

Seasonal and Spatial Variabilities of Litter Decomposition along a Climatic Gradient Within Mediterranean Forest in Southern France

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Abstract: To determine spatial and seasonal Variabilities of leaf litter decomposition an experiment was conducted along a northern-southern climatic gradient in the Mediterranean region (southern France). Four litter types of dominant trees (sweet chestnut, *Castanea sativa*; downy oak, *Quercus pubescens*; holm oak, *Quercus ilex* and Aleppo pine, *Pinus halepensis*) were decomposed in the fed of four plots (Cambo, Liouc, Montpellier and Pech-Rouge) corresponding to four forest types (downy oak, mixed downy - holm oak, holm oak and Aleppo pine forests). They differ also by their climatic characteristics. Litter-bags method was used. Litter decomposition was expressed by free-ash dry mass loss (LML, litter mass loss). Annual LML varied between 24% for downy oak at Pech-Rouge and 62% for sweet chestnut at Liouc. Between species, total LML was highest for sweet chestnut in the four plots and lowest for Aleppo pine, except at Pech-Rouge where downy oak presented the lowest LML. The two oaks occupied an intermediate position in terms of LML. Between plots, total LML was lowest at Pech-Rouge than in the other plots where LML did not differ significantly for sweet chestnut, downy oak and holm oak. On the other hand, for Aleppo pine the LML was lower at Cambo than at Montpellier and Liouc. Litter decomposition was also seasonal, maximum in autumn and minimum in winter. In summer and spring, the LML varied according to the plots. The variations of LML could be explained by climate (temperature and moisture) and/or plot characteristics.

Key words: Litter decomposition · Climate · Season · Mediterranean tree species

INTRODUCTION

General asynchronism between temperature and favorable conditions of humidity to biological activity has deep influenced on different ecological processes, especially organic matter cycle, which intervenes in the functioning of the Mediterranean ecosystem. Periodic fires also play a major role in mineralization of nutrients, but litter decomposition constitutes a key process in organic matter cycle during the inter-fire periods [1, 2]. Vegetation growing, nutrient use by vegetation cover and nutrient recycle seem to be more active during rainy seasons when the soils are moist and warm [3]. Humification processes in Mediterranean forests do not appear to present generally particular characters, but they are not constant during the year. In fact, they

generally stop or slow down during periods of summer-like dryness in low altitude forests and during winter, because of very low temperature in high altitude forests [4].

In Mediterranean region, several biological types coexist, the proper species of this region and the wide distribution species, but the presence of all these species in Mediterranean region is generally linked to a good capacity of the use of lowly available water resource and to their carbon balance [5]. Evergreen species with thick leaf cuticle are considered as physiologically adapted to dryness and low nutrients reserves [6]. In several regions of the world, evergreen species seem also to be associated with poor soil nutrients [7, 8] and would adapt to these regions by different means, including nutrient conservation by relatively slow litter decomposition [9].

In litter decomposition studies, the mean climatic variables needed to define the effects of climate on the rate of litter decomposition are temperature and humidity (of air or soil) and sometimes actual evapotranspiration (AET). The influences of each of these variables and their interactions have been reported in literature and their importance varies according to ecosystems under consideration [10]. Precipitation is considered as an indicator of environmental humidity. Fogel and Cromack [11] have shown that the rate of litter decomposition of Douglas fir was lower in sites where litter moisture is lower than where it's important. Likewise, Witford *et al.* [12] has found that precipitation and temperature explain about 50% of the variation of litter weight loss of *Creosotebush* in desert ecosystem. When arthropods are excluded, 90% of this variation was explained by precipitation and temperature.

Meentemeyer [13] used AET as climatic index. He showed that this index was positively correlated ($r=0.98$) with litter decomposition on 20 sites located in arctic climate, boreal, tempered and tropical climate. This model has been applied by Berg *et al.* [14] on pine leaf litter in Europe, including Mediterranean region and by Upadhyay *et al.* [15] on 10 leaf litter in central Himalaya. In the 2 cases, correlation between litter mass loss and AET was significant. However, this model presents the limits in desert systems, the predicted values of litter mass loss did not correspond to observed values. Witford *et al.* [12] attributed these differences to extreme environmental conditions in desert systems. Others studies have shown the existence of a good relationships between climatic variables and the rate of litter decomposition [16, 17, 10], but that the importance of climatic variables change with canopy structure and litter exposure. Witford [18] developed a climatic index for terrestrial ecosystems. It showed that moist forest with closed canopy (index=1) were least affected while the open systems, especially warm desert (index=10), were the most affected by climate.

