Effect of spatial and temporal patterns of stress and disturbance intensities in a sub-Mediterranean grassland

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Abstract
The present study examined a sub-Mediterranean pastoral system in the central Apennines (Italy) with a long history of grazing, where winter cold stress is alternated with summer drought stress. The research goals were to ascertain whether different floristic structures correspond to different stress conditions (xeric and semimesic), and whether peculiar functional plant traits (such as avoidance and tolerance mechanisms) respond to stress/disturbance intensities, and understand how vegetation reacts to changeable livestock pressure (through floristic and plant trait variations). Cluster analysis indicated that separate communities develop under different stress intensities. Other analyses highlighted how avoidance strategies predominate within the pastoral system. Observations of grazed and ungrazed patches conducted in 10-m transects revealed spiny cushion formation in semimesic grassland, where a brief period of overgrazing occurs in late summer, causing variations in plant community structure. All these results confirm the importance of historical grazing and current land use, showing how small disturbances and stress variations cause ecosystem responses. Best practices for management were identified. In xeric conditions, it is advisable that the intensity of disturbance be lessened, while in semimesic grassland overgrazing should be forbidden during the dry period, because it could facilitate the development of spiny patches, and subsequent spread of *Brachypodium rupestre*.

Keywords: *Avoidance/tolerance, floristic changes, functional plant traits, grazing management, stress and disturbance intensities, sub-Mediterranean grasslands*

Abbreviations: AWC, available water content; DFA, discriminant function analysis; FU, fodder unit; LU/ha, livestock units per hectare

Introduction

It is well known that grazing and its management act as driving forces in grassland ecosystems diversity determination (Hodgson & Illius 1996). However, throughout Europe, semi-natural calcareous grasslands are in strong decline in terms of extension, and threatened by management practice cessation (Sebastià et al. 2008). This trend is also observed within the Apennine sub-Mediterranean pastoral landscape (Catorci 2007), which is included in habitat 6210 by the 92/43/EEC Directive as "habitat of priority importance" (Biondi et al. 2009).

In order to further grassland biodiversity conservation, it is vital to identify the driving forces that affect plant community dynamics. In fact, considerable evidence supports the hypothesis that coexistence between herbaceous species is conditioned by stress and disturbance intensities (Grime 2001). They act in a very complex way, affecting the species' competitive ability, and thus plant community diversity (Lauenroth & Aguilera 1998; Wilson 1998). The general theory about the resistance of plants to grazing identifies two strategies that enable plants to survive and grow in grazed systems: avoidance and tolerance (Briske 1996). Milchunas et al. (1988) have hypothesized that the relative importance of these strategies diverges with increasing primary production that, in turn, is related to

environmental stress intensity (Tilman 1987; Berendse 1994; Silvertown et al. 1994). Bullock et al. (2001) affirm that this dichotomy may be simplistic. In fact, as Watkinson and Ormerod (2001) suggest, variations in the density or seasonality of grazing are key factors in understanding how grazing impacts on plant community composition. Thus, the competitive success of the different strategies depends on the relationship between resource availability in the environment and livestock pressure (Berendse 1985; Grubb 1992; Skarpe 2001). This understanding has been demonstrated by many studies conducted throughout the world (Noy-Meir et al. 1989; Chaneton & Facelli 1991; Tremont 1994; Biondini et al. 1998; Fensham et al. 1999; Dupré & Diekmann 2001; Pavlů et al. 2003; Altesor et al. 2006). However, there are few studies which refer to sub-Mediterranean grasslands (de Bello et al. 2006, 2007).

The study of trait distribution within a community affords useful information for understanding the mechanisms of plant community assemblage (McGill et al. 2006); in fact, the identification of functional traits concerning plant responses to stress and disturbance intensity provides further insight on plant community composition (Díaz et al. 2007; Navas & Violle 2009). Functional traits are defined as plant characteristics responding to dominant ecosystem processes (Gitay & Noble 1997; Hobbs 1997; Lavorel et al. 1997), and are used in assessing vegetation responses to different environmental factors, such as climate, disturbance, and land use (Díaz et al. 1999). As confirmed by many investigations, trait distribution within a community provides useful information for the comprehension and the prediction of plant community processes (McGill et al. 2006). On the basis of this theoretical framework, our study sought to verify whether the plant community composition in a sub-Mediterranean pastoral system is determined by avoidance and tolerance strategies, as hypothesized by Milchunas and Lauenroth (1993), and if these strategies are related to stress and disturbance intensities and timing. Hence, the research goals were: (a) to assess floristic differences occurring in the studied pastoral system, and to identify how they are associated to environmental stress and livestock disturbance intensity; (b) to determine whether the functional plant traits connected to avoidance and tolerance strategies show any particular patterns related to the identified stress/disturbance driving forces; (c) to define the relationships between plant traits, grassland patchiness, and livestock management (intensity and timing).

The final goal was to furnish some management guidelines for maintaining the biodiversity of Apennine pastures.

Materials and methods

Study area and current management

The study site (a farming system of about 200 ha) is located along the mountain ridge of the Umbria-Marche Apennines of central Italy (42°56′53″N 13°00′35″E), between 1100 and 1360 m a.s.l. (Figure 1); it is characterized by limestone lithotypes and belongs to the lower supratemperate bioclimatic belt (Biondi & Baldoni 1995; Biondi et al. 1995) in the temperate region (Rivas-Martínez & Rivas-Saenz 1996–2009). As reported in Catorci et al. (2009), the growing season (number of days with minimum temperature over 6°C) is 150–180 days/year (Table I). The plant landscape is composed of different secondary successional grasslands, interrupted by small beech copses and crop lands. As reported by Cesaretti et al. (2007), from a phytosociological point of view, the pastoral landscape is referred to *Brizo mediae-Brometum erecti brizetosum mediae* Biondi, Pinzi et Gubellini 2004 and *Potentillo cinereae-Brometum erecti potentilletosum cinereae* Biondi, Pinzi et Gubellini 2004 associations (Biondi et al. 2004) of *Phleo ambigui-Bromion erecti* alliance, *Brometalia erecti* order and *Festuco-Brometea* class (Biondi et al. 2005).

The seasonal trend of annual phytomass productivity is shown in Figure 2; in late summer, there is a lack of re-growth in both plant communities (Cesaretti et al. 2009). *Brizo mediae-Brometum erecti brizetosum mediae* has a higher productivity (a peak of 215.3 g/m^2) than *Potentillo cinereae-Brometum erecti potentilletosum cinereae* peak of productivity (57.4 g/m^2).

