seeders. This suggests that resprouters may have a competitive advantage. To test this hypothesis, we used a removal experiment to study the effect of the presence of the dominant tussock-grass *Ampelodesmos mauritanica* on the resprouting shrubs *Erica multiflora* and *Globularia alypum* and on the seeders *Rosmarinus officinalis* and *Pinus halepensis* three and four years after a wildfire. Water potential of target plants was also measured to see if *Ampelodesmos* removal increased water availability. *Ampelodesmos* marginally reduced growth of all target species but did not influence survival or water potential of any target species. Our results suggest that the effect of climatically influenced water stress was stronger than the effect of *Ampelodesmos* neighbours. Plant-plant interactions in this Mediterranean community are weak after fire and the magnitude of the *Ampelodesmos* effect does not differ between seeders and resprouters.

Keywords: Addition experiment; Grass expansion; Mediterranean shrubland; Neighbour; Removal experiment; Resprouting.

Nomenclature: Bolòs et al. (1990).

Introduction

The expansion of grass species around the world and their impact on native vegetation is becoming a prevalent topic in the conservation and management of natural areas (D'Antonio & Vitousek 1992; White et al. 1997). A shift from shrublands or woodlands to grasslands or savanna-type communities has been described as a consequence of changes in land use and disturbance regimes (Hughes et al. 1991; Wilson & Agnew 1992). For example, in Mediterranean communities, increased dominance of grasses and a reduction of woody species has been supposed to occur when communities are highly disturbed, and particularly when fires are highly frequent or intense (Naveh 1974; Masalles & Vigo, 1987; Zedler et al. 1983).

The outcome of grass-shrub interaction may depend on the species' life history stage and traits (Vilà & Sardans 1999) as well as on environmental conditions (Callaway 1997; Holmgren et al. 1997). Studies conducted in several communities such as tropical savannas (Knoop & Walker 1985), seasonally dry woodlands (D'Antonio et al. 1998), temperate grasslands (Romo & Eddleman 1987; Van Auken & Bush 1988) and Mediterranean shrublands (Schultz et al. 1955; Litav et al. 1963; Griffin 1971; Da Silva & Bartolome 1984) have found that woody seedling establishment, survival and growth can be limited by grasses. Grasses may outcompete juvenile woody plants by shading (Van Auken & Bush 1988) and by reducing water availability (Litav et al. 1963; Knoop & Walker 1985). However, grasses may not have a negative effect on seedlings if soil resources are not limited or if there is resource partitioning (Aarssen 1989; Brown & Archer 1990; Parrish & Bazzaz 1976). Furthermore, plant-plant interactions may be positive when severe physical conditions restrict resource acquisition (Callaway 1997).

Mediterranean-type ecosystems are characterized by dry summers and wet winters. It is widely assumed that in these ecosystems plants compete for water (Mooney & Dunn 1969; Vilà & Sardans 1999). Most field experiments have found that woody seedlings growing with grass neighbours have lower water potentials than plants without neighbours, indicating that water availability is lower when neighbours are present (Gordon et al. 1989; Momen et al. 1994). Even so, there is still disagreement about the effect of competition when there is water stress. According to Grime (1977) competition would be less important in communities with soil water deficiency because plant growth would be limited by water stress rather than by competition.

On the other hand, Mediterranean vegetation is frequently subjected to fire (Naveh 1974; Hanes 1977). Competition after fire may be weak because there is a reduction of above-ground plant cover and a greater availability of resources at the individual level (Grime 1977). Moreover, competition after fire depends on the

plant life form involved (Tyler 1996) and may also depend on regeneration strategies, i.e. whether they are seeders or resprouters during stand recovery after fire (Wells 1969; Naveh 1974; 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 stumps. Underground reserves of resprouters are mobilized during regrowth after fire, allowing plants to be independent of extrinsic resources (Canadell & López-Soria 1998). A greater and faster regeneration of resprouters compared to seeders suggests that long-lived species with the ability to survive after fire should have an overwhelming advantage in competition (Keeley & Zedler 1978). However, this hypothesis has not been tested, although it has sometimes been assumed to explain the relative abundance of these life history types in different Mediterranean communities (Smith et al. 1992; Whelan 1995).

