A soil population of *Glomeris marginata* (Villers, 1789) in a Mediterranean forest (Diplopoda, Chilognatha: Glomerida)

Antoni Serra, Eduardo Mateos & Carme Miquel

UNIVERSITAT DE BARCELONA

Departament de Biologia Animal, Facultat de Biologia
Avda. Diagonal, 645. E-08028 Barcelona, Spain.

INTRODUCTION

Glomeris marginata (Villers, 1789) is widely distributed across Europe. It is one of the most abundant saprophagous macroarthropods of the organic horizons of the soil, especially in Mediterranean sclerophyllous forests (Bertrand *et al.* 1987, David 1988, Bertrand & Lumaret 1992, David 1995, David *et al.* 1999). It has also been found abundantly in mesoxeric grasslands of Eastern Germany (Voigtländer & Duker 2001). Several studies show that it is a key species in the processes of decomposition of organic matter due to its high rate of litter consumption (Bocock 1963, Bertrand *et al.* 1987, David & Gillon 2002) and its relationship with microorganisms (Coûteaux *et al.* 2002) and earthworms (Bonkowski *et al.* 1998). The quantification of the effect of the activity of *G. marginata* on edaphic processes requires data on density and population biomass as well as on population composition, since different developmental stadia and also the two sexes may show different rates of consumption and assimilation of organic matter (David & Gillon 2002). In this study we present the temporal and spatial distribution of a population of *G. marginata* found in a Mediterranean forest soil. The large number of epimorphic individuals and the large amount of individuals in each larval stadium has allowed us to determine the population composition throughout the sampling period. A correlation algorithm has been determined to estimate an individual's biomass from a morphometric parameter (width of the second tergite). This algorithm has yielded the biomass of an average individual of the population as well as the biomass of an average individual of each developmental stadium.

METHODS

Location

Parc Natural de Sant Llorenç del Munt i Serra de l'Obac, 35 km north-west from Barcelona (Spain) (UTM coordinates 31TDG1411). Altitude: 870 m above sea level.

Forest characteristics

Sclerophyllous forest consisting mainly of *Quercus ilex* L. and *Pinus halepensis* Mill; the most common bush species was *Arbutus unedo* L. Litter was of the leptomoder type, with a mean pH of 5.88 (measured in 1:2.5 water).

Sampling

Samples were obtained in the field during 24 consecutive months from June 1991 to May 1993. In an experimental plot (40 x 40 m), three soil horizons were sampled: L/F, H, and A (leaf litter fall, humus and the first five cm of the mineral layer respectively). A cylindrical corer, 0.36 m in diameter (equivalent to 0.102 m^2), was used as the sampling device. Each monthly sample included five sampling units randomly taken. The faunal components were obtained with Berlese-Tullgren devices.

Numerical methods

Data obtained during these 24 months were grouped in two periods, the first one (first year) corresponding to the first 12 months (June 1991 to May 1992) and the second one (second year) to the last 12 (June 1992 to May 1993). Mean population density (ind·m^{-2}) and biomass (mg·m^{-2}) values were calculated in each soil horizon for each month (n=5), for each weather season (n=15), for each one of the two years (n=12) and for the whole sampling period (n=24).

The differences in density and biomass values between samples were compared by means of parametric Anova, *t*-test, nonparametric Kruskal Wallis (KW) and Mann-Whitney U-test methods. *A posteriori* comparisons were carried out using Student-Newman-Keuls (SNK). Spearman's correlation coefficient was used to relate abiotic parameters (mean monthly air temperature, monthly accumulated rainfall and soil water content in H and A horizons) to population density parameters.

Usher index (Usher, 1970) was used to estimate the vertical distribution of the *G. marginata* population through the soil profile. Arbitrary depth values were designated for each horizon, being 3 for L/F, 2 for H and 1 for A. For each monthly value of this index, a confidence interval of 95% was calculated using bootstrap technique (resampling with replacement, 10^4 iterations with sample size of 5 in each point).