The entire study area is characterized by intense livestock activity, with 150 cattle and 280 sheep reared for meat production. Cattle are free to graze throughout the area, while sheep are herded by shepherds.

Real livestock pressure is about 200–210 livestock unit per hectare (LU/ha); pastoral activities start in June and last until the end of October (Cesaretti et al. 2009). The grazers have different feeding behaviours and vegetation preferences: cattle opt for flat or semi-flat morphologies (Putfarken et al. 2008), while sheep graze mainly on the slopes. In spring and autumn, shepherds lead the flocks daily across the southern slopes of the grasslands (*Potentillo cinereae-Brometum erecti potentilletosum cinereae*), then to the northern ones (*Brizo mediae-Brometum erecti brizetosum mediae*). At noon, the sheep take a rest and ruminate inside beech copses, and in the afternoon they make the opposite journey. In summer, the flocks spend very little time in pastures with southern exposure, because the shepherds lead them directly to grasslands with northern exposure. Currently, the theoretical carrying capacity of the pastoral system is
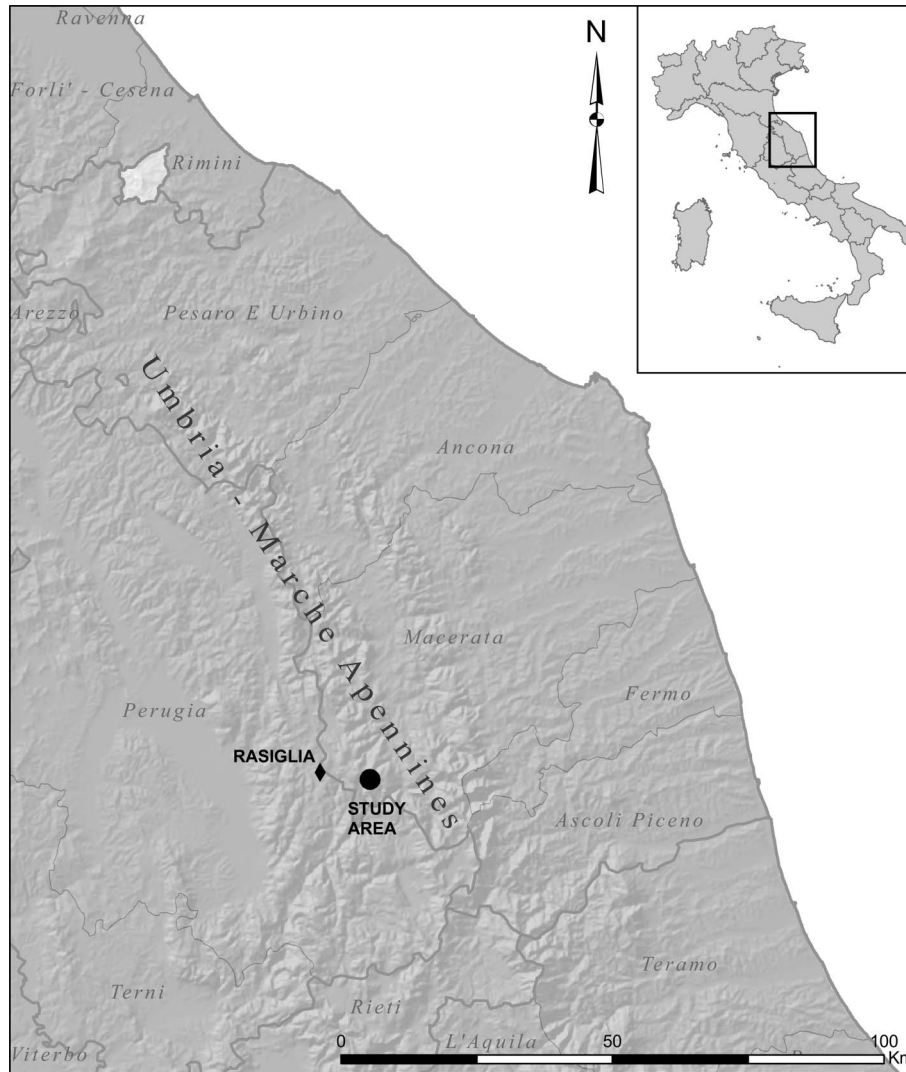
Figure 1. Localization of the study area.

Table I. Main bioclimatic characteristics of the study area (Orsomando et al. 2000; Catorci et al. 2009).

Mean annual temperature (°C)	Mean annual rainfall (mm)	Mean summer rainfall (mm)	Number of months with minimum temperature <0°C	Cold stress (number months)*	Length of growing period (number of days)
10–11	1200–1300	180–190	2–3	7–8	150–180

Note: *Number of months with cold stress, following the Mitrakos index (1982).

about 190–210 LU/ha (Cesaretti et al. 2009). Comparing the real livestock pressure (200–210 LU/ha) with the theoretical carrying capacity, it can be assumed that the pastoral system undergoes an optimal grazing pressure; consequently, the seasonal above-ground phytomass should be totally removed, hence there is no litter accumulation, and the expansion of dominant species should be contained. In this way, the pastoral system follows one of Grime's model conditions (1973, 2001), leading to

maximum floristic richness of the plant communities.

Data collection

The grassland vegetation relevés followed the Braun-Blanquet method (1964), and 20 relevés, having equivalent surfaces (100 m²), were performed. Floristic nomenclature followed Conti et al. (2005).
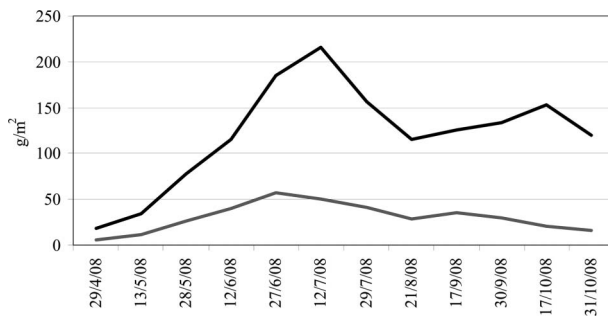
Figure 2. Seasonal productivity (g/m^2 of dry matter) of the two grasslands (grey indicates the grassland developing on *Potentillo cinereae-Brometum erecti potentilletosum cinereae*, while black indicates the one on *Brizo mediae-Brometum erecti brizetosum mediae*). Along the *x* axis, the growing period is reported (from the end of April to the end of October 2008; Cesaretti et al. 2009, modified).