Ampelodesmos mauritanica is a large, perennial tussock grass which is believed to be expanding in coastal shrubland communities of northern Catalonia (ORCA 1985) and the Balearic Islands due to its fast regrowth and seedling recruitment after fire (Castelló & Mayo 1987; Vilà et al. unpubl.). In Mallorca it forms extensive, tall, grass prairies dominated by this species, known as 'carritxeres'. In this study we investigated the effect of *Ampelodesmos* on the regeneration of four common woody Mediterranean species after fire. We studied the effect of *Ampelodesmos* on the regrowth of the shrub resprouters *Erica multiflora* and *Globularia alypum* and on seedling survival and growth of the shrub seeder *Rosmarinus officinalis* and the tree seeder *Pinus halepensis*. Our hypothesis was that because of the fast regrowth of resprouters compared to seeders, *Ampelodesmos* will have a greater negative effect on seeders than on resprouters. The study was conducted by *Ampelodesmos* removal experiments because they are one of the most reliable methods to assess plant interactions in the field (Aarssen & Epp 1990).

Material and Methods

Study species and study site

Ampelodesmos mauritanica (*Poaceae*) is a large, evergreen, resprouting tussock grass distributed in coastal limestone soils of the Mediterranean Basin, eastwards to western Greece. This species may not be native to Catalonia (NE Spain) and could have been introduced from Mallorca as equine forage (Montserrat 1989). However, there is no conclusive analysis to support the alien status of the species. *Ampelodesmos*

mauritanica plants can attain 1 m in diameter and produce one to 25 large inflorescences at the top of 2 - 3 m high reproductive stalks during spring (Bolòs et al. 1990). *Erica multiflora* (*Ericaceae*), *Globularia alypum* (*Globulariaceae*) and *Rosmarinus officinalis* (*Lamiaceae*) (*Erica*, *Globularia* and *Rosmarinus*, respectively hereafter) are evergreen sclerophyllous native shrubs ca. 1 m in height that typically occur in basic soils of the western Mediterranean Basin, where they are common components of the coastal shrubland (Bolòs et al. 1990). *Erica* and *Globularia* are able to resprout from underground structures after aerial biomass removal (e.g. by fire). In contrast, *Rosmarinus* plants die when above-ground biomass is removed and regeneration after fire takes place only by seed germination (Lloret 1998). *Pinus halepensis* (*Pinaceae*) is the most common pine species in western Mediterranean Basin lowlands. The successional significance of this species is controversial but it is largely accepted that seed recruitment and growth is favoured by fire (Masalles & Vigo 1987). *P. halepensis* does not resprout after fire.

The study site was located next to Can Grau in Parc Natural del Garraf, Barcelona (45° 73'N, 4° 02'E). The climate is Mediterranean with cool, wet winters and hot, dry summers. Mean annual precipitation at the nearest weather station (Vilanova i la Geltrú, 11 km to the southeast) is 548 mm. Mean annual temperature is 17° C. Mean maximum (31° C) and minimum (0.5° C) temperatures occur in August and January, respectively. Soils are Cretaceous limestones with a high presence of rock outcrops. The study site was burned by a wildfire in April 1994.

In September 1996, when we started the study, *Ampelodesmos* (40.4 ± 3.3 % plant cover and 10307 ± 762 plants/ha), *Globularia* (10.2 ± 1.3 % and 11447 ± 1164 plants/ha) and *Erica* (6.5 ± 0.8% and 11009 ± 851 plants/ha) were the most common species in the study site. At this time, *Ampelodesmos* plants were 57.2 ± 1.9 cm (± S.E.) tall and 65.7 ± 3.2 cm² in crown diameter. *Erica* and *Globularia* plants were less than 40 cm tall and had 38.6 ± 3.8 and 20.5 ± 2.8 resprouts, respectively. Density of *Rosmarinus* was 9582 ± 1555 seedlings/ha, but the seedlings were only 8.1 ± 0.9 cm tall and the mean basal area was 1.3 ± 0.1 mm². Density of *Pinus* was low (2807 ± 469 seedlings/ha). These seedlings were all one or two years old (i.e. all germinated after the fire). We are confident that seedling mortality due to competition before they were tagged was low (Lloret 1998). Forbs and grasses, excluding *Ampelodesmos*, accounted for 25% of the total plant cover. Before the fire, the vegetation was a shrubland 1 m tall dominated by the same species with sparse *Pinus* (Lloret 1998).

Spatial patterns of target plants

In order to test for negative spatial associations between *Ampelodesmos* and resprouting target species, 42 plots of 1 m radius were randomly selected and the number of *Erica*, *Globularia* and *Ampelodesmos* plants was counted. A negative correlation between the number of *Erica* or *Globularia* and *Ampelodesmos* was tested by a Spearman rank analysis.