The Morisita dispersion index (Morisita 1962, cited in Elliott 1977) was used to estimate the horizontal distribution of the population.

Climatology (Figure 1, Table 1)

The climate of this region is typically Mediterranean. Figure 1 depicts the total rainfall and mean monthly temperatures recorded during the sampling period. Climatology varied between the first and second years. The second year showed a lower mean temperature, a more abundant rainfall and higher water content in the soil (Table 1) than the first one. It had an exceptionally rainy summer and a very dry winter, while the first year showed a typically Mediterranean climate, including a period of hydric stress in the summer.

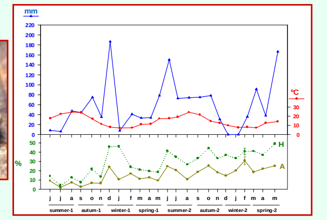

Figure 1. Above: Accumulated monthly rainfall (mm) and mean temperatures (ºC) recorded during the sampling period (data obtained from the climatology station of Terrassa (Barcelona, Spain). Below: Hydric content (%) in horizons H and A calculated as water percentage in weight.

	Temperature (ºC)	Accumulated rainfall (mm)	Water content horizon H % ± s.e.	Water content horizon A % ± s.e.
1st year	14.99 ± 1.87	596.70	20.68 ± 3.82	9.96 ± 1.76
2nd year	14.18 ± 1.63	812.10	37.65 ± 1.72	20.83 ± 1.54
Mean	14.58	704.40	29.16	15.39

Table 1. Mean temperature (ºC), accumulated rainfall (mm) and mean water content (%), for the first year, for the second year and for the 24 months period (Mean). s.e.=standard error.

		EPIMORPHIC males ind·m^{-2} ± s.e	EPIMORPHIC females ind·m^{-2} ± s.e	ANAMORPHIC stadium II ind·m^{-2} ± s.e	ANAMORPHIC stadium III ind·m^{-2} ± s.e	ANAMORPHIC stadium IV ind·m^{-2} ± s.e	ANAMORPHIC stadium V ind·m^{-2} ± s.e	TOTAL ind·m^{-2} ± s.e
L/F	1st	1.19 ± 0.5	1.39 ± 0.62	0.16 ± 0.2	0.00	0.23 ± 0.2	0.17 ± 0.2	3.14 ± 1.2
	2nd	2.0 ± 0.8	1.18 ± 0.45	0.12 ± 0.1	0.40 ± 0.3	0.62 ± 0.3	0.36 ± 0.3	4.68 ± 1.2
	Mean	1.59 ± 0.5	1.29 ± 0.38	0.14 ± 0.1	0.20 ± 0.2	0.43 ± 0.2	0.26 ± 0.2	3.91 ± 0.8
H	1st	11.09 ± 1.7	7.59 ± 2.30	1.69 ± 1.1	1.84 ± 0.9	4.66 ± 1.5	1.25 ± 1.0	28.1 ± 4.8
	2nd	7.59 ± 1.9	7.05 ± 1.84	2.86 ± 2.2	4.32 ± 1.5	1.81 ± 0.9	1.54 ± 0.7	25.17 ± 6.3
	Mean	9.34 ± 1.3	7.32 ± 1.44	2.3 ± 1.2	3.08 ± 0.9	3.24 ± 0.9	1.40 ± 0.6	26.65 ± 3.9
A	1st	3.59 ± 0.9	2.44 ± 0.86	0.89 ± 0.5	0.70 ± 0.33	1.02 ± 0.4	0.35 ± 0.3	8.99 ± 2.1
	2nd	2.78 ± 1.2	1.37 ± 0.57	2.95 ± 2.3	2.23 ± 1.74	0.62 ± 0.3	0.63 ± 0.4	10.58 ± 4.2
	Mean	3.18 ± 0.7	1.91 ± 0.52	1.92 ± 1.2	1.47 ± 0.9	0.82 ± 0.3	0.49 ± 0.2	9.79 ± 2.3
T	1st	15.88 ± 2.1	11.43 ± 2.4	2.74 ± 2.3	2.54 ± 1.1	5.91 ± 1.9	1.77 ± 1.0	40.27 ± 6.1
	2nd	12.36 ± 2.6	9.6 ± 2.2	5.93 ± 4.5	6.95 ± 2.9	3.05 ± 1.3	2.53 ± 0.9	40.42 ± 10.2
	Mean	14.12 ± 1.7	10.5 ± 1.6	4.34 ± 2.3	4.75 ± 1.6	4.48 ± 1.2	2.15 ± 0.7	40.34 ± 5.8
%		*35.00*	*26.05*	*10.76*	*11.77*	*11.11*	*5.33*	*100*