Ten soil samples were collected and then analysed by the Marche Region agrochemical analysis and research laboratories to identify the soil features (according to the methodological standards established by Italian ministerial decree 13/09/99). The soil depth was measured directly in the field using a graduated pole. The thermo-pluviometric data are from a station close to the study area (Rasiglia), where data have been recorded for a period of 30 years and published in Orsomando et al. (2000).

In order to collect data on the relationship between grass-growing capacity and herbivore intake, relevés of available above-ground phytomass were done in the grazed pastures during 2007 and 2008 (from April to October). Circles of 0.2 m^2 were mown every 15 days at 2–3 cm height from ground level (in order to simulate the sheep bite). A total of 840 circles were harvested during the growing season. For investigating which avoidance and/or tolerance strategies are employed by the different species forming the pastures, information from the literature (Pignatti 1982; Grime et al. 1988; Kerguélen & Plonka 1989; Klotz et al. 2002; Roggero et al. 2002; Ballelli & Bellomaria 2005; Klimešová & Klimeš 2006) and field observations were used. For each species identified by the relevés, 15 functional plant traits were considered: leaf distribution (rosette and non-rosette growth forms), spines, hairs, leaf texture (mechanical defences), chemical defences (toxic and repelling compounds), unpalatability, prostrate form, early flowering (escape strategies), and re-growth capacity. All these mechanisms were considered as avoidance strategies, except re-growth capacity, which is a tolerance strategy. Unpalatability is an agronomic assessment of feed value, and it was included in the set of evaluated traits in order to understand which morphological or chemical characteristics are related to this forage feature. Presence of clonal ability through rhizomes, tap roots, stolons, bulbs, and tubers was evaluated as well.

At the close of the grazing season, in order to test the effects of grazer selectivity and to understand why some patches were not grazed, 20 transects, each 10 m long and 0.5 m wide, were applied; floristic composition, species cover values (%), and size of patches not eaten were recorded.

Data processing and statistical analysis

To highlight significant differences in plant communities' floristic richness and functional compositions, the following procedures were performed.

Species cover values were converted, according to the Van der Maarel scale (1979), and then subjected to cluster analysis through Syntax 2000 software (Podani 2001), using the group average method, ratio scale coefficient with Euclidean distance.

For available water content (AWC) and water deficit graphs of both plant communities, Armiraglio's spreadsheet was applied (Armiraglio et al. 2003), using the mean values of the soil parameters (depth, texture, and skeleton percentage), and the average monthly rainfall and temperature data. Independent *t*-tests for means with standard errors (SE) were performed for all the soil and environmental parameters (showing normal distribution of data), using SPSS 13.0 software (2005).

Concerning plant community productivity, green biomass was oven-dried for 48 h at 90°C until constant weight, and then weighed.

The calculation of the daily instantaneous carrying capacities (LU/ha), defined as the number of theoretic LU that can be nourished for a given day in a given area (Pardini 2006), is achieved through the Bittante et al. (1993) formula:

$$\text{LU/ha} = \left[\frac{\text{FU/ha year}}{3000/365 \times D} \right]$$

where FU (fodder unit) represents the nutritional value of the forage, considering that 1 kg of dry grassland phytomass is equal to 0.69 FU (FU = kg/ha dry matter × 0.69); *D* is the period the livestock stay in the grassland (=1 because we considered the daily instantaneous carrying capacity). The actual livestock pressure is obtained by considering that six sheep are equivalent to 1 LU.

Multivariate discriminant function analysis (DFA) was carried out to identify the most discriminant plant traits (showing normal distribution of data) for each plant community pointed out by the cluster analysis. The matrix subjected to the DFA procedure uses presence/absence data weighted by Van der Maarel cover values. Then, Pearson correlation analysis was performed for all the traits and both plant communities, in order to identify positive relationships between plant traits.

For patchiness analysis, data from transects were statistically processed considering cover percentage of dominant species inside the ungrazed portion, frequency of dominant species, and combinations of dominant species and patch size. Pearson's correlation coefficient (r) was calculated to verify whether there was a statistical relationship between cover values of dominant species within ungrazed patches, and patch size. DFA and Pearson's correlation analysis were carried out using SPSS 13.0 software (2005).

Results

Floristic analysis

Cluster analysis (Figure 3) reveals a clear separation between relevés (Appendix 1): cluster I includes relevés carried out on the south-facing grassland, while cluster II groups the relevés of the north-facing grassland. In accord with the phytosociological placement reported in Cesaretti et al. (2007), the former cluster refers to *Potentillo cinereae-Brometum erecti potentilletosum cinereae* (relevés 1–10), while the latter belongs to *Brizo mediae-Brometum erecti brizetosum mediae* (relevés 11–20).

Environmental characterization

Table II shows the means with SE of the soil parameters considered in both plant communities (texture, percentage of sand, silt and clay, N content, skeleton, depth, pH, and AWC). From these data,

the changing parameters, identified by independent t-tests, are skeleton ($p < 0.01$), depth ($p < 0.001$), pH ($p < 0.05$), and AWC ($p < 0.01$).

Water deficit area graphs for south- and north-facing slopes show a longer period of water scarcity for the xeric community, and briefer drought stress for the semimesic one (Figure 4).

Phytomass production and carrying capacity

The dry matter of available phytomass (g/m^2) and the daily instantaneous carrying capacity (LU/ha) during the grass-growing period (from April to October) are reported in Tables III and IV, respectively, and show that there is a notable decrease in August. From the comparison with the real mean daily instantaneous grazing pressure, it emerges that the daily instantaneous carrying capacity is very low between August 15 and September 15 (Table IV). Given that the mean of total daily instantaneous carrying capacity in this period is 22 LU/ha, and that real livestock pressure is 200 LU/ha, it can be calculated that the herd needs 9.1 ha daily to feed regularly. Since the available surface of the pastoral system is about 200 ha, there is insufficient fodder available to sustain animals for the whole month (200 ha/9.1 daily ha = 22 days).