Negative spatial association between *Ampelodesmos* and *Rosmarinus* was not tested by this method because *Rosmarinus* seedlings were too small compared to *Ampelodesmos* plants (see Study species and study site) and interference might occur at a smaller spatial scale than for *Erica* and *Globularia*. Instead, we measured the distance between all individuals of both species in five randomly placed 20 m × 2 m belts. We expected to find that *Rosmarinus* seedlings were not located next or close to *Ampelodesmos*. The spatial association between *Pinus* seedlings and *Ampelodesmos* was not examined because the density of *Pinus* seedlings was very low.

Removal and addition experiments

To assess the effects of *Ampelodesmos* on target plant performance a removal experiment was conducted. Existing *Erica* and *Globularia* resprouting shrubs and *Rosmarinus* seedlings were chosen for the study. However, *Pinus* seedlings were planted because their density was very low at the study site.

In September 1996, 30 randomly selected *Erica* and *Globularia* resprouting plants and 30 *Rosmarinus* seedlings that were at least 2 m apart were selected. The length of three randomly selected branch tips of *Erica* and *Globularia* were tagged in order to measure branch growth. In January 1997, 80 2-yr old *Pinus halepensis* seedlings were planted 20 cm from the base of randomly chosen *Ampelodesmos* plants, making sure that they were planted below the canopy of *Ampelodesmos*. *Pinus* seedlings were obtained from a nursery and came from the region. Mean (\pm S.E.) height was 16.8 ± 0.3 cm and mean (\pm S.E.) basal area was 2.8 ± 0.05 mm². Planting the *Pinus* seedlings is not expected to have substantially disturbed the root system of *Ampelodesmos* because of the limited extension of removed ground. Because it rained the day before planting and the soil was moist, we did not water the seedlings after planting.

Half of the target plants of each species were selected as controls and in the remaining plants all *Ampelodesmos* plants within a 1-m radius for *Erica* and *Globularia* sprouts, and 0.5 m for *Rosmarinus* and *Pinus* seedlings were clipped at ground level. Observational exploration of target plant root systems and

previous removal experiments suggested that the removal radii chosen were wide enough to reduce competition and that larger radii would not further decrease the intensity of competition (Vilà & Terradas 1995a; Vilà et al. 1998). *Ampelodesmos* neighbours were clipped every four months to keep plant interference to a minimum. Most *Ampelodesmos* did not resprout after being clipped three times. We did not remove underground structures to prevent soil disturbance which could influence plant growth (Aarssen & Epp 1990).

Sprout and seedling biomass at the time of treatment was estimated using allometric equations obtained by measuring sprouts and seedlings randomly selected from plants growing in the same area (Table 1). In September 1998, the number of *Erica* and *Globularia* sprouts was counted. The relative increase in tagged branch length in September 1997 and 1998 was calculated as $(L_{t_2} - L_{t_1})/L_{t_1}$, where L_{t_2} = length at a time t_2 and L_{t_1} = length at a previous time, t_1 . Above-ground biomass of all treatment species was harvested. Material was weighed after drying at 80 °C for 96 hr. The relative increase in biomass was calculated as $(B_{t_1} - B_{t_0})/B_{t_0}$, where B_{t_1} = biomass at harvesting time and B_{t_0} = estimated biomass before treatment.

Target plants water potential

To assess water stress as a function of *Ampelodesmos* presence, we measured pre-dawn and midday water potential with a Scholander pressure bomb. For *Erica* and *Globularia*, water potential was measured in two branches of five randomly selected plants in mid June and mid July 1998 as a measure of spring (when plants are still growing) and summer potentials, respectively. Different plants were sampled for spring and summer measurements. For *Rosmarinus* and planted *Pinus* seedlings, water potential was measured in two branches of five randomly selected plants in September 1998, before harvesting. Water potential in seedlings was not measured earlier because the seedlings were very small and the procedure would have disturbed the plants.

Table 1. Allometric equations to estimate *Erica multiflora* and *Globularia alypum* sprout biomass and *Rosmarinus officinalis* and *Pinus halepensis* seedling above-ground biomass.