Table 2. Mean monthly density value (ind·m^{-2}) and standard error (s.e.) of *Glomeris marginata* for males and females, anamorphic stadia and total population in the first year (1st, n=12 month), in the second year (2nd, n=12 month) and in the whole sampling period (Mean, n=24 month) for each one of the sampled soil horizons (L/F, H, A) and for the whole of the soil profile (T).

		EPIMORPHIC males mg·m^{-2} ± s.e	EPIMORPHIC females mg·m^{-2} ± s.e	ANAMORPHIC stadium II mg·m^{-2} ± s.e	ANAMORPHIC stadium III mg·m^{-2} ± s.e	ANAMORPHIC stadium IV mg·m^{-2} ± s.e	ANAMORPHIC stadium V mg·m^{-2} ± s.e	TOTAL mg·m^{-2} ± s.e
L/F	1st	51.2 ± 20.9	152.2 ± 80.4	0.1 ± 0.1	0.00	1.3 ± 1.3	1.6 ± 1.6	206.4 ± 92.2
	2nd	168.2 ± 72.7	146.9 ± 53.7	0.1 ± 0.1	0.8 ± 0.6	3.5 ± 1.9	2.9 ± 2.0	322.4 ± 91.6
	Mean	109.7 ± 38.9	149.5 ± 47.3	0.1 ± 0.1	0.4 ± 0.3	2.4 ± 1.2	2.2 ± 1.2	264.4 ± 64.7
H	1st	661.1± 91.0	645.6 ± 198.4	1.1 ± 0.6	3.3 ± 1.7	20.2 ± 6.3	16.7 ± 13.4	1348.5 ± 262.8
	2nd	493.6 ± 105.9	722.8 ± 164.4	2.5 ± 2.0	9.9 ± 3.4	12.2 ± 6.9	10.7 ± 4.1	1251.9 ± 270.1
	Mean	577.6 ± 70.5	684.2 ± 126.3	1.8 ± 1.0	6.6 ± 2.0	16.2 ± 4.6	13.7 ± 6.9	1300.2 ± 184.6
A	1st	208.6 ± 52.3	179.8 ± 75.1	0.6 ± 0.4	3.7 ± 2.7	3.8 ± 1.4	3.6 ± 2.7	400.1 ± 124.0
	2nd	194.9 ± 94.1	144.7 ± 64.5	2.4 ± 1.9	5.3 ± 4.3	3.0 ± 1.6	8.6 ± 4.7	358.9 ± 4.2
	Mean	201.7 ± 52.6	162.3 ± 48.6	1.5 ± 1.0	4.5 ± 2.5	3.4 ± 1.0	6.1 ± 2.7	379.5 ± 92.0
T	1st	921.4 ± 120.1	977.7 ± 258.3	1.8 ± 0.9	7.0 ± 3.0	25.3 ± 8.1	21.9 ± 13.5	1955.1± 344.4
	2nd	856.8 ± 147.3	1014.4 ± 201.4	5.1 ± 0.9	16.0 ± 7.0	18.7 ± 8.3	22.2 ± 7.6	1933.2 ± 341.4
	Mean	889.1± 93.2	996.0 ± 160.2	3.4 ± 2.0	11.5 ± 3.9	22.0 ± 5.7	22.1 ± 7.6	1944.1 ± 237.1
%		*45.73*	*51.23*	*0.17*	*0.59*	*1.13*	*1.14*	*100*

Table 3. Mean monthly biomass value (mg·m^{-2}) and standard error (s.e.) of *Glomeris marginata* for epimorphic stadia (males and females), anamorphic stadia (stadium II to stadium V) and total population in the first year (1st, n=12 month), in the second year (2nd, n=12 month) and for the whole sampling period (Mean, n=24 month) for each one of the sampled horizons (L/F, H, A) and for the whole of the soil profile (T).