Climatic effects on litter decomposition vary according to scale of studies. In fact, according to LaCaro and Rudd [19], the rate of litter decomposition is not affected by precipitation and temperature in humid tropical forest. These results were positive for their sites only, but other studies have given contrary results. Thus, Dyer *et al.* [20] have found a higher coefficient of determination, about 0.78, between climatic and rate of litter decomposition, measured on 104 sites from all over the world. Santos *et al.* [21] have also showed significant influence of precipitation gradient on the litter mass loss of *Larrea tridentata* in American desert system.

Studies of litter decomposition in natural conditions, on one site only, allows with difficulty to estimate climatic effects on litter decomposition rate, but differences between species may be clearly observed. To separate climatic effect from others parameters, Upadhyay *et al.* [22] placed the same litter type on at least 5 different sites with varying precipitation and temperature gradient. In the Mediterranean region, the few studies analyzing site variation of litter decomposition have been realized on at most 3 sites [23, 24].

The aim of this study is to determine spatial and seasonal variability of litter decomposition of Mediterranean evergreen and deciduous species. Effects of climate on litter mass loss in natural conditions were also discussed. So, four litter types belonging to tree species were decomposed in field along a climatic gradient on four sites with the same soil type but varying by soil organisms, rainfall and temperature gradient.

MATERIALS AND METHODS

Study Site: Experimental site is located in Mediterranean region in southern France (lat. 43°08' to 43°58'N and long. 3°08' to 4°00'E; altitude 40 to 708 m asl). The permanent sites were chosen along a northern-southern climatic gradient in 4 distinct forest types, ranging from La Fage mountain to Narbonne plain and corresponding to *Quercus pubescens* forest (Cambo site), mixed *Q. Pubescens* - *Q. ilex* forest (Liouc site), *Q. ilex* forest (Montpellier site) and *Pinus halepensis* forest (Pech-Rouge site). Geographical location of four plots and their important characteristics are given in Figure 1 and Table 1.

The Climate of study area is sub-humid Mediterranean type according to Emberger [25], with mean annual precipitation about 770 mm, mean annual temperature about 14.4°C, pluviothermic formula of Emberger about 80. Water deficit according to Turc formula extended from April to September [26]. Calculated mean annual precipitation for 30 years varied from 478 (Pech-Rouge) to 1154 mm (Cambo). Although there is a marked inter-annual variation of precipitation between sites (Table 1). During the period of our experiment from March 1993 to February 1994, the measured annual precipitation varied between 1060 and 1500 mm, with an increase from 108 (Liouc) to 725 mm (Pech-Rouge) compared to normal precipitation. Rainfall at Pech-Rouge increased greatly, 3 times higher than mean annual. Rainfall distribution during year was seasonal and the differences among sites were much more marked in

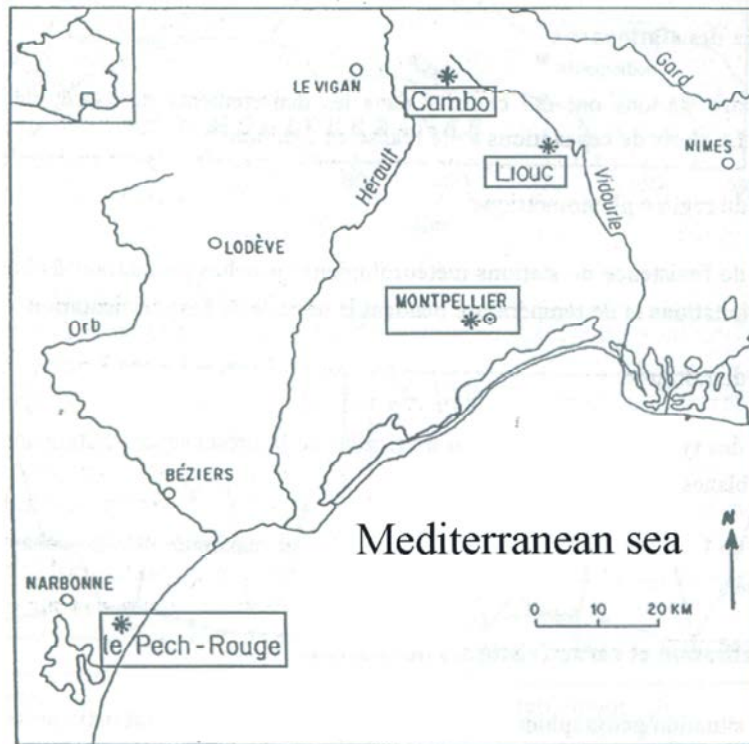


Fig. 1: Location of study plots in Mediterranean region (Southern France).