Species	Equation	r^2	n
<i>Erica</i>	$\ln B = -5.10 + 1.38 \ln L + 0.43 \ln Y$	0.93	30
<i>Globularia</i>	$\ln B = -1.59 + 2.30 \ln D$	0.88	67
<i>Rosmarinus</i>	$\ln B = -5.67 + 1.64 \ln D + 1.45 \ln H$	0.93	39
<i>Pinus</i>	$\ln B = -3.32 + 0.81 \ln D + 0.97 \ln H$	0.71	99

B = above-ground dry biomass Y = number of branches per sprout
 L = sprout length D = basal diameter
 H = seedling height

Root profiles

Root profiles of adult *Ampelodesmos* and the two shrubs *Globularia* and *Erica* were analysed from road-cuts. Vertical superficial layers (ca. 20 cm) were hand-cleared and the number of roots more than 0.5 mm and 1 mm in diameter were counted in 10 cm intervals along a 20 cm wide, vertical transect which started beneath the centre of each plant and ended when bed-rock was encountered. Five *Ampelodesmos*, four *Globularia* and three *Erica* plants were sampled by this procedure. Root profiles for *Pinus* and *Rosmarinus* are not shown because the seedlings were too small (16.79 ± 0.31 and 8.09 ± 0.91 cm in height, respectively) and any attempt to excavate the soil would have disturbed the seedlings.

Statistical analysis

The number of sprouts and the relative increase in branch length for *Erica* and *Globularia* in 1997 and 1998 were compared by a two-way ANOVA with species and competition treatment as the main factors. The relative increase of above-ground biomass for *Erica*, *Globularia*, *Rosmarinus* and *Pinus* was also compared with a two-way ANOVA with species and competition treatment as the main factors. The effect of the competition treatment on target plant water potential was compared with a repeated measures analysis with *Ampelodesmos* removal, species and season as the main effects and time of the day as the repeated measure. Season was not considered a repeated measure because sampled plants were different for spring and summer measurements. Water potential in *Pinus* seedlings was analysed separately because measurements were conducted in a different season. Data were $\ln(x + 1)$ transformed before analysis when necessary to meet the assumptions of parametric statistics.

Results

Spatial patterns of target plants

We did not find negative spatial associations between *Erica*, *Globularia* or *Rosmarinus* and *Ampelodesmos*. In fact, abundance of *Erica* was positively correlated to *Ampelodesmos* (Spearman rank correlation coefficient = 0.4; two-tailed p -value = 0.02). In contrast, the abundance of *Globularia* was not correlated to that of *Ampelodesmos* (Spearman rank correlation coefficient = -0.2; tied p -value = 0.1). Similarly, abundance of *Rosmarinus* seedlings was independent of distance from *Ampelodesmos* plants. The distribution of distances was strongly skewed, with most *Rosmarinus* located next or close to *Ampelodesmos* plants. The distance between the two species ranged from 10 cm to 2 m (mean \pm S.E. = 70.1 ± 4.4 cm).

Effects of *Ampelodesmos* removal

Pinus seedling mortality was identical (20%) with and without *Ampelodesmos*. The difference in *Rosmarinus* seedling survival with *Ampelodesmos* (7%) and without (13%) was also non-significant ($\chi^2 = 0.36$; $p > 0.05$).

While *Erica* had more sprouts than *Globularia* they did not differ in relative increase of branch length (Table 2, Fig. 1). *Ampelodesmos* removal did not significantly affect branch length but showed a trend ($p = 0.06$) towards decreasing the number of sprouts of both species, i.e. of facilitation (Table 2, Fig. 1).

The relative increase of above-ground biomass was significantly higher in *Rosmarinus* than in the other target species (Fig. 2). *Ampelodesmos* removal marginally increased this variable ($p = 0.05$) but the effect was not significantly different between species (Table 2, Fig. 2). Target plants with *Ampelodesmos* removed accumulated 18.6% more biomass than plants with *Ampelodesmos*.

Table 2. Two-way ANOVA of the effect of *Ampelodesmos mauritanica* removal on the number of sprouts in *Erica multiflora* and *Globularia alypum*, the relative increase of tagged branch length in *E. multiflora* and *G. alypum* in 1997 and 1998, and the relative increase of aboveground biomass in *E. multiflora*, *G. alypum*, *Rosmarinus officinalis* and *Pinus halepensis* two years after treatment. SS = Sum of squares.