RESULTS AND DISCUSSION

Biomass estimates (Figure 2)

Fresh weight was obtained for 105 alive specimens of *G. marginata* of different ages and sizes after having kept them fasting for 48 hours. Width of body segments 1, 2 and 5 was measured for each one of those 105 specimens and regression algorithms of these widths against fresh weight were calculated. The algorithm corresponding to the width of segment 2 (T2) showed the highest regression coefficient. Algorithms based on the widths of segments 1 and 5 were discarded.

Figure 2 shows the regression function between fresh weight of the individual and width of its second body segment. This function is $B = 0.456\cdot (T2)^{3.189015}$ (n=105, R^2= 0.943, F=1719.4, p< 0.000), where B is the biomass value (fresh weight) in mg and T2 is the width of the second segment in mm. All specimens collected during the study period were measured and their biomasses were inferred through that algorithm.

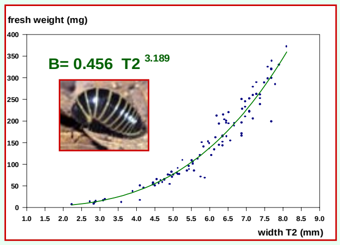

Figure 2. Regression function between individual fresh weight in grams and the width in millimetres of the second tergite (T2) of *Glomeris marginata*.

Population composition (Tables 2 and 3)

Monthly mean density and biomass of the total population was 40.34 ind.m^{-2} (Table 2) and 1944.1 mg·m^{-2} (Table 3) respectively. Epimorphic stadia represent 61% of the density and 97% of the biomass, with mean monthly values of 24.6 ind·m^{-2} and 1885 mg·m^{-2}. Anamorphic stadia showed mean monthly values of 15.7 ind·m^{-2} and 59 mg·m^{-2}.

The sex ratio did not vary between the two years of sampling, achieving values of 1.37 and 1.29 respectively. Although it was a ratio above 1, the male population (14.1 ind·m^{-2}) did not show a density value significatively higher than that of the female population (10.5 ind·m^{-2}) along the two study years. These sex ratio values were not very different from those found by Heath *et al.* (1974) in *G. marginata* populations captured with pit-fall traps (sex ratio 1.25). This steadiness in the sex ratio value seems to be differentiating *G. marginata* from other species, such as *G. balcanica* where sex ratio values have been measured between 0.43 and 1.83 (Iatrou & Stamou 1991).

According to David & Gillon (2002), the higher the biomass of an individual is, the higher its rates of consumption and assimilation of organic matter are. These authors found that rates achieved by females were significantly higher that those achieved by males in experiments of consumption of *Quercus ilex* leaves. Similarly, different consumption and assimilation rates between individuals belonging to different developmental stadia could be expected. Because of that, models quantifying the degree of contribution of *G. marginata* to the processes of decomposition of edaphic organic matter must take into account the population composition in terms of developmental stadia or biomass ranks.

Distribution in time (Figures 3 and 4)

For each one of the soil horizons, no significant differences were found in density (Figure 3) and biomass (Figure 4) values between months, seasons or years. Moreover, Spearman's rank correlation analyses between monthly mean density values in different horizons and abiotic parameters (temperature, rainfall, water content in the soil) showed that no significant differences occurred between mean density values of the *G. marginata* population and any of these factors. This steadiness of population density and biomass values indicates that *Glomeris marginata* is a species that shows a high degree of independence from local climatic conditions.

