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Positive fire–grass feedback in Mediterranean Basin woodlands

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Abstract

Fires can mediate switches between alternative vegetation types which may be more flammable and thus reinforce fire spread. We tested if there is a positive feedback between the expansion of the tussock grass *Ampelodesmos mauritanica* (hereafter *Ampelodesmos*) and fire hazard in Mediterranean Basin communities and its relation to tree cover decline. The effect of fire on *Ampelodesmos* population structure was analysed by surveying stands burned at different fire frequencies. The effect of vegetation dominated by *Ampelodesmos* on fire behaviour compared to other species coexisting in the community was predicted by the Rothermel fire propagation model BEHAVE. There was a negative correlation between pine cover and percentage of *Ampelodesmos* plants. *Ampelodesmos* mortality after fire is very low. Recently burned stands had a higher proportion of reproductive plants and higher seedling density than unburned stands. The high temperatures reached during fire may kill seeds, the higher seedling recruitment results from fast resprouting and higher seed production of burned plants compared to unburned plants 1 year after fire. Simulations with the BEHAVE fire model predict that *Ampelodesmos* increases fire intensity and spread because of its high accumulation of fuel load and standing dead material. The results suggest that there is a positive relationship between *Ampelodesmos* abundance and fire regime which increases the invasive potential of this grass and the fire risk of the community where it dominates. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: *Ampelodesmos mauritanica*; BEHAVE; Fire regime; Grass expansion; Ecological feedback; Post-fire regeneration; Rothermel model

1. Introduction

Positive feedback switches in vegetation are processes by which initial differences in vegetation types are magnified and stabilized by environmental factors, hence becoming more suitable for one vegetation type and less for the alternative type (Wilson and Agnew, 1992). Fire-mediated switches are common. Over the last decades frequency and extension of fires have increased at a global scale (Mueller-Dombois and Goldammer, 1990) and a positive feedback between grass expansion and susceptibility to fire has been

described for some ecosystems (Hughes et al., 1991; D'Antonio and Vitousek, 1992), such as in forest/savanna systems, in which the higher fire tolerance and flammability of grasses promote their expansion in detriment of forests and woodlands (Vogl, 1974; Menaut et al., 1990; Woodcock, 1992).

Although it is generally held that in Mediterranean vegetation there is a relatively fast recovery of structure and composition after fire (Hanes, 1971; Trabaud, 1994), and even after frequent fires, characteristic dominant taxa remain because most species regenerate by vegetative means (Trabaud and Lepart, 1981), an increase of grassland and a reduction of woody vegetation specially tree species has been proposed when these communities are highly disturbed, and particularly when fires are frequent or intense (Bolòs,

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1962; Naveh, 1974; Masalles and Vigo, 1987; Zedler et al., 1983). In the Mediterranean Basin, the number of wildfires and the size of burned areas has increased since the 1960s as a consequence of alterations in land use and climatic change (Piñol et al., 1998). However, quantitative evidence of grass/fire positive feedbacks and involved mechanisms have rarely been provided for Mediterranean communities (Naveh, 1974).

The mechanisms involved in grassland/woodland switches could be related to vegetation response after fire and vegetation effects on fire regime. Fire may modify the relative abundance of some species through their different responses to burning and post-fire conditions. Some species are able to resprout from canopy or below-ground organs after fire (Trabaud, 1987). Indirectly, fire may also promote seedling recruitment by stimulating seed germination after breaking hard seed coats or by depleting allelopathic substances which inhibit germination. Fire also reduces competitors and increases the availability of open spaces and resources, favouring both resprouting (Vilà and Terradas, 1995) and seedling recruitment (Tyler, 1995; Lloret, 1998). Early successional species with a high ability to regenerate by both resprouting and seedling recruitment may be favoured by high fire frequency. Many perennial grasses are able to resprout from rhizomatous structures after fire (Kucera, 1981; Silva et al., 1991; Mark, 1994), and although their seeds do not seem able to survive at high temperatures (Daubenmire, 1968), their seedlings may be abundant after fire (Mark, 1994; Odgers, 1996) as a consequence of resource increase or germination stimulation by smoke (Baxter et al., 1994). In contrast, non-resprouting trees such as pines, although they produce cones which may survive heat and release seeds during fire, will not be favoured by fire frequency. Pines require several years before they produce cones and if fire is very frequent there will not be a seed bank able to germinate after fire.

Changes in vegetation features linked to fuel properties may bear changes in community flammability and fire spread (Van Wilgen and Van Hensbergen, 1992). Grasses are highly combustible and produce extensive and fast moving fires (Kucera, 1981; Bradstock and Gill, 1993; Bond and Van Wilgen, 1996) because they have low moisture content and a high portion of fine biomass and standing dead material (Vogl, 1974). To forecast the flammability consequences of grass

expansion into woodlands, we have to describe dominant species in terms of fuel types and their possible contribution to fire spread. Such a goal is possible by using fire-spread models that depend on the fuel properties of the dominant species in the community (Rothermel, 1972; Van Wilgen et al., 1990).