Source	No. of sprouts			Branch length (1997)			Branch length (1998)			Biomass		
	df	SS	p	df	SS	p	df	SS	p	df	SS	p
Species (S)	1	8.08	0.0001	1	0.05	0.42	1	0.006	0.76	3	48.02	0.0001
<i>Ampelodesmos</i> (A)	1	1.14	0.06	1	0.04	0.48	1	0.0002	0.95	1	2.69	0.05
A \times S	1	0.11	0.55	1	0.01	0.69	1	0.06	0.32	3	0.24	0.95
Residual	56	17.06		55	4.04		55	3.51		141	94.31	

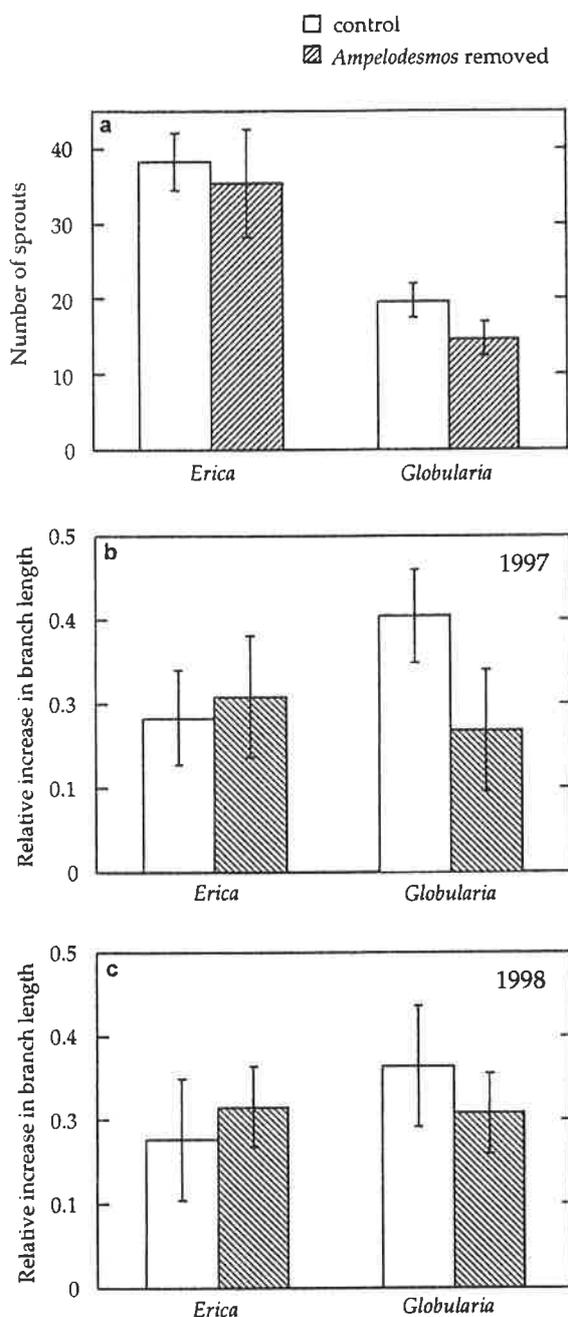


Fig. 1. Effect of *Ampelodesmos mauritanica* removal on mean (\pm S.E.) number of sprouts (in 1997) and relative increase of tagged branch length in *Erica multiflora* and *Globularia alypum* (in 1997 and 1998).

Target plant water potential

Rosmarinus xylem pressure potentials could not be measured because they were too low (< -5 Mpa). *Erica* and *Globularia* pre-dawn and midday xylem pressure potentials did not differ significantly between control plants and plants with *Ampelodesmos* removed ($F_{1,31} = 0.4$; $p = 0.5$, Fig. 3). For these species, water potentials were

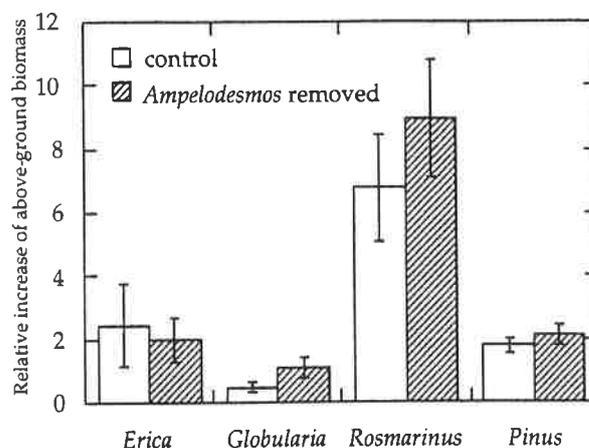


Fig. 2. Effect of *Ampelodesmos mauritanica* removal on mean (\pm S.E.) relative increase of above-ground biomass in *Erica multiflora*, *Globularia alypum*, *Rosmarinus officinalis* and *Pinus halepensis*.

more negative in summer than in spring ($F_{1,31} = 21.07$; $p = 0.0001$) and in *Globularia* more than in *Erica* ($F_{1,31} = 27.8$; $p = 0.0001$). *Ampelodesmos* removal had no significant effect on *Pinus* seedling xylem pressure potentials in September ($F_{1,8} = 0.6$; $p = 0.5$), (Fig. 3). As expected, for all species water potentials were more negative at midday than pre-dawn ($F_{1,8} = 6.3$; $p = 0.04$ for *Pinus* and $F_{1,31} = 93.9$; $p = 0.0001$ for *Erica* and *Globularia*).