Table 1: Characteristics of four forest type sites. Rainfall formula indicates the seasonal precipitation in percentage of annual precipitation. asl: above sea level

Site characteristics	Sites			
	Cambo	Liouc	Montpellier	Pech-Rouge
Latitude:	43°58'N	43°53'N	43°38'N	43°08'N
Longitude:	3°48'E	4°00'E	3°51'E	3°08'E
Altitude (m) asl:	708	97	60	40
Distance from sea (km):	50	40	12	1.4
Vegetation:	Downy oak	Holm oak & downy oak	Holm oak	Aleppo Pine
Soil organisms	Mesofauna	Mesofauna	Mesofauna and fungi	Fungi
Mean annual rainfall (mm) for 30 years	1154	966	755	478
Rainfall for 93/94:	1505	1146	1066	1203
Rainfall formula for 93/94 (%)				
Autumn	41.56	46.06	49.94	58.34
Spring	26.61	19.65	23.03	23.83
Winter	20.24	23.57	19.68	13.76
Summer	11.58	10.72	7.65	4.07

summer, when rainfall is lower (Table 1 and Figure 2). Mean seasonal temperature were higher in summer (about 21.5 to 22°C) and lower in winter (about 5 to 9°C). It differed between sites only in winter. In the latter season the minimum seasonal temperature increased from Cambo (1.70°C) to Pech-Rouge (5.46°C).

A good description of soils of the study area is found in the studies of Bottner [27]. The soils are generally a fersialitic one and the parent material is weathered calcareous [28].

Litter Types: Species selected for this experiment were a range of contrasting Mediterranean species: one coniferous tree species (*Pinus halepensis* Miller) and three broad-leaved tree species including a deciduous species (*Castanea sativa* Miller), a marcescent one (i. e. a deciduous species in to which withered leaves remain on the tree for several months, *Quercus pubescens* L.) and evergreen one (*Quercus ilex* L.). The distribution of sweet chestnut (*C. sativa*) is much wider than that of the Mediterranean climate. In contrast, two species,

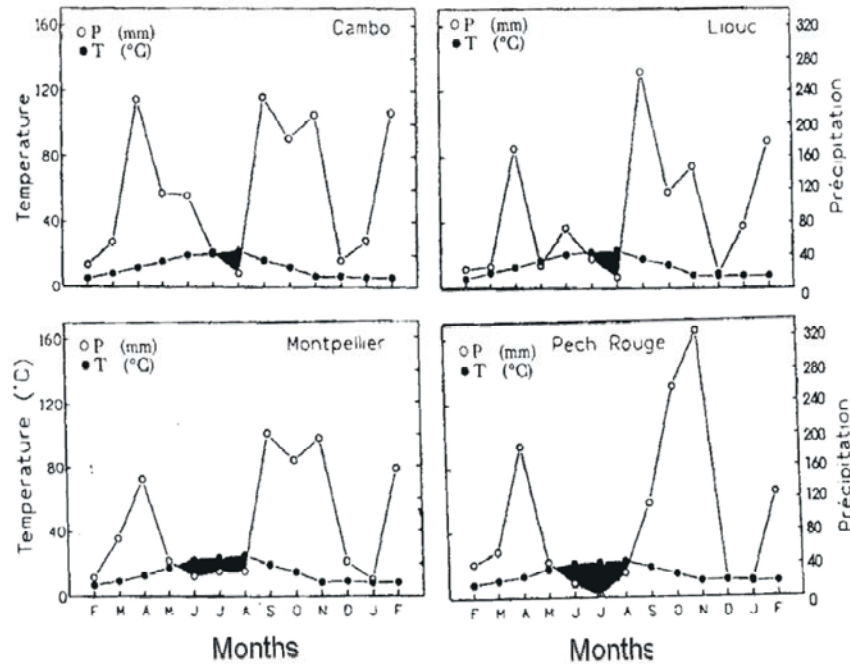


Fig. 2: Monthly mean temperature (solid point) and mean precipitation (open point) for one year (93/94). Black areas show dry seasons vary from 2 to 4 months according to sites.

holm oak (*Q. ilex*) and Aleppo pine (*P. halepensis*) are strictly limited to the Mediterranean climate. Downy oak (*Q. pubescens*) represents an intermediate case, being widely distributed, but much more abundant in Mediterranean zones.