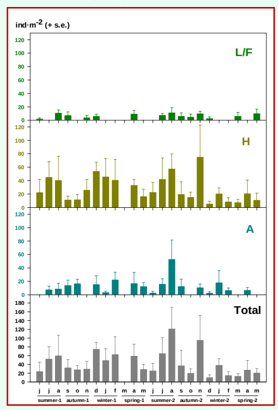

Figure 3. Mean monthly density values (and associated standard errors) showed by the whole of the *Glomeris marginata* population in each one of the soil horizons (L/F, H, A) and in the whole of the soil profile (Total).

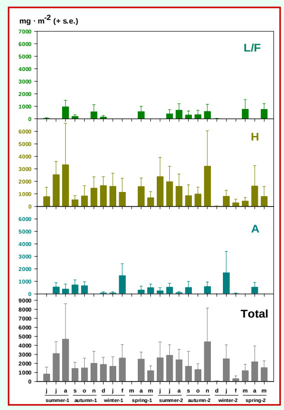

Figure 4. Mean monthly biomass values (and associated standard errors) showed by the whole of the *Glomeris marginata* population in each one of the soil horizons (L/F, H, A) and in the whole of the soil profile (Total).

Distribution in space (Figure 5)

Significant differences between monthly mean densities (n=24, KW p=0.000, SNK p<0.05) and biomasses (n=24, KW p=0.000, SNK p<0.05) were found between the different soil levels. Mean values in level H (26.65 ind·m^{-2} and 1300.2 mg·m^{-2}) were significantly higher than those in A (9.79 ind·m^{-2} y 379.5 mg·m^{-2}) and L/F (3.91 ind·m^{-2} y 264.4 mg·m^{-2}). Mean values in A were significantly higher than those in L/F.

In most months, *G. marginata* occured across the whole of the soil profile, as shown by the 95% confidence intervals of the Usher index in Figure 5. During some months, basiccally the winter period of both years, the species tended to move towards the deepest horizon. Nevertheless, these fluctuations shown by the Usher index were not significant and they were not correlated with environmental parameters. Unlike other authors (Bocock & Heath 1967), we can not talk about vertical migrations along the soil profile during the annual cycle: the population was located preferably in horizon H, as some other studies pointed out before (Schubart 1934, Blower 1955).

Concerning horizontal distribution, Morisita index monthly values for each one of the horizons were always higher than one, which indicated that the species was distributed in patches. This kind of horizontal distribution is found in most edaphic arthropods, since it seems to favour their search for nourishment and protection or their reproductive activity (Blower 1969, Banerjee 1967).

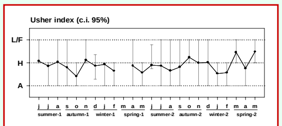

Figure 5. Vertical distribution of *Glomeris marginata* density calculated from the Usher index. Confidence intervals (95%) estimated using bootstrap technique.

Recruitment (Figures 6 and 7)

Considering that stadium I of postembrionary development in *G. marginata* is found inside the egg, the time of recruitment corresponds to the apparition of individuals in stadium II. In the studied population, individuals in stadium II appeared all through the sampling period (Figure 6). Similarly, the whole set of anamorphic stadia occured continuously during the two years of study (Figure 7).

According to Heath *et al.* (1974), although egg-laying in *G. marginata* mostly happens in April, May and June, females can lay eggs all through the year. Our results, with the appearance of individuals in stadium II along all seasons of the annual cycle, confirmed this capability.

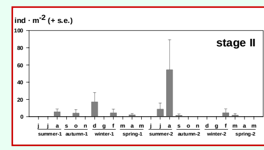

Figure 6. Mean monthly density values of *Glomeris marginata* specimens in anamorphic stadium II in the whole of the soil profile.

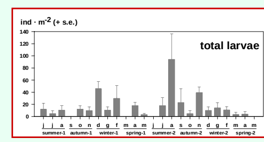

Figure 7. Mean monthly density values of all *Glomeris marginata* specimens in anamorphic stadia in the whole of the soil profile.