Root profiles

Most *Ampelodesmos* roots were concentrated in the upper 20 cm, but in deep soil they can achieve up to 1 m depth (Fig. 4). In contrast, root distribution of *Globularia* and *Erica* shrubs was more homogeneous along the soil profile. Paired *t*-tests of root density per dm^2 between the upper 20 cm and the lower layer for the three species showed that differences were only significant in the grass (*Ampelodesmos*: *t*-value = 14.4; $p < 0.0001$; *Globularia*: *t*-value = 1.7; $p = 0.2$; *Erica*: *t*-value = 2.4; $p = 0.1$). Roots more than 1 mm thick were less abundant in *Ampelodesmos* than in the shrubs and were almost exclusively present in the upper layer, whereas *Globularia* and *Erica* always developed roots over 1 mm diameter that reached the bedrock. Density of roots over 1 mm diameter in the profile layers below 20 cm showed significant differences between *Ampelodesmos* and both shrubs ($F_{2,11} = 26.1$; $p = 0.0002$, post-hoc Scheffé-test (see Zar 1984) $p < 0.01$ for both *Ampelodesmos* vs. *Globularia* and vs. *Erica*).

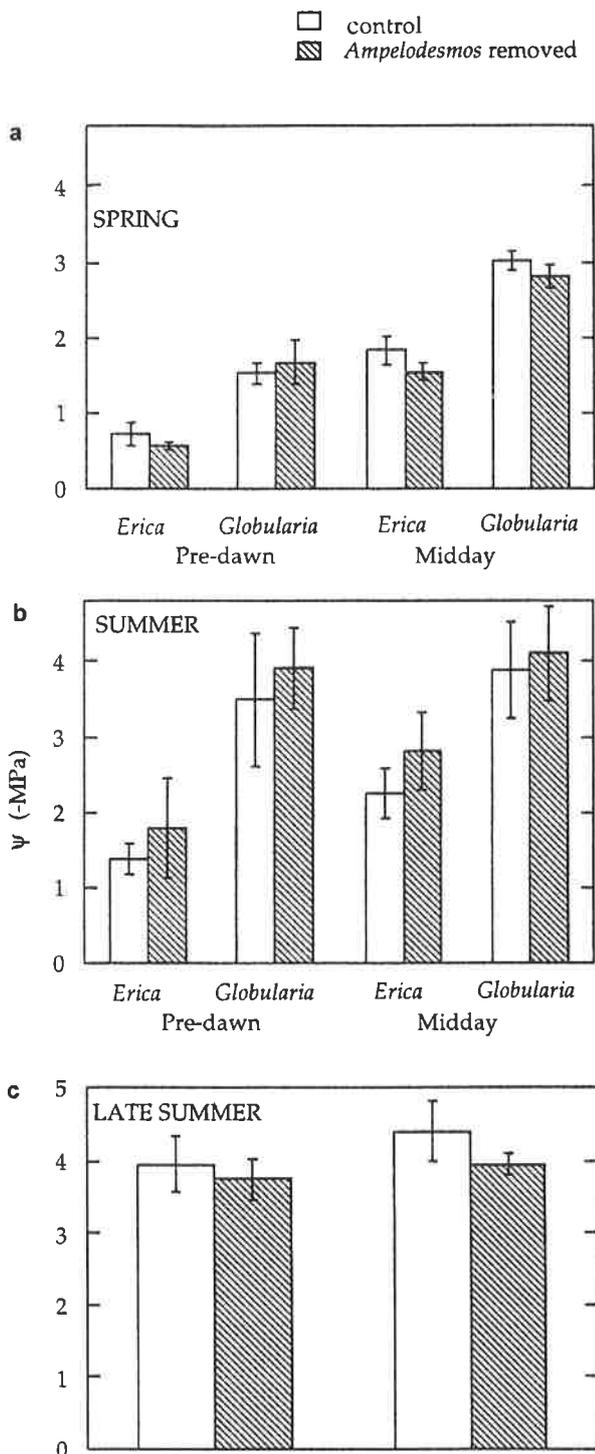


Fig. 3. Effect of *Ampelodesmos mauritanica* removal on *Erica multiflora*, *Globularia alypum* and *Pinus halepensis* mean (\pm S.E.) pre-dawn and midday xylem pressure potential, in spring, summer and late summer. *Ampelodesmos mauritanica* removal had a non-significant effect.