Ampelodesmos mauritanica is a perennial tussock grass that has been suggested to be expanding in shrubland communities of northeastern Spain (ORCA, 1985) and the Balearic Islands (Castelló and Mayol, 1987). In Mallorca, it forms extensive and thick tall grass prairies almost dominated by this species known as "carritxeres" (similar in structure to Mexican "zacatales") which are supposed to be favoured by fire (Castelló and Mayol, 1987). In this study, we investigate the effect of fire on the population structure and abundance of *A. mauritanica* and the effect that this species may have on tree cover and fire behaviour. Our hypothesis is that if (1) grass populations increase under high fire frequency regime, and (2) the grass increases the fire hazard by increasing fire intensity and speed, we can suggest that there is a positive feedback between grass expansion and fire hazard (Wilson and Agnew, 1992). We base this hypothesis on the ability of *A. mauritanica* plants to survive and to establish after fire and the high flammability of this species. The first premise was tested by conducting a survey to evaluate grass abundance and fecundity, and seedling establishment on areas that had been burned at different fire frequencies in the last decades. This premise would be reinforced if pines decrease while *Ampelodesmos* increases. We also analysed the direct effect of temperature on seed germination under laboratory conditions. The second premise was tested by simulating fire behaviour from a fuel model based on structural plant flammability parameters.

2. Material and methods

2.1. Study species and study sites

A. mauritanica (Poiret) T. Durand et Schinz (Poaceae) is a large, C₃, tussock grass distributed in coastal, dry places of the Mediterranean Basin, eastwards to western Greece. Plants may attain 100 cm in diameter and produce 1–25 large inflorescences at the top of 2–3.5 m high reproductive stalks during the

spring (Bolòs et al., 1990). Seeds are wind dispersed in late summer and fall. *Ampelodesmos mauritanica* (*Ampelodesmos* hereafter) vigorously resprouts after aerial biomass removal (clipping or burning). *Ampelodesmos* may be exotic in Catalonia and could have been introduced from the Balearic Islands as equine forage (Montserrat, 1989). *Ampelodesmos* may be expanding in Catalonia (ORCA, 1985) and Mallorca due to its fast regeneration after fire (Castelló and Mayol, 1987).

Two study sites in Catalonia (NE Spain) were surveyed to analyse the effect of fire on *Ampelodesmos* populations. One site was the Garraf Natural Park (Garraf hereafter) located about 30 km south of Barcelona. The area (almost 10 000 ha) is a karstic massif ranging from sea level to 600 m altitude. The climate is typically Mediterranean. Mean annual rainfall is 550 mm, with a pronounced summer drought (only 100 mm of rainfall from June to August). Mean annual temperature is 17°C. Mean maximum and minimum temperatures are reached in July (28°C) and January (0.5°C), respectively. The vegetation is dominated by evergreen, sclerophyllous shrublands 1.5 m high and *Pinus halepensis* open forests (Bolòs, 1962). In Garraf, there are three types of areas according to their fire history: small, scattered areas that have remained unburned for at least the last 20 years, a 7000 ha area that was burned in July 1982 and finally, a 4800 ha area within the 7000 ha area that was burned again in April 1994. Therefore, for the last 20 years, there has been a mosaic of unburned, once burned and twice burned areas, respectively.

The second site was located approximately 7 km northeast of the Garraf Natural Park, near Vallirana town (Vallirana hereafter). The climate is similar to that described for Garraf, and vegetation is dominated by a 50-year old *P. halepensis* forest with a dense understorey dominated by *Ampelodesmos* and sclerophyllous shrubs. In July 1995, a wildfire burned a 300 ha surface.

2.2. Extensive survey at a regional scale

An extensive survey was conducted in Garraf from January to March 1996. Thirty 10 × 10 m² stands were randomly chosen from a 500 × 500 m² grid map in each unburned and twice burned areas, and 32 stands in once burned areas. A simple character-

ization of these stands was made considering the fire history, the aspect (north or south), the topographical location (steep or flat areas, many of which are more than 50-year old fields), and the presence of rock outcrops (in more or less than 30% of the total soil surface).

We estimated the plant size and the presence of reproductive stalks in all *Ampelodesmos* plants within each stand. The size of *Ampelodesmos* plants was estimated as the cylinder volume calculated from the height of the plant vegetative part and the crown area calculated from the mean value of the longest canopy diameter and the perpendicular to it. Previous allometric analysis demonstrated that the cylinder volume (V , m³) of the plant was a good prediction of plant biomass (W , g) ($\ln W = -5.67 + 828 \ln V$, $r^2 = 0.914$, $n = 51$). Vegetation cover of perennial species in each stand was estimated using the point intercept sampling procedure by detecting the presence of species every 0.5 m along the four sides of the stand quadrat and in a 10 m transect situated in the middle of the stand. Thus in each stand a total of 94 points were recorded to estimate cover of perennial species. Correlation analysis was conducted to test if *Ampelodesmos* performance was negatively correlated to shrub and tree cover species.