Biomass of different developmental stadia (Table 4, Figures 8 and 9)

The value of individual mean biomass was obtained for each anamorphic and epimorphic stadium (Table 4). This value, estimated from the regression algorithm, can be considered as the standard individual biomass of each stadium and it allows a biomass to be assigned to an individual once its developmental stadium is known. The values of individual mean biomass of the whole anamorphic stadia (3.92 mg), of the epimorphic stadia (74.12 mg) and that of a type individual of the *G. marginata* population (47.87 mg) were determined.

Although differences were not statistically significant, the value of individual mean biomass of males (62.1 mg) was considerably lower than that of the females (90.3 mg). Because of that, even though the value of male population density was higher than that of the female population, the value of male population biomass (889.1 mg·m^{-2}) was lower than that of the females (996 mg·m^{-2}). Nevertheless, those differences were not statistically significant either.

Epimorphic stadia (males and females) showed a wide range of individual biomass values: between 10 and 190 mg in males (Figure 8) and between 10 and 230 mg in females (Figure 9). Frequency distribution was biased towards lower biomass values, which showed that most males and females of the studied population were relatively small.

From data obtained by Heath *et al.* (1974) with specimens from a mixed deciduous woodland in north-west England, male (56.1 mg) and female (172.3 mg) individual biomass values were estimated. The male value is similar to the one we calculated in our study population (62.1 mg), while that of the females is considerably higher than the one we obtained (90.3 mg). It must be taken into account, though, that those specimens came from a very different habitat and that they were collected in spring only.

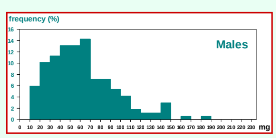

Figure 8. Frequency distribution of the male population of *Glomeris marginata* according to individual fresh weight ranges in milligrams.

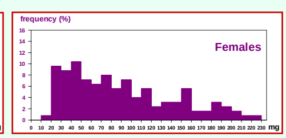

Figure 9. Frequency distribution of the female population of *Glomeris marginata* according to individual fresh weight ranges in milligrams.

	Stadium	number of tergites	number of pairs of legs	n	mg ± se	rank (mg)
ANAMORPHIC	I	8	3		---	---
	II	8	8	42	0.77 ± 0.03	0.50 - 1.08
	III	9	10	52	2.13 ± 0.07	1.27 - 3.24
	IV	10	13	55	4.72 ± 0.18	1.81 - 8.05
	V	11	15	26	10.89 ± 0.86	5.64 - 26.86
	MEAN ANAMORPHIC STADIA BIOMASS			175	3.92 ± 0.28	0.50 - 26.86
EPIMORPHIC	VI- XVI (♂) (♂)	12 12	19 17	168 125	62.1± 2.5 90.3 ± 4.7	10.3 - 185.5 19.2 - 225.9
	MEAN EPIMORPHIC STADIA BIOMASS			293	74.12 ± 2.62	10.3 - 225.9
MEAN INDIVIDUAL BIOMASS				468	47.87 ± 2.27	0.50 - 225.9

Table 4. Mean individual biomass (mg±s.e.) of *Glomeris marginata* for each developmental stadium calculated using the regression algorithm $B= 0.456\cdot (T2)^{3.189015}$. n=number of individuals in each stadium. Rank=minimum and maximum biomass values.

Comparison against other localities (Table 5)

Table 5 shows different density and biomass data obtained by different authors in Mediterranean (Bertrand *et al.* 1987, Bertrand & Lumaret 1992, David 1995, David *et al.* 1999) and Atlantic (David 1988) ecosystems. Comparisons between different values in this table must be made with a certain caution due to the different sampling methods used, the different types of soil and edaphic horizons considered. Nevertheless, mean monthly density and biomass values obtained in our study (40.34 ind.m^{-2} and 1944.1 mg·m^{-2}) were relatively low when compared to other forests in the Mediterranean region.