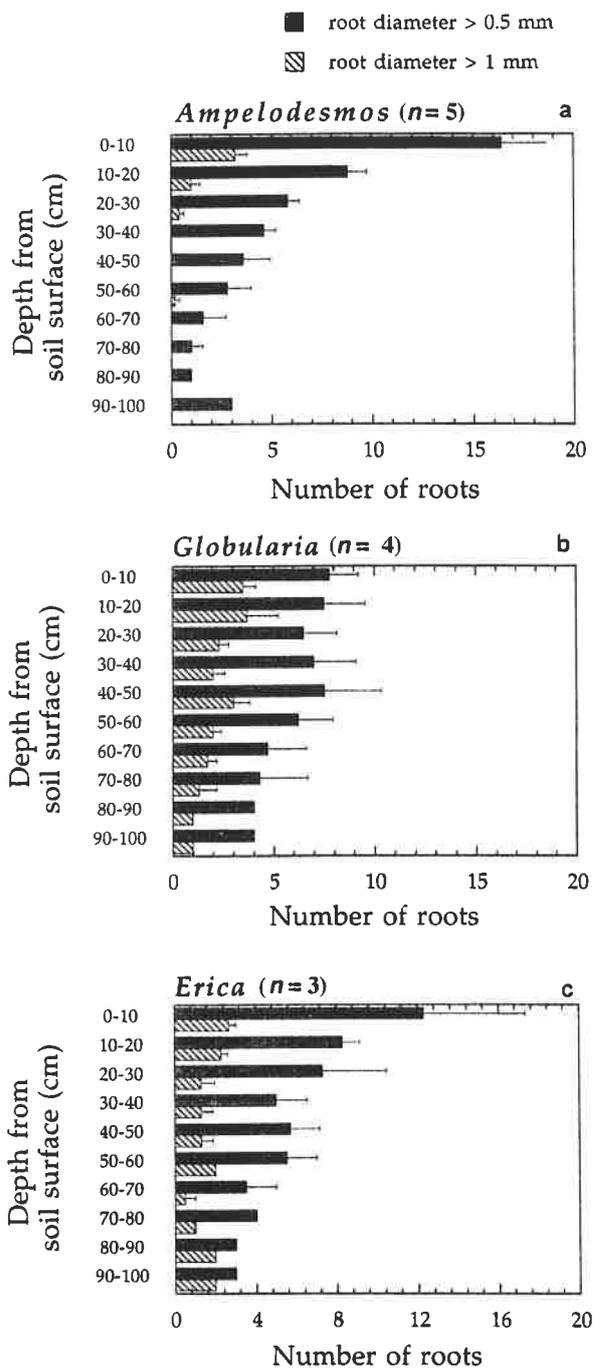


Fig. 4. Root density (number of roots per dm²) for roots with diameter > 0.5 mm and > 1.0 mm (mean + S.E.) of *Ampelodesmos* (n = 5), *Globularia* (n = 5) and *Erica* (n = 3) in each 10-cm depth increment below soil surface along 20-cm wide, vertical transects, which started beneath the centre of each plant and ended at the bedrock.

Discussion

Our results do not support the hypothesis that *Ampelodesmos* has a greater negative effect on seeders than on resprouters after fire. *Ampelodesmos* had only a marginal significant effect on target plant performance and this effect did not differ between species. Competitive effects were difficult to detect because there was high variability among individuals. *Ampelodesmos* removal slightly increased target plant biomass suggesting weak competition. For resprouters it decreased the number of sprouts, suggesting that self-thinning among sprouts takes place earlier when the grass is removed (Vilà & Terradas 1995a). Other studies have also shown that grasses do not always have a strong effect on woody species' performance (Parrish & Bazzaz 1976; Aarssen 1989). This situation has been described in Mediterranean communities (Williams & Hobbs 1989), and in savannas where the effect of grasses on woody plants at the establishment stage is variable depending on the interaction with soil resources, mainly water, biotic interactions and fire (O'Connor 1995; Scholes & Archer 1997).