In the twice burned stands, we registered the percentage of *Ampelodesmos* mortality after fire by counting burned rhizomes that had not resprouted. Because of the small size of seedlings and because they tend to be more numerous than mature shrubs, seedling abundance was recorded in six 20 × 20 cm² subplots randomly selected within each stand.

The effects of fire history (unburned, once burned or twice burned), aspect (N or S), slope (sloped or flat) and presence of rock outcrops (high or low) on *Ampelodesmos* features (cover, density of seedlings and adults, seedling/adult ratio and percentage of reproductive adults) were analysed by a general linear model approach, following the JMP procedure (Anonymous, 1992) which gives the significance of each effect by F -tests calculated after removing each effect from the whole model. A model that included all four independent variables was built for each dependent variable. The values of the independent variables were discrete and followed the previously described characterization. Absence of collinearity between independent variables was checked by likelihood tests. The effect of fire was analysed by ANOVA and the

Fisher-test was used for a posteriori pairwise comparisons. Data of all dependent variables, except the percentage of reproductive adults, were $\log(x + 1)$ transformed in order to normalize residuals.

To assess the effect of positive spatial autocorrelation as a consequence of the non-uniform distribution of stands through the landscape (the unburned stands are more scattered than those in burned areas), we performed partial Mantel tests for the two main structural and demographic variables of *Ampelodesmos* populations (cover and adult density), following the MANTEL program of the “R package” (Legendre and Vaudor, 1991). Using this test, we analysed the significance of the fire history treatment when the effects of the spatial location are kept constant (Fortin and Gurevitch, 1993). The variable distance matrix was calculated from the differences in *Ampelodesmos* cover and adult density, and the geographic distance matrix was computed using the Euclidean distance between all pairs of stands. The significance of the normalized Mantel statistics r was assessed by performing 500 iterations after randomly permuting the arrangement of the elements of the distance matrix.

2.3. Intensive survey at a local scale

In January 1997, an intensive survey comparing *Ampelodesmos* population structure in a burned and in an adjacent unburned area was conducted on a south-facing hill in Vallirana. We believe that vegetation structure was similar in both areas before the fire because the density of the dominant shrub *Arbutus unedo* and *Ampelodesmos* were not significantly different (Wilcoxon signed rank test for *A. unedo*, $Z = -1.78$, $p = 0.07$; *Ampelodesmos*, $Z = -0.10$, $p = 0.92$). Furthermore, aerial photographs taken before the fire show that canopy structure and tree density were similar in the burned and in the unburned areas.

Six paired stands were selected along the burned boundary. Each paired stand consisted of one $10 \times 5 \text{ m}^2$ stand in the burned area and one $10 \times 5 \text{ m}^2$ stand in the unburned one. Stands were smaller than in the extensive survey because *Ampelodesmos* density was higher at this site. The distance between stands was at least 100 m to prevent seed dispersal among stands. We estimated plant size as in the extensive survey and we counted the current year

reproductive stalks in all *Ampelodesmos* plants. Vegetation cover was estimated by the point intercept sampling procedure by detecting the presence of species every 0.5 m along the four sides of each stand. Seedling abundance was recorded in ten $20 \times 20 \text{ cm}^2$ subplots randomly selected within each stand.

In November 1997, one stalk per plant from 20 randomly selected plants in each burned and unburned stands was chosen to compare seed production and pre-dispersal seed predation. The total number of sound, aborted and predated seeds per stalk was counted. Pre-dispersal seed predation was detected if there was a small hole in the glume.

Seedling recruitment after fire before resprouting *Ampelodesmos* plants produce seeds was checked in May 1998 in two additional areas in Garraf that burned in July 1997. If there were seedlings, they germinated from burned seeds or from the seed bank.

2.4. Effect of temperature on seed germination

The direct effect of burning on seed germination was tested by heating seeds in the oven at the following treatments of temperature and time: high heating — 300°C , 5 min; 200°C , 5 min; and 200°C , 1 min; moderate heating — 105°C , 15 min; and 105°C , 5 min; low heating — 70°C , 60 min, 70°C , 15 min; and 70°C , 5 min and control. Each treatment was applied to 100 seeds, which were placed in 10 Petri dishes containing pot soil (Composana, BASF®) in the dark in a greenhouse (mean $T = 25^\circ\text{C}$, dark conditions). Pot soil had 80–90% organic matter and mineral composition was 150 N, 27.2 P, 74.7 K and 75.37 Mg mg/l. Treatments were selected in order to simulate heating at different soil depths in Mediterranean garrigues (Trabaud, 1979). Darkness also provided a better simulation of burning conditions in the soil. Seeds had been collected from randomly chosen stalks from the recently burned stand (2 year since last fire).