Analysis of functional plant traits

Overall, 113 species were found in the study area; all of them having one or more traits which can be considered avoidance/tolerance strategies (Table V).
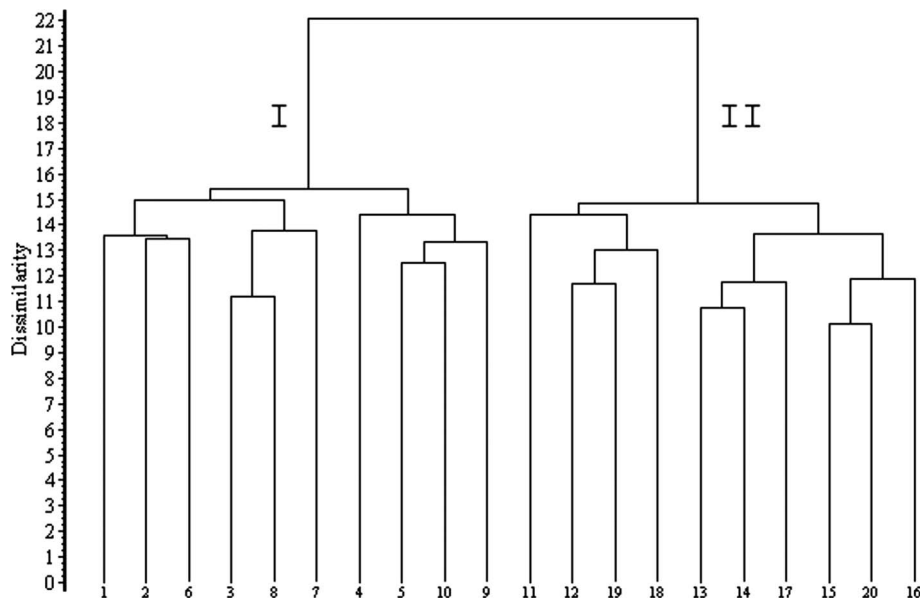
Figure 3. Cluster analysis outcome highlighting the separation between the two studied plant communities; relevés 1–10 belong to *Potentillo cinereae-Brometum erecti potentilletosum cinereae* and relevés 11–20 refer to *Brizo mediae-Brometum erecti brizetosum mediae*.

DFA (Wilks' Lambda $p < 0.005$) performed within xeric (*Potentillo cinereae-Brometum erecti potentilletosum cinereae*) and semimesic (*Brizo mediae-Brometum erecti brizetosum mediae*) plant communities identified hairs and leaf texture as the most significant traits characterizing the xeric community, while the discriminants for the semimesic community are leaf distribution (rosette form), chemical defences, spines and, to a lesser degree, re-growth capacity, prostrate form, and unpalatability. The plant community group centroids of functional traits are separated along the function linear axis: the negative values correspond to xeric pasture, whereas the positive part refers to semimesic grassland (Table VI).

Table II. Soil and environmental features (means ± SE) of the grasslands developing on south- and north-facing slopes with the results of independent *t*-tests to compare means (***$p < 0.001$; **$p < 0.01$; *$p < 0.05$).

Parameters	South-facing	North-facing
Texture	Clayey	Clayey
Sand (%)	10.12 ± 1.38	8.06 ± 0.91
Silt (%)	36.98 ± 2.88	31.76 ± 3.01
Clay (%)	52.9 ± 4.01	60.18 ± 3.36
Total N (g/kg)	6.6 ± 0.98	6.89 ± 0.49
Skeleton (%)**	75 ± 2.6	47 ± 5.76
Depth (cm)***	13.8 ± 1.88	28 ± 1.14
pH*	5.44 ± 0.05	5.7 ± 0.07
AWC**	7.3 ± 0.72	35.3 ± 3.32
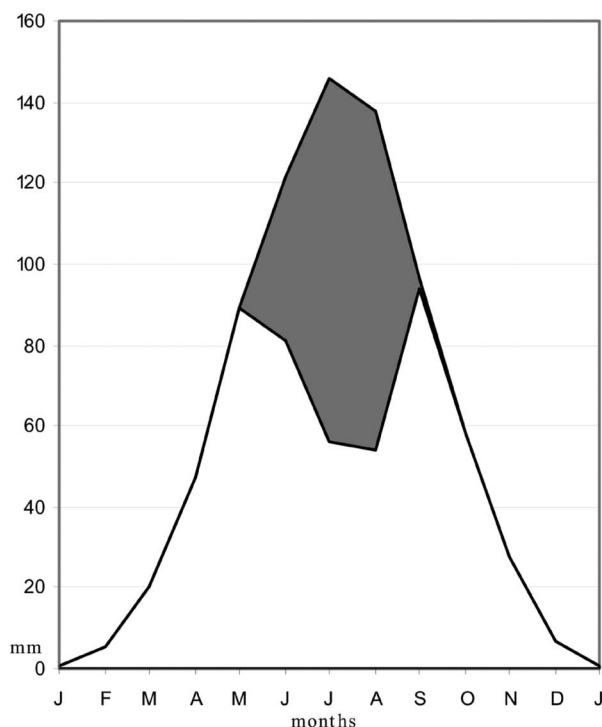
Correlations between traits

Some traits are correlated with each other, as indicated by Pearson's correlation analysis. Particularly evident are the relationships between unpalatability and leaf texture, chemical defences, prostrate form and, secondarily, leaf distribution (rosette form) and presence of stolons. Other statistically significant correlations are listed in Table VII.

Patchiness analysis

Examination of the 10-m transects indicates the presence of ungrazed patches. Within the uneaten patches, three dominant species (Appendix 2) for cover and frequency were identified (*Brachypodium rupestre* with 88% frequency, followed by *Astragalus sempervirens* with 82%, and *Eryngium amethystinum* with 58%). The outcome of Pearson's correlation coefficient (r) for the relationship between species cover and patch size shows a direct relation between *B. rupestre* cover and patch size ($p < 0.01$), while this relationship is inverse for *A. sempervirens* ($p < 0.01$) and *E. amethystinum* ($p < 0.05$; Table VIII).

Discussion

Functional plant traits

As proposed by many authors (e.g. Catorci & Gatti 2010; Mårtensson & Olsson 2010), soil AWC and

Figure 4. Grey indicates the water deficit area (months) for south-facing (left) and north-facing (right) environments.

Table III. Available phytomass expressed as g/m^2 (means $\pm$ standard deviations) in xeric and semimesic conditions.