Several reasons may explain the weak competition between *Ampelodesmos* and woody species after fire. First, the low water pressure potentials in target plants at midday and summer provide evidence that water availability was low and, according to Grime (1977), water stress would decrease plant growth and competition. Second, at the first stages of succession competition would be less intense than in mature stands due to the smaller size of above-ground plant organs, which would decrease resource demand relative to that available (Sousa 1984). The decrease of competition after fire compared to mature stands has already been described in Mediterranean shrublands by Vilà & Terradas (1995b) by means of removal experiments and may be related to greater space and light availability at the plant level after fire. The reverse explanation could also be true. *Ampelodesmos* plant cover only accounted for 42% of the total vegetation cover. The high variability in the response parameters measured could be a result of the presence of other neighbour species which could compete with target plants. In a multispecies stand, competition is diffuse. Plants do not compete with a single neighbour species but with an array of species (Mitchley 1987). In our study, it is feasible that *Ampelodesmos* removal did not release target plants from competition because other neighbour species were present. Other studies have shown that any single species, even if dominant, does not contribute much to the neighbourhood effect (Vilà et al. 1998).

The reasons for the weak competitive effect of *Ampelodesmos* are probably different for resprouters

(*Erica* and *Globularia*) and for seeders (*Rosmarinus* and *Pinus*). *Ampelodesmos* has a fibrous root system that dominates the upper portion of the soil profile, while resprouters have an extensive root system that exploits a larger volume of soil at depth. Although we have not observed root segregation between grasses and resprouters, our study supports the idea that resprouters are better able to exploit deeper layers of the soil than grasses (Canadell et al. 1996). Moreover, regrowth in resprouting shrubs depends largely on the storage of resources in subterranean structures and the bud bank (sprout recruitment) which, in turn, are positively correlated to pre-disturbance plant size (James 1994; Canadell & López-Soria 1998). Plant size including underground structures is the result of the history of the individual plant, i.e., past competition and past disturbances. Thus, during the regeneration stage after fire, regrowth may depend more on intrinsic factors than on extrinsic ecological interactions.

Overall, *Ampelodesmos* may have an ameliorating effect on seedlings that may counterbalance any negative effect. Light may not be a limiting factor during regeneration after fire (Kummerow et al. 1985; Moreno & Oechel 1988, 1992). For example, shading did not have a negative effect on seedling survival and growth for *P. halepensis* (Broncano et al. 1998). Instead, *Ampelodesmos* may protect seedlings from direct irradiance in the dry season (Valiente-Banuet et al. 1991). In the same community, no significant differences in seedling survival of woody species in open areas and beneath vegetation have been found (Lloret 1998).

Ampelodesmos can have an indirect negative effect on woody species because fire interacts with competition by increasing the susceptibility to flame damage in crowded vegetation (Ne'eman et al. 1992; Scholes & Archer 1997). Grasses accumulate fine fuels and increase the intensity of fires (Schultz et al. 1955; Zedler et al. 1983; Harradine 1991). Fire behaviour models predict that *Ampelodesmos* would produce more intense fires than co-occurring dominant species (Vilà et al. in press) and this could increase mortality of both woody seeders and resprouter species (Lloret & López-Soria 1993).

The dominance and the expansion of *Ampelodesmos* cannot be explained by a competitive effect on woody species at the regeneration stage. We believe that the cause of *Ampelodesmos* expansion is due to the plant's life history characteristics rather than to its negative effect on the vegetation. Prolific seed production in occasional years has been suggested to be a cause of high spread of certain species (Lonsdale et al. 1988). *Ampelodesmos* recovers more rapidly after fire as compared to other resprouting species (López-Soria &

Castell 1992) and it has episodic high seed production, high seed germination and high seedling recruitment (Vilà & Lloret 2000) which may account for its expansion.

Our results do not exclude the possibility that competition between *Ampelodesmos* and woody species increases at later stages of succession when canopies are closed and under other environmental conditions. A species responds to neighbours differently depending on its life history stage (Fowler 1986; Vilà & Sardans 1999) specially in woody plants. Removal experiments have shown that in these Mediterranean communities, adult neighbours have a negative effect on the growth of the target resprouting plant (Vilà et al. 1994; Vilà & Terradas 1995a) but competition may not occur after fire (Vilà & Terradas 1995b). In conclusion, we expected the grass to exert a strong effect on the shrubs and designed our experiment accordingly. Contrary to expectations, the effect was too weak relative to the plant-to-plant variation to be detected with the sample size chosen. For resprouters, this interpopulation variation could result from differences in plant size before treatment and the variability in the type and abundance of target plant neighbours. For seeders, water stress was very high and water availability may limit seedling growth more than the presence of *Ampelodesmos*.

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