Seeds were checked once a week from November 1996 to January 1997 and were considered to have germinated if both radicle and cotyledon had emerged from the seed coat. The effect of heating treatment on final germination percentage was analyzed with an ANOVA after arcsinus transformation of data. The Scheffé-test was used for posteriori pairwise comparisons.

2.5. Fire behaviour

In July 1997, we estimated plant structural characteristics related to flammability for the following dominant species growing in the once burned area in Garraf: *Ampelodesmos*, the short perennial grass *Brachypodium retusum* (Pers.) Beauv, the seeder shrub *Rosmarinus officinalis* L., and the resprouter shrub *Quercus coccifera* L. The parameters that we used were fuel depth, fuel load and area to volume ratio of fuel <6 mm diameter in both standing dead and live materials (Pyne, 1984). Fuel load and area to volume ratio of >6 mm parts were also estimated for dead material in *Q. coccifera*.

These parameters were sampled by randomly choosing three homogeneously covered plots ($0.6 \times 0.6 \text{ m}^2$) for each species. We clipped and collected at ground level all plant material, which was divided into dead and live parts in the laboratory. Two class diameters were considered: less or greater than 6 mm. All plant portions were then weighed after being oven dried at 105°C to constant mass. Area to volume ratio (A/V) is the ratio between $\pi R^2/\pi R^2 H$ for leaves, and $2\pi RH/\pi R^2 H$ for twigs, where R is the ratio of the leaf surface or twig thickness and H the thickness of the leaf or the height of the twig. A/V for leaves was estimated by the formula $A/V = 1/H$ for leaves and $A/V = 2/R$ for twigs. H and R were measured with a micrometer.

We built a fuel model package for each species with the NEWMDL model of the BEHAVE package (Rothermel, 1982; Burgan and Rothermel, 1984) and we compared fire spread and fire intensity under four fire hazard scenarios, defined by different wind speed, dead fuel moisture and live fuel moisture levels (Table 1). Values of these parameters were obtained from the literature (Van Wilgen and Richardson, 1985) and from estimations on fuel moisture carried out by Piñol and Ogaya (1997) for a year on some of the same species and regions (Viegas et al., 1998) (Table 1).

3. Results

3.1. Extensive survey at the regional scale

Fire was the only factor with a significant effect on *Ampelodesmos* cover, the density of adults and

Table 1

Weather parameters and fuel moisture contents used in fire behaviour simulation

Degree of fire hazard	Low	Moderate	High	Extreme
Wind speed (m/s)	0.5	2	5	7
Slope ($^\circ$)	0	0	0	0
Dead fuel moisture (%)	10	8	6	4
Live fuel moisture (%)				
<i>A. mauritanica</i>	125	100	75	50
<i>B. retusum</i>	100	75	50	30
<i>Q. coccifera</i>	175	150	100	75
<i>R. officinalis</i>	175	125	100	75

seedlings, the seedling/adult ratio and the percentage of reproductive adults (Table 2). The density and cover of adults was the lowest in the unburned stands and the highest in the twice burned stands (Table 3). Partial Mantel tests indicated that the effect of fire history was significant on the percentage of *Ampelodesmos* cover and adult density when the effect of the spatial location was kept constant ($r = 0.072$, one-tail probability $p = 0.036$; $r = 0.176$, one-tail probability $p = 0.002$, respectively). Pine (*P. halepensis* and *P. pinea*) cover followed the opposite trend: it was the lowest in the twice burned stands (0.5%) and the highest in the unburned stands (42.1%).

The plant size distribution indicates that old stands have a higher frequency of large plants than burned stands. However, in burned stands small size plants have higher fertility than in old stands (Fig. 1). In unburned stands, where *P. halepensis* and *P. pinea* have developed a 5–10 m high canopy, there was a significant negative correlation between pine cover and the percentage of reproductive adults ($r = -0.50$, $p = 0.017$, $n = 22$). Three years after fire, plant cover in twice burned stands was not significantly different than that observed in once burned and unburned stands and the percentage of resprouting was very high: only 15 out of 1829 plants (0.82%) did not resprout. *Ampelodesmos* plant cover was only negatively correlated to *Q. coccifera* cover, the dominant shrub of the region, in unburned stands ($r = -0.41$, $p = 0.026$, $n = 30$).

Unburned stands had less than 40 seedlings/m², while there were around 200 seedlings/m² in both once and twice burned stands (Table 2). Seedling density was positively correlated with the density of reproductive adults (ln–ln transformation of variables,

Table 2

Significance of effects of environmental variables of *Ampelodesmos* population parameters, calculated from general linear model applied to the extensive survey data. All the variables, except the percentage of reproductive plants, were $\log(x + 1)$ transformed. For each environmental variable, the number of stands per class are given as the footnotes