Fresh fallen leaf litter was collected at the period of maximum leaf-fall, that is in autumn for sweet chestnut and Downy oak, in spring for holm oak and in summer for Aleppo pine, from near Montpellier. All leaf litter was stored in laboratory after air-drying before using.

Litter Bags Experiment and Dry Litter Mass Loss Measuring: Litter-bag method was used. Eighty bags (twenty for each species) of 1-mm mesh, except for that of *P. halepensis* (0.5 mm), containing 10 ± 0.001 g of air-dried litter were placed on the soil surface of each plot at the end of February 1993. Five replicates of each species were removed randomly on each plot after 3, 6, 9 and 12 months, respectively at the end of May (spring), August (summer), November 1993 (autumn) and February 1994 (winter). All samples were dried in a ventilated oven at 60°C until a constant weight was gotten weighed and then ground in a cyclone mill through a 1-mm mesh.

The ash content of all the litter samples was determined by NIRS [29], which enabled us to calculate the ash-free litter mass loss (LML, litter mass loss).

Data Analysis: One way ANOVA (species, sites or seasons) was used on litter mass loss to test specific, spatial and seasonal variability. These analysis were followed by mean comparison using Scheffer's test at $p < 0.05$. Simple and multiple linear regressions between LML and initial litter properties, between LML and environmental factors (rainfall, temperature, altitude) were also calculated.

RESULTS

Annual Litter Mass Loss: After one year of field incubation, total litter mass loss differed significantly between species in each of four sites ($F = 37.9, 41.4, 17.9$ and $50.5, p < 0.001$, respectively for Cambo, Liouc, Montpellier and Pech-Rouge). This litter mass loss varied between 24% (*Q. pubescens*) at Pech-Rouge and 62% (*C. sativa*) at Liouc. Mean comparison, showed that total LML was highest for *C. sativa* in four sites (Figure 3a). It was lowest for *P. halepensis* except at Pech-Rouge. The 2 oaks species occupied an intermediate position. In Pech-Rouge, it was *Q. pubescens* which presented the lowest LML whereas *P. halepensis* with *Q. ilex* occupied an intermediate position.

After one year of litter decomposition, total LML differed significantly between sites for all species ($F = 15.9, 34.6, 32.6$ at $p < 0.001$ and 7.6 at $p < 0.01$,