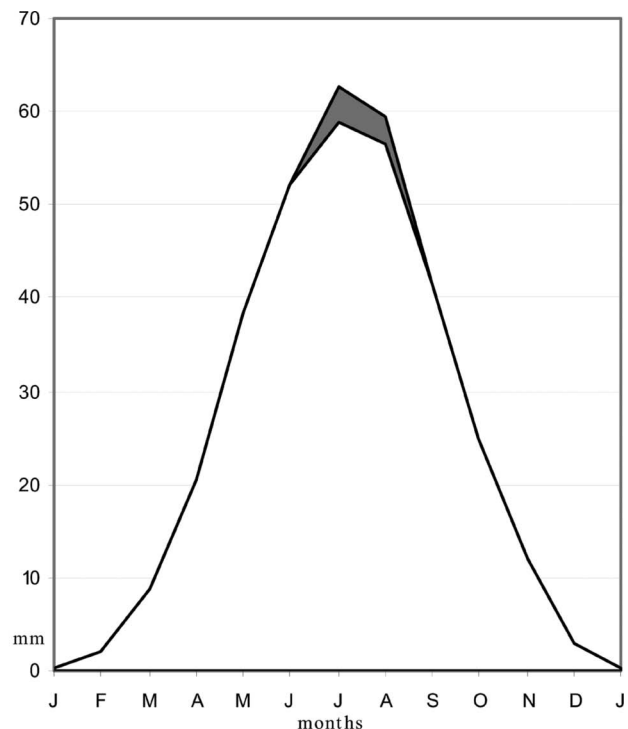| Period	Xeric	Semimesic
01 April	2.4 ± 1.9	3.6 ± 1.5
15 April	5.9 ± 3.8	7.1 ± 5
01 May	21.4 ± 5.5	45.2 ± 4.8
15 May	48.7 ± 6.1	54.7 ± 8.2
01 June	67.7 ± 10.5	85.6 ± 5.8
15 June	80.8 ± 15.3	101.1 ± 13.2
01 July	45.2 ± 14.8	84.9 ± 4.2
15 July	30.9 ± 7.6	73.7 ± 3.8
01 August	20.2 ± 1	47.5 ± 5.2
15 August	5.8 ± 0.8	17.8 ± 5.8
01 September	2.5 ± 0.5	4.7 ± 4.5
15 September	17.8 ± 8	29.7 ± 9.4
01 October	28.5 ± 10.4	53.5 ± 16.2
15 October	45.2 ± 12.6	74.9 ± 18.2

Table IV. Daily instantaneous carrying capacity (LU/ha) for xeric and semimesic conditions, and for the total pastoral system (total LU/ha).

Period	Xeric	Semimesic	Total
01 April	2	3	5
15 April	5	6	11
01 May	18	38	56
15 May	41	46	87
01 June	57	72	129
15 June	68	85	153
01 July	38	72	110
15 July	26	62	88
01 August	17	40	57
15 August	**5**	**15**	**20**
01 September	**2**	**4**	**6**
15 September	**15**	**25**	**40**
01 October	24	45	69
15 October	38	63	101

Note: The late summer period is indicated in bold.

Table V. Number of analyzed species with relative number of avoidance/tolerance plant traits.

Number of species	Number of plant traits
3	8
11	7
19	6
24	5
25	4
21	3
7	2
4	1
0	0

Table VI. Traits with corresponding standardized canonical discriminant function coefficients (Function 1: values of the first discriminant function), and function at group centroids (Wilks' Lambda $p < 0.005$).

Traits	Function 1
Leaf distribution	9.054
Spines	8.515
Hairs	-15.220
Leaf texture	-20.319
Unpalatability	3.114
Chemicals	8.804
Prostrate form	5.533
Re-growth capacity	5.858

Clusters	Centroids
1	-13.872
2	13.872

fact that all the collected species show one or more avoidance/tolerance strategies. Moreover, the significant correlation between unpalatability, leaf texture, chemical defences and stolons also confirms the adaptation to historical grazing disturbance (Crofts & Grayson 1999).

The differential plant traits of the xeric grassland were hairs and leaf texture that could play a dual role; they can reduce evapotranspiration and at the same time render the leaves unpalatable to grazers, as proven by Pearson's correlation analysis.

In semimesic conditions, either avoidance mechanisms (rosette form, chemical substances, spines, prostrate form, and unpalatability) or tolerance strategies (re-growth capacity) occur. Rosette and prostrate growth forms are escape mechanisms allowing plants to avoid the bite of herbivores because their leaves are located close to the ground level (Kahmen & Poschlod 2008). Re-growth capacity is typical of productive environments, providing the ability to compete when the potential for resource uptake is high relative to loss of tissues (Maschinsky & Whitham 1989; Skarpe 2001). Pearson's correlation analysis showed significant correlations between re-growth strategy and storage organs (rhizomes); probably this occurs as a consequence of the not very high productivity of sub-Mediterranean grassland ecosystems, where the plants need stored resources for leaf re-growth after animals have grazed it. The importance of avoidance strategies in the semimesic environment is coherent with Sternberg et al. (2000), who proposed that under continuously heavy grazing, species draw advantage from rosette leaf distribution, chemical defences, and spine traits. As mentioned, the studied grassland system undergoes a summer overgrazing period. Hence, the interaction between summer drought stress and overgrazing may be considered as the driving force enhancing

pH can be viewed as the driving forces for ecosystem differentiation. Moreover, in accord with Milchunas and Lauenroth (1993), both plant communities are strongly affected by historical grazing, as seen by the

Table VII. Significant Pearson correlation values between analyzed traits ($^{**}p < 0.01$; $^*p < 0.05$).

Traits	Leaf texture	Unpalatability	Chemical defences	Prostrate form	Early flowering	Rhizome	Tubers
Leaf texture		0.839**	0.827**	0.767**			
Unpalatability	0.839**		0.839**	0.679*			
Chemical defences	0.827**	0.839**		0.692*			
Prostrate form	0.767**	0.679*	0.692*				
Tap root				0.939**			
Stolons		0.691*					
Re-growth capacity						0.706*	
Leaf distribution	0.703*						
Hairs			0.646*				
Bulbs					0.677*		
Clonal ability							0.653*

Note: Void cells correspond to outcomes that are not significant.

Table VIII. One-tailed (r) Pearson correlation coefficients for the considered species ($^{**}p < 0.01$; $^*p < 0.05$).