	Whole model			Partial regressions											
	d.f.	F-ratio	p	Fire ^a			Aspect ^b			Soil surface ^c			Topography ^d		
				d.f.	F-ratio	p	d.f.	F-ratio	p	d.f.	F-ratio	p	d.f.	F-ratio	p
Adult density (m ⁻²)	5	7.38	<0.0001	2	15.85	<0.0001	1	0.87	0.35	1	1.28	0.26	1	0.08	0.78
Plant cover (%)	5	4.46	0.001	2	9.97	0.0001	1	0.17	0.68	1	0.55	0.46	1	0.05	0.83
Reproductive plants (%)	5	4.15	0.002	2	7.29	0.001	1	0.51	0.48	1	1.42	0.24	1	0.32	0.57
Seedling density (m ⁻²)	5	2.27	0.054	2	4.85	0.010	1	0.55	0.46	1	0.33	0.57	1	0.03	0.86
Seedling/adult ratio	5	3.26	0.01	2	5.08	0.008	1	1.66	0.20	1	1.42	0.24	1	0.04	0.84

^a Unburned: 30 stands; once burned: 32 stands; twice burned: 30 stands.

^b North: 48 stands; south: 44 stands.

^c Low rock outcrops: 68 stands; high rock outcrops: 24 stands.

^d Flat: 33 stands; slope: 59 stands.

unburned stands: $r^2 = 0.34, p = 0.0007$; once burned stands: $r^2 = 0.58, p < 0.0001$; twice burned stands: $r^2 = 0.26, p = 0.0038$). Seedling/adult ratio was higher in once and twice burned stands than in unburned stands (Table 3).

3.2. Intensive survey at the local scale

Two and a half years after fire, although *Ampelodesmos* cover was not significantly different than in the adjacent unburned stand, *Ampelodesmos* plants were larger (Table 4) and only one out of 338 plants (0.29%) did not resprout after fire. Standing flower stalks demonstrated that *Ampelodesmos* produces new inflorescences the following year after fire. There were significant differences for reproductive characters between burned and unburned plants; the percentage of reproductive plants was significantly higher in

burned stands and these plants bore more reproductive stalks than the unburned plants (Fig. 2). However, the number of seeds per stalk was lower and the percentage of predated and aborted seeds was higher in burned plants. As in the Garraf extensive survey, seedling densities were significantly lower in the unburned stands (Table 4). In May 1998, we did not find seedlings in areas recently burned in July 1997 in Garraf, but seedlings were present in nearby unburned areas.

3.3. Effect of temperature on seed germination

High heating treatment had a lethal effect on seeds. However, seed germination was very high in the other treatments and it was not significantly different among moderate, low and control treatments ($F_{5,54} = 2.03, p = 0.09$) (Table 5).

Table 3

Characteristics (mean + S.E.) of *Ampelodesmos* populations in areas with different fire history in Garraf^a

	F-value	Unburned (n = 30)	Once burned (n = 32)	Twice burned (n = 30)
Adult density (m ⁻²)	17.46***	0.20 ± 0.05 a	0.43 ± 0.06 b	0.68 ± 0.06 c
Plant cover (%)	11.01***	15.60 ± 3.50 a	22.90 ± 4.00 b	35.76 ± 3.30 c
Reproductive plants (%)	9.04***	30.30 ± 5.58 a	49.48 ± 5.26 b	58.66 ± 2.88 b
Seedling density (m ⁻²)	5.39**	37.50 ± 15.57 a	220.96 ± 85.16 b	182.08 ± 53.52 b
Seedling/adult ratio	6.73**	152.42 ± 60.40 a	346.38 ± 101.32 b	260.09 ± 65.87 b

^a Values followed by different lower case letters are significantly different.