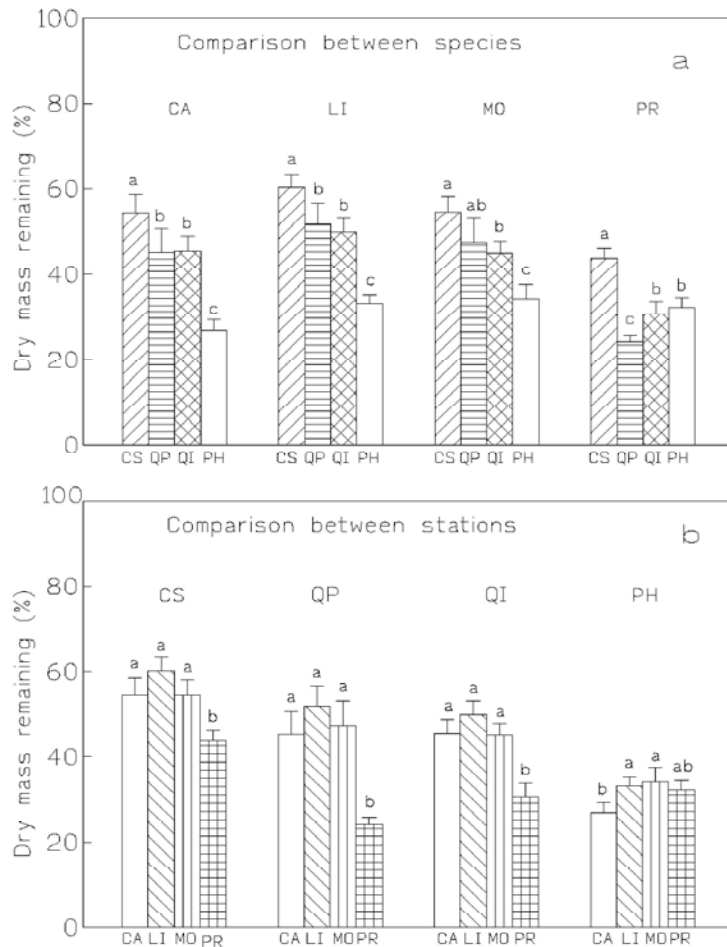


Fig. 3: Annual LML (Mean \pm SE), comparison (a) between species in each of four plots and (b) between plots for each of four species. Two different letters indicate the mean values of LML are significantly different. Species: *C. sativa* (CS), *Q. pubescens* (QP), *Q. ilex* (QI) and *P. halepensis* (PH). Plots: Cambo (CA), Liouc (LI), Montpellier (MO) and Pech-Rouge (PR).

respectively for *C. sativa*, *Q. pubescens*, *Q. ilex* and *P. halepensis*). It varied from 44% (Pech-Rouge) to 62% (Liouc) for *C. sativa*, from 24% (Pech-Rouge) to 52% (Liouc) for *Q. pubescens*, from 31% (Pech-Rouge) to 50% (Liouc) for *Q. ilex* and from 27% (Cambo) to 33% (Montpellier) for *P. halepensis* (Figure 3b). Mean comparison shows that for *C. sativa*, *Q. pubescens* and *Q. ilex* the LML were lower at Pech-Rouge than in other plots where they did not differ significantly between them (Figure 3b). On the other hand, for *P. halepensis* the total LML was significantly lower at Cambo than at Liouc and Montpellier.

Seasonal Litter Mass Loss: Seasonal LML (or LML per season) is the LML corresponding to every 3 months of field decomposition. Mean seasonal LML (or mean LML

per season) is the average of seasonal LML of 4 plots for each species or of 4 species at each plot.

One way analysis (species factor) showed that mean seasonal LML differed significantly between species at each season ($F=3.4$, $p<0.05$; 5.9 $p<0.01$; 22.2 , $p<0.001$, respectively for spring, summer and autumn), except in winter. During the last season, differences between species were insignificant ($F=2.8$ and $p>0.06$) (Figure 4a). In summer and autumn, *C. sativa* species presented the highest LML and *P. halepensis* species the lowest. It was in autumn that differences between species were more important.

The mean seasonal LML differed significantly between plots only in spring and in summer ($F=16.3$ and 37.9 at $p<0.001$, 0.5 and 2.4 at $p>0.06$). In autumn and winter, differences between plots were insignificant.