Species		Patch size (cm^2)
B. rupestre	Correlation coefficient (r)	0.480**
	N	69
A. sempervirens	Correlation coefficient (r)	−0.423**
	N	64
E. amethystinum	Correlation coefficient (r)	−0.278*
	N	45

Note: N, number of samples.

avoidance responses in the semimesic plant community as well. Thus, as stated by Briske (1996), stress and disturbance levels act in concert in the definition of the winning strategies within the plant community.

In the semimesic community, plants can deploy a broader range of strategies (as shown by the higher number of significant traits highlighted by DFA), while in xeric grasslands, they have fewer significant traits, and thus the opportunity to apply only a few strategies, indicating a more selective condition. These observations are in agreement with Grime (2001) and Navas and Violle (2009) about the possibility of developing more functional types (thus higher floristic richness) in more productive environments.

Furthermore, during the spring and early summer (when there is no water scarcity), semimesic grasslands are highly productive systems, featuring mainly species with a tolerance strategy (re-growth capacity). Instead, during the drought period and under heavy herbivore pressure (overgrazing), these strategies are not suitable, because water scarcity blocks tissue re-growth, and different strategies are necessary. Some species react by drying the above-ground phytomass temporarily (entry in a quiescent state) until the autumn rainfall. In sub-Mediterranean landscapes, this process of quiescence can be seen

as an avoidance strategy in addition to re-growth capability. Species with summer green leaves must have strong avoidance responses, such as a prostrate growth form, spines, or chemical defences. An example of winner species having dual advantage adaptations is *Teucrium chamaedrys*, with its late flowering strategy (a temporal niche allowing this small species to avoid the plant community flowering peak), and total unpalatability because of the presence of particular chemical substances, and hairs. Another such species is *A. sempervirens*, whose green leaves are protected by spines during the drought period. This model is coherent with the outcomes of other studies examining the relationship between vegetation changes and rainfall/grazing intensity (Biondini et al. 1998; Koukoura et al. 1998).

Evolutionary model

The relationship between stress and disturbance intensity affects the functional response of plant communities, but can also lead to changes in plant community structure, favouring the creation of patches. Indeed, transect analysis indicated patch formation in the semimesic grassland; these are characterized by spiny species, such as *A. sempervirens* and *E. amethystinum*, and by unpalatable species with tough and silica-rich leaves (*B. rupestre*). The smaller, ungrazed patches are dominated by spiny species (*A. sempervirens* and *E. amethystinum*), while *B. rupestre* dominates larger patches, as evidenced by Pearson's correlation coefficient (r) analysis.

Based on these observations, it is possible to formulate an evolutionary model that relates grazer management and seasonal stress patterns. In the first phase, spiny species (favoured by high intensity of stress and disturbance) create small cores that the sheep avoid; in fact, sheep can choose single leaves or shoots from the sward, biting them close to the ground level because of their narrow mouth, with lips

able to manipulate plants prior to biting them (Hofmann 1989). Moreover, grazers choose plants according to a wide range of factors, such as season, forage availability, and animal condition, breed and gender (Hulme et al. 1999; Sebastià et al. 2008). Young leaves of *B. rupestre* are eaten by sheep (Ellenberg 1988); thus, inside *A. sempervirens* cushions, small and young individuals can establish themselves and grow undisturbed, thereby becoming dominant and replacing the smaller spiny species to form bigger patches. The spread and fusion of two or more patches allow the affirmation of the *B. rupestre* community. This species has dominant features (*sensu* Grime 1973, 2001) such as large size, strong vegetative reproductive capacity (with marked lateral spreading), growth from basal meristems (Stebbins 1972), and high phytomass production. Moreover, the silica-rich leaves render this species poorly palatable to sheep (Grime et al. 1988), thus ensuring the formation of a large amount of litter, and a consequent decrease in floristic diversity (Bonanomi & Allegrezza 2004; Bonanomi et al. 2009).

This evolutionary model based on a facilitation process (Callaway & Pugnaire 2007) between *B. rupestre* and *A. sempervirens* offers an explanation for the *B. rupestre* encroachment process in sub-Mediterranean mountains that is very different from those described for central and northern European mesic pastures. In such mesophylous grasslands, it was demonstrated that the competitive ability of *Brachypodium pinnatum* (vicariant of *B. rupestre* in central and northern Europe) is enhanced when nitrogen levels increase (Bobbink et al. 1988; Willems et al. 1993) or when a reduction in grazing pressure occurs (Buckland et al. 2001). However, the model hypothesized in this work for the spread of *B. rupestre*, via facilitation mechanisms, does not exclude that undergrazing and nitrogen enrichment phenomena might also play an important role in sub-Mediterranean environments. Rather, this model, by explaining why the *B. rupestre* expansion process also occurs in pastoral systems that undergo optimal disturbance, can help in defining best practices for grazing management that optimize biodiversity conservation.

Conclusions

Our findings show that, for biodiversity conservation, the disturbance intensity in more stressed conditions (xeric) should be lessened by allowing fewer animals to graze, or by allowing them to do so for a shorter period of time. In semimesic conditions, temporary summer overgrazing should be forbidden because it may promote the formation of spiny patches and the spread of *B. rupestre*. In addition, an alternative management solution could be mechanical removal

(mowing) of *A. sempervirens* patches or late summer grazing by very low selective herbivores, such as donkeys or horses (Hofmann 1989; Crofts & Grayson 1999). In fact, Endresz et al. (2005) demonstrated that, for *B. pinnatum*, repeated occurrence of shoots lost in consecutive years could deplete the reserves of perennating organs, and ultimately lead to the plant's death.

The considerations described above seem to indicate that problems with *B. rupestre* expansion and management are not related to conditions of undergrazing only, but also to changes in livestock composition. In fact, traditionally (until the 1950s), the livestock grazing in these areas were sheep, goats, mules and/or horses, a situation that made it impossible for one or several poorly palatable species to predominate (Crofts & Grayson 1999). In addition, shepherds often removed spiny and toxic species, and sometimes performed controlled burning of the grassland. Nowadays, the full range of pastoral activities is no longer present (e.g. goats, mules, and horses are not present, burning and removal are not done anymore), provoking the sort of changes in grassland ecosystems described in this paper.

Finally, while the findings of this study agree with those in the literature, they highlight how, in sub-Mediterranean grasslands, winter cold stress alternated with summer drought stress cause a more complex trait response than that observed in temperate regions, and arid or sub-arid contexts.