** $P < 0.001$.

*** $P < 0.0001$.

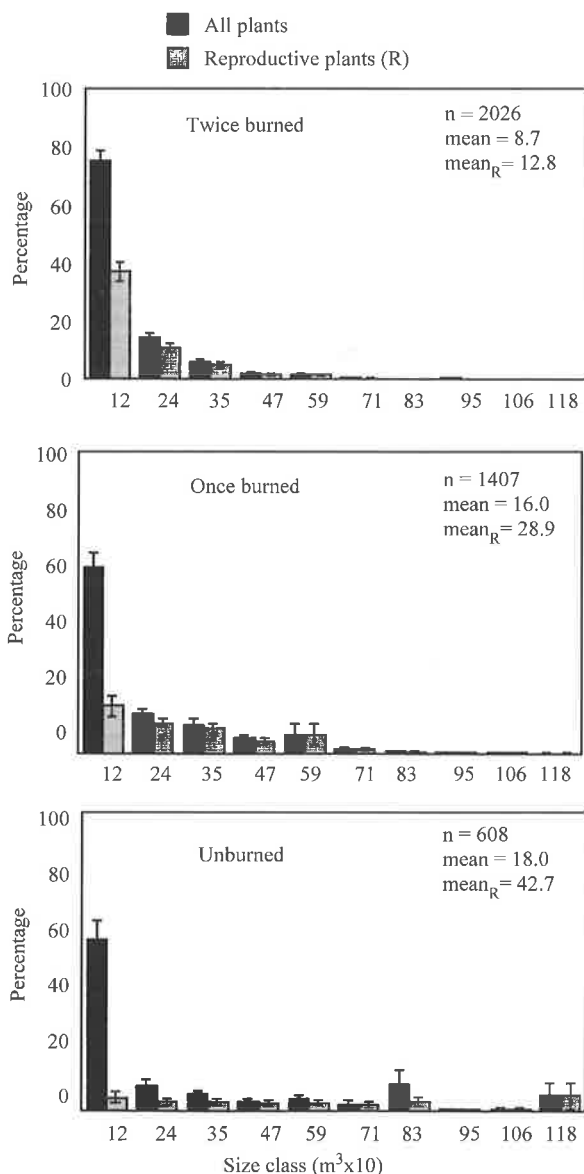


Fig. 1. Size distribution of *Ampelodesmos* plants at sites with different fire history in Garraf.

3.4. Fire behaviour

The fuel model built for *Ampelodesmos* is close to Model III from the BEHAVE system, while the model built for *B. retussum* is close to Model I and the ones for the remaining species *Q. coccifera* and *R. officinalis* are similar to Model V. *Ampelodesmos* produces a high and dense carpet of dead leaves from which

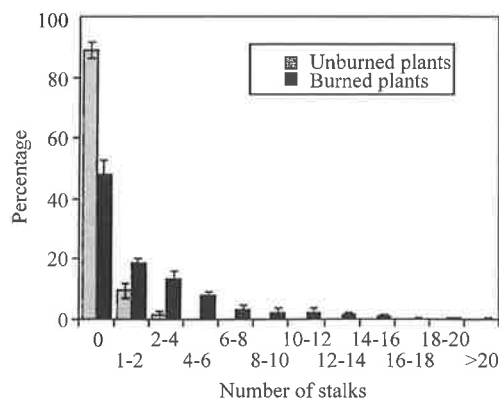


Fig. 2. Distribution of number of stalk per plant in burned and adjacent unburned *Ampelodesmos* plants in Vallirana.

originate high values of dead fuel load and depth (Table 6). The average percentage of standing dead biomass was 60.5 (S.E. = 6.14) in *Ampelodesmos*, while this value was 41.1 (S.E. = 4.63), 28.9 (S.E. = 1.69), and 13.1 (S.E. = 1.89) for *B. retussum*, *Q. coccifera*, and *R. officinalis*, respectively. Under all four scenarios of fire hazard, the model predicted the highest values of both simulated rate of fire spread and simulated fire intensity for *Ampelodesmos* (Fig. 3). Differences in fire spread become greater with increasing fire hazard, while differences in fire intensity show a more regular pattern. The low predicted values for both fire parameters in the other grass species (*B. retussum*) were due to its smaller plant size. *R. officinalis* also had a low rate of fire spread and fire intensity due to low values of dead fuel load and low area/volume ratio.

4. Discussion

4.1. Grass expansion and pine cover reduction after fire

Adult and seedling density of *Ampelodesmos* were greater with increasing fire frequency. The process by which burned stands show higher *Ampelodesmos* density may be associated with (i) high regeneration and survival rate after fire and (ii) competitive advantage over other shrubland species or avoidance of competitive exclusion by larger, later successional species, particularly pines.

Table 4

Characteristics of *Ampelodesmos mauritanica* in a burned and in an adjacent unburned stand in Vallirana^a

Character	Burned stand	Unburned stand	<i>p</i> ^b
Plant density (ha ⁻¹)	10700 ± 1380 a	11260 ± 1078 a	0.92
Plant cover (%)	83.63 ± 5.36 a	64.28 ± 15.20 a	0.34
Plant volume (m ⁻³)	0.36 ± 0.07 a	0.29 ± 0.1 b	0.03
Reproductive plants (%)	49.75 ± 5.00 a	11.13 ± 2.71 b	0.03
Stalks/plant	2.55 ± 0.35 a	0.18 ± 0.04 b	0.03
Seeds/stalk	233.65 ± 37.78 a	432.10 ± 69.05 b	0.006
Seedling density (m ⁻²)	217.65 ± 50.60 a	50.42 ± 15.77 b	0.03
Aborted seeds (%)	72.93 ± 5.40 a	37.52 ± 3.77 b	0.000
Predated seeds (%)	5.75 ± 1.02 a	1.70 ± 0.44 b	0.001

^a Values followed by different lower case letters are significantly different.^b Wilcoxon signed rank test except for seeds/stalk, % aborted seeds and % predated seeds that were compared by a *t*-test.

Ampelodesmos plants show a very high resprouting ability. Post-burn regrowth from buds surviving at ground level is known to occur in grasses (Vogl, 1974). Although fire characteristics are not identical among fires, our findings suggest that *Ampelodesmos* recovers quickly and successfully after fire compared to co-occurring shrubs: more than 99% of *Ampelodesmos* plants survived after fire, while survival rates in resprouting shrubs of the same region range from 40 to 90% (López-Soria and Castell, 1992).