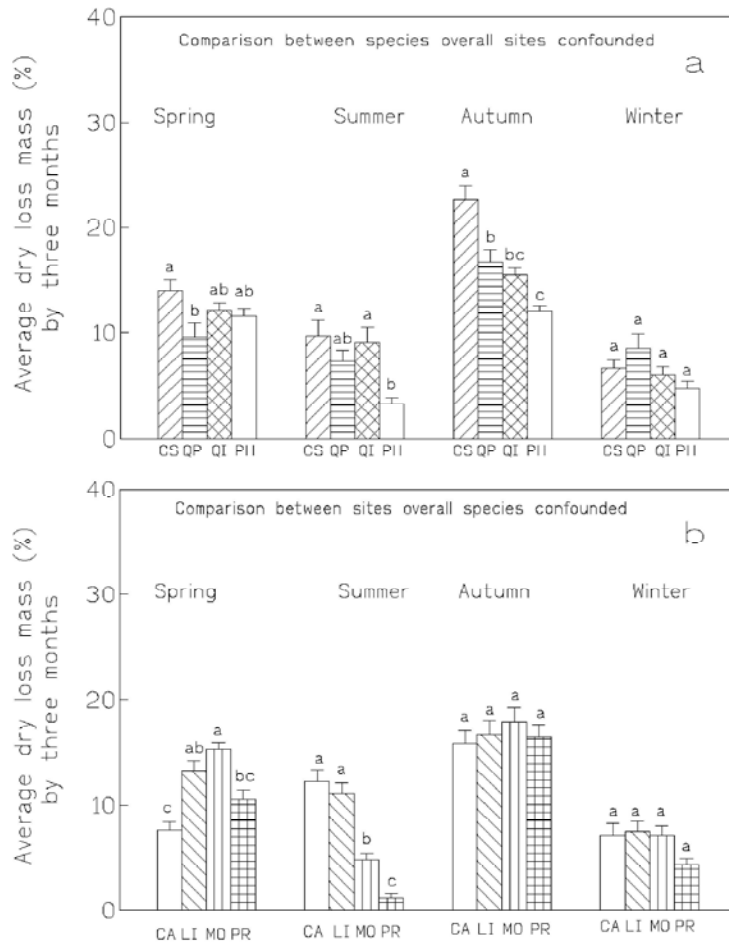


Fig. 4: Seasonal LML (Mean \pm SE), comparison (a) between species all sites included and (b) between sites all species included. Two different letters indicate the mean values of LML are significantly different. Species: *C. sativa* (CS), *Q. pubescens* (QP), *Q. ilex* (QI) and *P. halepensis* (PH). Plots: Cambo (CA), Liouc (LI), Montpellier (MO) and Pech-Rouge (PR).

In spring, it is at Liouc and Montpellier that the greatest LML occurred and at Cambo the least (Figure 4b). On the other hand, in summer, they were at Cambo and Liouc that occurred the highest mean seasonal LML whereas they were less important at Montpellier and almost null at Pech-Rouge.

Mean seasonal LML differed significantly between seasons in the four plots ($F = 14.3, 12.1, 46.9$ and 68.0 , at $p < 0.001$, respectively for Cambo, Liouc, Montpellier and Pech-Rouge). In these four plots, it was in autumn that the greatest LML occurred (Figure 5a). On the other hand, seasons during which mean seasonal LML were the lowest varied according to plots. They occurred in winter and spring at Cambo, in winter and summer at Montpellier and Pech-Rouge.

For all species, mean seasonal LML differed significantly between seasons ($F = 34.6, 11.6, 18.7$ and 55.4 , at $p < 0.001$, respectively for *C. sativa*, *Q. pubescens*, *Q. ilex* and *P. halepensis*). The most important mean seasonal LML still occurred in autumn and the lowest in summer and winter (Figure 5b). On the other hand, the role played by spring varied according to species. During this season which corresponds to the first three months of field decomposition, the mean seasonal LML were lower than in autumn for *C. sativa* and *Q. pubescens* whereas it was almost equivalent to that in autumn for *Q. ilex* and *P. halepensis*.

Relationships Between Initial Litter Characteristics and Litter Mass Loss (LML): Initial litter properties were determined by Gillon *et al.* (1994). The C and N content of