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Appendix 1

Number of relevés	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Presence
Altitude (m a.s.l.)	1200	1220	1260	1210	1200	1250	1265	1300	1240	1210	1340	1320	1330	1320	1240	1270	1290	1310	1300	1280	
Exposure	SO	SO	OSO	S	SE	SO	S	SE	S	S	N	ONO	N	NNO	N	ONO	ONO	N	N	N	
Slope (°)	25	30	35	5	25	15	20	30	25	20	20	30	30	25	25	20	25	30	30	20	
Cover (%)	100	98	98	65	90	90	90	98	90	85	100	100	100	100	100	100	100	100	100	100	
Surface (m²)	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	
Species																					
Bromus erectus Huds. subsp. *erectus*	2	2	2	2	2	2	2	2	2	2	4	4	4	4	4	4	4	4	4	4	20
Helianthemum nummularium (L.) Mill. subsp. *obscurum* (Celak.) Holub	2	2	1	2	2	2	2	1	2	2	+	+	+	+	+	+	+	+	+	+	20
Avenula praetutiana (Parl. ex Arcang.) Pignatti	2	2	2	+	3	+	3	2	2	2	1	2	+	+	1	+	1	1	2	+	20
Helianthemum oelandicum (L.) DC. *incanum* (Willk.) G. López	1	1	3	2	1	1	1	3	2	1	+	+	1	2	+	+	+	1	2	+	20
Hieracium pilosella L.	1	1	1	2	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	20
Eryngium amethystinum L.	1	1	1	+	1	1	+	1	1	1	+	+	1	+	+	1	+	+	+	+	20
Sanguisorba minor Scop. subsp. *balearica* (Bourg. ex Nyman) Muñoz Garm. & C. Navarro	1	1	1	+	+	1	+	+	1	1	1	1	+	+	+	+	+	+	1	1	20
Plantago media L. subsp. *media*	1	+	+	+	1	1	1	+	+	+	+	+	+	+	+	+	+	+	+	+	20
Thymus praecox Opiz subsp. *polytrichus* (Borbás) Jalas	+	2	2	3	3	+	2	2	3	3	+	2	1	2	2	2	2	1	2	2	20
Koeleria lobata (M. Bieb.) Roem. & Schult.	+	1	+	1	1	1	+	1	+	1	1	1	1	1	1	1	1	1	1	1	20
Trinia glauca (L.) Dumort. subsp. *carniolica* (A. Kern. ex Janch.) H. Wolff	+	+	+	+	+	+	+	+	+	+	1	1	1	1	1	1	1	1	1	1	20
Valeriana tuberosa L.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	20
Anthyllis vulneraria L. subsp. *weldeniana* (Rchb.) Cullen	1	1	.	2	2	2	1	1	.	2	+	+	+	2	+	+	+	1	+	2	18
Thymus longicaulis C. Presl subsp. *longicaulis*	2	2	.	1	1	2	.	1	1	2	1	1	1	1	1	1	1	1	1	1	18
Knautia purpurea (Vill.) Borbás	1	1	+	1	1	1	1	1	+	.	1	.	+	1	1	1	1	.	1	1	18
Coronilla minima L. subsp. *minima*	.	1	2	2	2	2	.	1	2	2	1	1	1	2	1	1	1	.	1	2	18
Brachypodium rupestre (Host) Roem. & Schult.	2	3	2	.	1	.	1	2	3	2	+	.	1	1	+	1	+	+	.	1	16
Trifolium montanum L. subsp. *rupestre* (Ten.) Nyman	2	2	2	.	.	2	2	2	.	.	2	2	1	2	2	2	2	1	2	2	16
Cerastium arvense L. subsp. *suffruticosum* (L.) Ces.	1	1	1	1	+	1	1	1	1	+	1	.	+	1	.	1	.	+	1	.	16
Cyanus triumfetti (All.) Dostál ex Á. & D. Löve	+	1	1	+	+	+	+	+	1	1	+	+	+	.	+	+	+	+	+	.	16
Armeria canescens (Host) Ebel	+	+	+	.	+	+	+	+	+	.	1	.	+	+	1	1	1	.	+	+	16
Leontodon cichoraceus (Ten.) Sanguin.	1	.	+	.	+	.	+	1	.	+	3	2	1	+	1	+	1	3	2	1	16

(continued)

Appendix 1 (*Continued*).

Species																			
Helianthemum apenninum (L.) Mill. subsp. apenninum	16
Globularia meridionalis (Podp.) O. Schwarz	14
Astragalus sempervirens Lam.	14
Saxifraga bulbifera L.	14
Sedum sexangulare L.	14
Polygala nicaeensis Koch subsp. mediterranea Chodat	14
Hippocrepis comosa L. subsp. comosa	14
Luzula multiflora (Ehrh.) Lej.	12
Galium corrudifolium Vill.	12
Myosotis alpestris F.W. Schmidt	12
Medicago lupulina L.	12
Plantago argentea Chaix s.l.	12
Coeloglossum viride (L.) Hartm.	12
Anthyllis vulneraria L. subsp. polyphylla (DC.) Nyman	10
Carex caryophyllea Latourr.	10
Trifolium campestre Schreb.	10
Potentilla incana P. Gaertn., B. Mey & Scherb	10
Muscari neglectum Guss. ex Ten.	10
Plantago lanceolata L.	10
Poa alpina L. subsp. alpina	10
Gymnadenia conopsea (L.) R. Br.	10
Senecio provincialis (L.) Druce	10
Phleum hirsutum Honck. subsp. ambiguum (Ten.) Tzvelev	10
Festuca stricta Host subsp. trachyphylla (Hack.) Patzke ex Pils	10
Anthoxanthum odoratum L. subsp. odoratum	10
Luzula campestris (L.) DC.	10
Rhinanthus minor L.	10
Briza media L.	10
Filipendula vulgaris Moench	10
Onobrychis viciifolia Scop.	10
Potentilla rigoana Th. Wolf	10
Trifolium ochroleucum Huds.	10
Lotus corniculatus L. subsp. corniculatus	10
Primula veris L. subsp. suaveolens (Bertol.) Gutermann & Ehrend.	10
Cynosurus cristatus L.	10

Appendix 1 (*Continued*).