The survival rates of *Ampelodesmos* seeds after heating treatments were similar to the observed values for other grasses (Daubenmire, 1968). These results indicate that although some seeds buried in the soil may survive after fire, those lying in the upper part of the litter or still in the inflorescences will be killed by fire. The negative effect of fire by burning seeds is counteracted by the fast resprouting of *Ampelodesmos* and high production of seeds the first summer after

fire, which can quickly refill the soil seed bank and allow seedling recruitment. Furthermore, *Ampelodesmos* has a pseudo-persistent seed bank because there are always seeds in the soil but their density fluctuates

Table 5

Germination percentage (mean ± S.E.) of *Ampelodesmos* seeds 98 days after high (H), moderate (M) and low (L) heating treatments

Heating treatment	Germination (%)
Control	84 ± 5.2
L (70°C, 5 min)	89 ± 3.8
L (70°C, 15 min)	86 ± 4.3
L (70°C, 60 min)	79 ± 4.7
M (105°C, 5 min)	72 ± 4.7
M (105°C, 15 min)	74 ± 5.8
H (200°C, 1 min)	0
H (200°C, 5 min)	0
H (300°C, 5 min)	0

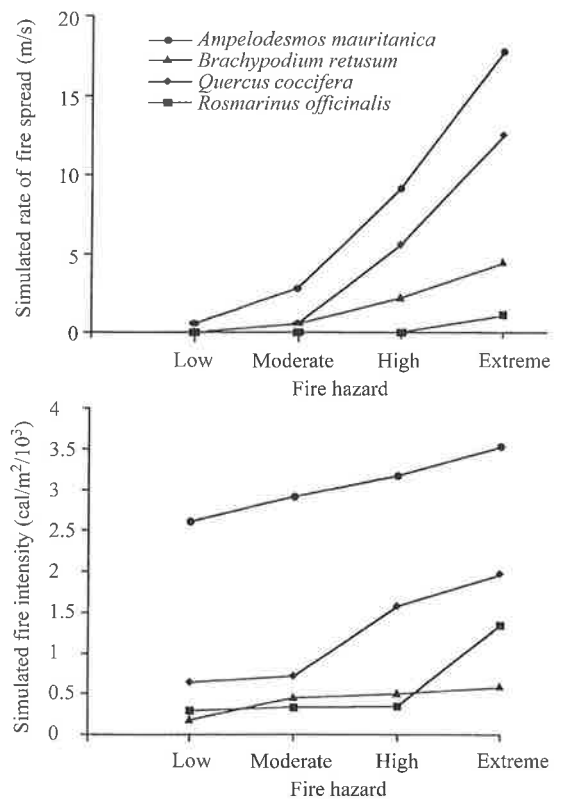


Fig. 3. Simulated rate of fire spread and fire intensity for four Mediterranean species at different degrees of fire hazard (see Table 6).

Table 6

Parameters used for each species to simulate fire behaviour using the BEHAVE model

	Dead				Live		
	Fuel load (t/ha)		Area/volume (mm ⁻¹)		Fuel load (t/ha) (<6 mm)	Area/volume (mm ⁻¹) (<6 mm)	Depth (cm)
	<6 mm	>6 mm	<6 mm	>6 mm			
<i>A. mauritanica</i>	12.0		33		5.9	35	75
<i>B. retusum</i>	1.4		37		1.9	33	18
<i>Q. coccifera</i>	5.3	0.2	45	15	8.3	40	72
<i>R. officinalis</i>	2.9		12		11.3	14	68

in parallel with seedfall due to short seed life-span and high post-dispersal seed predation (Vilà and Lloret, 2000). As for other Mediterranean species, survival of seedlings emerging from fire-stimulated seed production is expected to be greater than survival of seedlings emerging in periods between fire (Lloret, 1998).

The positive correlation between seedling density and reproductive plant density also supports the hypothesis that seedling density is greater in burned stands because of the higher percentage of reproductive plants and the higher seed production per plant. The higher percentage of aborted and predated seeds in burned plants does not seem to modify this trend because burned plants bore on average four times more viable seeds than unburned ones.

An increase of seed production has also been found in recently burned grasslands and savannas (Daubenmire, 1968; Coutinho, 1982; Canales et al., 1994; Mark, 1994). Lower seed production in unburned stands may also be associated with competition with large shrubs and trees and it may reflect reduced individual growth rates (Silva et al., 1991) or changes on the light quality produced by shading (Pfitsch and Peracy, 1992). Establishment limitations may also keep seedling density of *Ampelodesmos* low in old stands due to the lack of safe sites and overstorey shading. In savanna communities protected from fire, standing necromass suppresses seedling recruitment by shading, limiting space and nutrient availability (Vogl, 1974). These recruitment limitations may also occur in Mediterranean old stands where *Ampelodesmos* is a component of the understorey.