In general, in Mediterranean forest soils, *G. marginata* shows higher values of population density and biomass (from 20 to 212 ind·m^{-2} and from 222.5 to 10800 mg·m^{-2}) than it does in temperate climate forests (from 0.66 to 51.84 ind·m^{-2} and from 1.12 to 676.2 mg·m^{-2}). These values highlight the capability of this species to face the strong changes that characterise Mediterranean climatology, allowing it to increase population densities and biomasses even in extreme situations (Haacker 1968, Stamou *et al.* 1984, Read & Martin, 1990, Iatrou & Stamou 1991, Dunger & Steinmetzger 1981). This capability would explain the absence of significant correlations between density values of our population and temperature, rainfall and soil humidity, which results into the fact that changes in those parameters do not provoke relevant fluctuations in population density values. It is interesting pointing out that Sustr (1996), studying different *Glomeris* species (*G. marginata*, *G. balcanica*, *G. hexasticha*) found that *G. marginata* is the best adapted one to the type of climate where it lives.

Table 5 shows also that, even though population biomass values are lower in temperate climates than they are in Mediterranean ones, individual mean biomass values tend to be higher in temperate climates. Nevertheless, we must consider that different studied populations may have a different population composition, which would affect individual biomass values.

PLACE	FOREST		ind·m^{-2}	mg·m^{-2}	REF.
Massif d'Ingrannes Orléans, FRANCE	(*Quercus petraea* + *Q.robur*) (79%); *Fagus sylvatica* (19%)	TEMPERATE CLIMATE	51.84 16.05	676.2 276.8	1
"	(*Quercus petraea* + *Q.robur*) (72%); *Pinus sylvatica* (21%)		10.4	585	
"	*Pinus sylvestris* (99%)		4.32	132	
"	*Pinus sylvestris* (98%)		3.78 ---	195.5	
"	(*Quercus petraea* + *Q.robur*) (96%);		3.74 1.05	280 2.68	
"	(*Quercus petraea* + *Q.robur*) (89%); *Carpinus betulus*		2.6	142.2	
"	(*Quercus petraea* + *Q.robur*) (44%); *Pinus sylvatica* (38%)		1.9 1.6	411.6 166.8	
"	*Pinus sylvestris* (86%); *Betula* (12%)		1.8	136.8	
"	(*Quercus petraea* + *Q.robur*) (32%); *Fagus sylvatica* (36%); *Pinus sylvatica* (30%)		1.76	115.5	
"	*Pinus sylvestris* (93%)		0.66	1.12	
Puechabon Montpellier, FRANCE	Evergreen oak forest *Quercus ilex*	MEDITERRANEAN CLIMATE	212	7800	2
Saint Gély du Fesc Montpellier, FRANCE	*Quercus coccifera*		124.1	3150	3
Puéchabon Montpellier, FRANCE	*Quercus ilex*		70.2	4000	3
Chêne vert de Puéchabon	*Quercus ilex* + *Q.pubescens*		50-100	7200-10800	4
Sant Llorenç del Munt Barcelona, SPAIN	*Quercus ilex*, *Arbutus unedo*, *Pinus halepensis*		40.34	1944.1	PRESENT ESTUDY
Mas de Cazarils Montpellier, FRANCE	Wooded sites *Quercus ilex* + *Q.pubescens*		≈ 33	---	5
"	Mixed semi-open sites herbs and dwarf shrubs		≈ 22	---	5
"	Semi-open sites shrubs and youg oaks		≈ 21	---	5
Saint Gély du Fesc Montpellier, FRANCE	*Quercus ilex* litterfrazing		20	222.5	3

Table 5. Population density (ind·m^{-2}) and biomass (mg·m^{-2}) values obtained by different authors in different forests of temperate and Mediterranean climates. Values ≈ # have been extrapolated from figures published by the author. Ref=References: 1= David (1988), 2 = David (1995), 3 = Bertrand & Lumaret (1992), 4 = Bertrand *et al.* (1987), 5 = David *et al.* (1999).

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