Species																	
Bunium bulbocastanum L.	10
Hieracium cymosum L.	10
Ranunculus neapolitanus Ten.	8
Arenaria serpyllifolia L. subsp. *serpyllifolia*	8
Viola eugeniae Parl. subsp. *eugeniae*	8
Arabis hirsuta (L.) Scop.	8
Leontodon crispus Vill. subsp. *crispus*	8
Galium verum L. subsp. *verum*	6
Teucrium chamaedrys L. subsp. *chamaedrys*	6
Veronica orsiniana Ten. subsp. *orsiniana*	6
Dactylorhiza sambucina (L.) Soó	6
Centaurea ambigua Guss. s.l.	6
Carex macrolepis DC.	6
Gentiana verna L. subsp. *verna*	6
Minuartia verna (L.) Hiem subsp. *collina* (Neilr.) Domin	6
Allium sphaerocephalon L.	6
Crocus vernus (L.) Hill subsp. *vernus*	6
Linum catharticum L. s.l.	6
Campanula glomerata L.	6
Senecio scopolii Hoppe & Hornsch. ex Bluff & Fingerh.	6
Trifolium pratense L. subsp. *pratense*	6
Ranunculus breyninus Crantz	6
Festuca circummediterranea Patzke	4
Crepis lacera Ten.	4
Aira caryophyllea L. subsp. *caryophyllea*	4
Bellis perennis L.	4
Cirsium lobelii Ten.	4
Ranunculus millefoliatus Vahl	4
Colchicum lusitanum Brot.	4
Linum trigynum L.	4
Teucrium montanum L.	4
Orchis pauciflora Ten.	4
Achillea millefolium L. subsp. *millefolium*	4
Dianthus monspessulanus L.	4
Asperula cynanchica L.	4
Centaurea jacea s.l.	4
Dianthus sylvestris Wulfen subsp. *sylvestris*	4
Campanula micrantha Bertol.	4
Carduus carlinifolius Lam. subsp. *carlinifolius*	4
Veronica chamaedrys L.	2

(*continued*)

Appendix 1 (*Continued*).

Species														
Bromus hordeaceus L. s.l.	+	.	.	.	.	.	.	.	.	.	.	.	.	2
Salvia pratensis L. subsp. pratensis	+	.	.	.	.	+	.	.	.	.	.	.	.	2
Hypericum perforatum L.	.	+	.	+	.	+	.	.	.	.	.	.	.	2
Erysimum pseudorhaeticum Polatschek	.	+	+	.	.	.	.	.	.	.	.	.	.	2
Tragopogon pratensis L. subsp. pratensis	.	+	.	+	.	.	.	+	.	.	.	.	.	2
Orchis ustulata L.	.	.	.	.	+	.	.	.	+	.	+	.	.	2
Cruciata glabra (L.) Ehrend. s.l.	.	.	.	.	+	.	.	.	.	.	+	.	.	2
Vicia sativa L. subsp. sativa	.	.	.	.	+	.	.	.	.	.	+	.	.	2
Rumex acetosella L. subsp. angiocarpus (Murb.) Murb.	.	.	.	.	+	.	.	.	.	.	.	+	.	2
Orchis mascula (L.) L. subsp. mascula	.	.	.	.	.	.	+	.	+	.	.	.	.	2
Bupleurum baldense Turra	.	.	+	.	.	.	.	.	+	.	.	.	.	2
Allium vineale L.	.	.	+	.	.	.	.	.	.	.	+	.	+	2
Bupleurum falcatum L. subsp. cernuum (Ten.) Arcang.	.	.	1	.	.	.	.	.	.	.	1	.	.	2
Leucanthemum adustum (W.D.J. Koch) Gremli	.	.	.	.	.	.	+	.	+	.	.	.	.	2
Trifolium alpestre L.	.	.	+	.	.	.	+	.	.	.	+	.	.	2
Trifolium repens L. subsp. repens	.	.	+	.	.	.	.	.	.	.	.	+	.	2

Appendix 2

| Ungrazed patch | cover values (%) | | | Patch surface (cm^2) |
	Astragalus sempervirens	*Eryngium amethystinum*	*Brachypodium rupestre*	
1	90	0	0	300
2	40	10	20	1000
3	40	10	20	750
4	20	10	60	2900
5	10	5	30	5100
6	40	0	10	350
7	70	0	0	100
8	60	10	10	150
9	80	0	0	100
10	60	0	10	100
11	30	0	50	100
12	30	20	20	350
13	10	20	70	750
14	40	20	20	1400
15	50	0	20	300
16	50	0	40	2850
17	20	10	60	1350
18	70	0	10	300
19	30	10	50	1300
20	80	0	10	100
21	40	5	40	1300
22	30	0	40	1300
23	10	5	50	2000
24	20	15	40	700
25	5	0	70	2000
26	0	5	80	1200
27	80	0	0	100
28	0	1	80	10000
29	0	0	90	100
30	0	1	80	10000
31	0	1	70	10000
32	0	0	60	1200
33	0	0	80	10000
34	5	1	60	2800
35	5	1	5	2800
36	40	0	30	1950
37	0	0	0	1200
38	40	0	20	1900
39	0	80	0	300
40	40	5	20	700
41	40	0	5	1900
42	20	20	40	1850
43	10	0	60	2800
44	0	0	70	50
45	50	5	30	2750
46	40	0	10	1200
47	20	0	0	700
48	30	5	10	1150
49	15	5	10	1150
50	50	0	10	3900
51	70	0	0	300
52	10	0	40	1150
53	50	10	20	700
54	0	1	30	1150
55	10	10	50	500
56	0	0	0	100
57	40	1	60	950
58	30	10	40	1100
59	50	0	30	200
60	40	0	10	350

(*continued*)

Appendix 2 (*Continued*).

| Ungrazed patch | cover values (%) | | | Patch surface (cm^2) |
	Astragalus sempervirens	*Eryngium amethystinum*	*Brachypodium rupestre*	
61	5	5	50	1600
62	20	1	60	5000
63	60	0	30	350
64	40	1	50	300
65	0	1	30	700
66	0	10	20	300
67	10	0	10	1100
68	5	0	30	900
69	30	1	50	7900
70	40	10	20	700
71	50	10	5	700
72	70	1	5	900
73	60	1	5	500
74	70	5	1	700
75	70	5	10	700
76	60	5	5	700
77	60	5	10	700
78	60	20	5	350