In our study system, although regeneration of shrubs and pines occurs after fire, the fast vegetative growth of *Ampelodesmos* probably allows it to colonize space and to become the dominant species in the

community. However, if the period without fire is long enough, the tree and shrub canopy may close over the grass understorey and the grasses would be suppressed, as expected from a classical successional model (Escarré et al., 1983). The negative correlations between pine cover and *Ampelodesmos* reproductive performance, and between *Q. coccifera* and *Ampelodesmos* cover support this hypothesis. Vegetation changes due to grass burning have been suggested to occur in other Mediterranean regions. In California, fires which burn annual grasslands may contribute to the expansion of coastal sage scrub and the recession of chaparral (Oberbauer, 1978). Haidinger and Keeley (1993) have also suggested that high fire frequency may favour a conversion from shrubland to herbaceous ecosystems dominated by non-native species. A dense grass cover may inhibit the establishment of shrub and tree seedlings (Berkowitz et al., 1995).

4.2. Flammability of *Ampelodesmos*

Although we recognize that the BEHAVE models that we have built are single-species fuel models and usually Mediterranean vegetation is a mixture of several species which together form a fuel bed, in our study system it is realistic to compare species because in some cases they form almost monospecific stands (i.e. *Ampelodesmos* forms prairies known as “carrizxeres” and *Q. coccifera* forms shrublands known as “garrigues”).

For the BEHAVE fuel models which consider grasslands as a distinctive fuel type, fire behaviour will be strongly dependent on fuel load (Rothermel and Philpot, 1973). Although short Mediterranean grasses have low fuel load (Trabaud, 1985) (e.g. *B. retusum* dead fuel load is 1.4 t/ha), *Ampelodesmos* achieves a

considerable size, accumulates a large amount of dead leaves and is able to produce fuel loads more than 1 m in depth. Stands dominated by *Ampelodesmos* catch fire more readily and in conditions less suitable for propagation than short grasses. Therefore, fire frequency could increase. Fire intensity is expected to decrease when the interval between fires is short, but here we show that higher fire intensity and spread occur sooner in stands dominated by *Ampelodesmos* than in stands covered by other species, because the faster fuel accumulation in *Ampelodesmos* areas.

Maintenance of flammable grassland communities associated with high fire recurrence has been proposed to be a self-reinforcing process leading to stable plant communities, and it is known to occur in temperate and tropical grasslands (Vogl, 1974; Archibold, 1995). Most studies on vegetation flammability and fire behaviour in Mediterranean regions consider shrublands and forests, which are the dominant formations (Rothermel and Philpot, 1973; Van Wilgen and Van Hensbergen, 1992; Viegas et al., 1998). However, grass–fire interaction has been less studied in these communities (but see the Bradstock and Gill, 1993, study on the increase of flame size due to the presence of the grass *Triodia irritans* in Australia). We do not know if the spatial distribution of past wildfires can be explained by past distribution of grass abundance in the landscape, but the simulation models predict that high *Ampelodesmos* densities promote an increase of fire spread and intensity.

4.3. Management implications

These findings contribute to our understanding that in the studied Mediterranean landscapes the patterns of grass abundance and fire hazard may be connected. Although, experimental fires should be conducted to obtain conclusive proof, we believe that our study supports that both premises needed for a positive feedback between fire and grass have been found: there is a positive effect of fire on *Ampelodesmos* population size within the community and *Ampelodesmos* also has a positive effect on fire hazard. The conversion of shrublands and pine forests to grassland-type formations has important implications for fire management.

Ampelodesmos is very abundant in northern coastal communities of the Balearic Islands. In Mallorca,

prescribed fires at a 4-year frequency are conducted by peasants in order to obtain fresh forage for sheep and goats (Castelló and Mayol, 1987). This practice was even more frequent in the past. Old records describe *Ampelodesmos* cleaning and burning at a higher frequency to obtain domestic animal forage and fibre production (Salvador, 1987). Thus in these communities, the fire–grass cycle has been reinforced by man. Given that nowadays there is a low to moderate grazing demand, we do not recommend using this fire management tool because fire enhances the dominance of *Ampelodesmos* in the community and consequently increases fire hazard. An increase in fire hazard does not only result in expensive fire prevention and fire fighting programs but also on catastrophic damage to private properties, including agricultural and urbanized areas. Furthermore, frequent fires and the dominance of *Ampelodesmos* stands reduce tree establishment and tree cover.

Under the current trend of increasing fire frequency due to alterations in land use and climatic change (Piñol et al., 1998), we suggest that there could be a shift from thicket to grassland-type formations. These changes may be locally persistent, leading to important changes at a landscape level (Woodcock, 1992). Although *Ampelodesmos* appears to become more abundant in localities where it was previously present, its ability to colonize new, potentially suitable areas remains to be investigated. Therefore, more accurate forecasts on the fire–grass interaction consequences need an increasing knowledge of the mechanisms involved in the grass–woody vegetation interaction and in the ability of *Ampelodesmos* to expand its distribution area by seed dispersal.

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