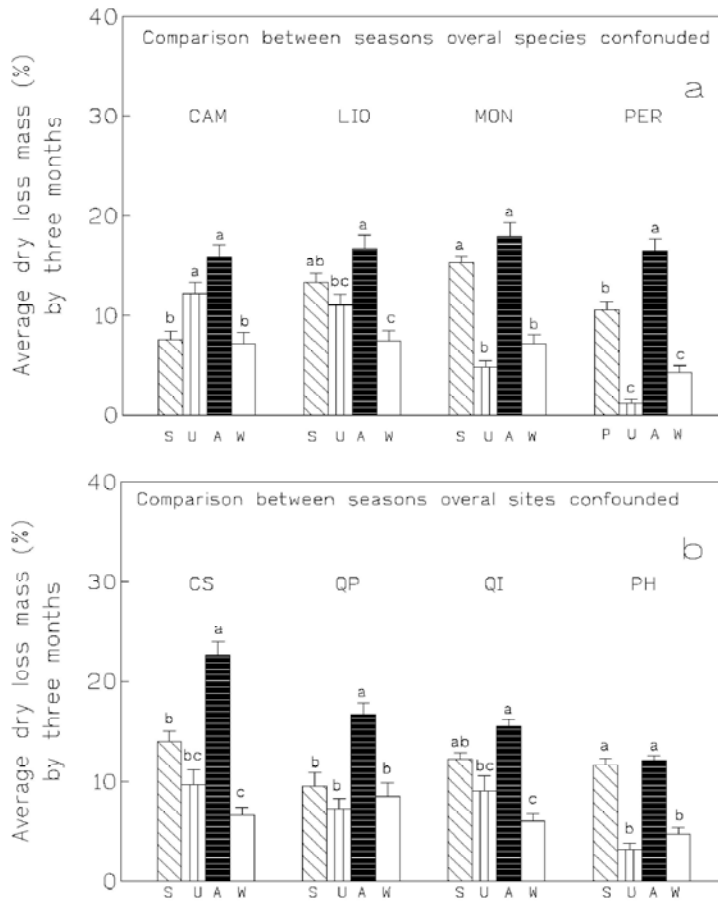


Fig. 5: Seasonal LML (Mean \pm SE), comparison (a) between seasons all species included in each of plot and (b) between seasons all plots included for each species. Two different letters indicate the mean values of LML are significantly different. Species: *C. sativa* (CS), *Q. pubescens* (QP), *Q. ilex* (QI) and *P. halepensis* (PH). Plots: Cambo (CA), Liouc (LI), Montpellier (MO) and Pech –Rouge (PR). Seasons: spring (P), summer (E), autumn (A) and winter (H).

Table 2: Initial characteristics of four leaf litter types. ND: non determine. LSM: leaf specific mass.

Litter properties	litter types			
	<i>C. sativa</i>	<i>Q. pubescens</i>	<i>Q. ilex</i>	<i>P. halepensis</i>
C (%)	49.7	50.8	52.5	56.7
N (%)	0.72	0.77	1.00	0.66
C/N ratio	68.8	66.4	51.7	86.1
Thickness (10^{-5} m)	14.0	21.4	25.9	ND
Density (kg. m^{-3})	400	414	708	721
LSM (g.m^{-2})	56	87	184	ND

litter varied little between species (Table 2), from 50 to 53% for C, with exception of *P. halepensis*, which contained 57% and from 0.7 to 1% for N. The litter also differed in their thickness (14 – 26 10^{-5} m). The leaf specific mass (LSM) varied from 1 to 3 and their density between 1 and 2.

Only the C/N ratio correlated significantly with LML after 12 months of field decomposition. This correlation was significantly with LML only at Cambo ($r = -0.98$, $n = 4$ and $p < 0.05$) and Liouc ($r = -0.97$, $p < 0.05$).

DISCUSSION

Litter Mass Loss after One Year Litter Decomposition: Annual litter mass loss varied between 24% (*Q. pubescens*) at Pech-Rouge and 62% (*C. sativa*) at Liouc. Compared to data from literature concerning Mediterranean leaf litter, these obtained annual LML were among the highest (Table 3). Litter decomposition of *Q. pubescens* and *P. halepensis* has been studied *in situ* on field, under pine and oak forests in Marseille region [30]. The two species lost an average of 48% (*P. halepensis*)

Table 3: Comparison between annual dry litter mass loss (LML) of Mediterranean plant species. P: annual precipitation (mm)

Region	P(mm)	LML (%)	litter types	Reference
South of Africa	200	20	<i>Leucospermum parile</i>	[40]
Australia		25	<i>Eucalyptus pauciflora</i>	[1]
		39	<i>E. delegatensis</i>	[1]
	570	47	<i>E. microcarpa</i>	[49]
California	440-480	15-19	<i>Ceanothus megacarpus</i>	[41]
	440-480	20-24	<i>Salvia mellifera</i>	[41]
	1080-1710	6.8-31.2	<i>Pinus ponderosa</i>	[49]
Spain	500-600	35-42	<i>Quercus rotundifolia</i>	[38]
	500-1600	42-62	<i>Fraxinus angustifolia</i>	[23]
		10-50	<i>Q. pyrenaica, Q. suber</i>	[23]
Spain, France	568-969	32-37	<i>Quercus pyrenaica</i>	[32]
		26-34	<i>Quercus lanuginosa</i>	[32]
France	770	23-27	<i>Quercus ilex</i>	[42]
Greece	449	22-24	<i>Quercus coccifera</i>	[50]
	600-900	37	<i>Arbutus unedo</i>	[51]
		33	<i>Quercus coccifera</i>	[51]
Italy	988	16	<i>Pinus pinaster</i>	[43]
		28	<i>Arbutus unedo</i>	[43]
		37	<i>Quercus cerris</i>	[43]
		37	<i>Quercus suber</i>	[43]

and 55% (*Q. pubescens*) of their original mass in 26 months of litter decomposition. In our study, the LML was from 27% (Cambo) to 34% (Montpellier) for *P. halepensis* and from 24% (Pech-Rouge) to 51% (Liouc) for *Q. pubescens*. One year of our study, the LML went beyond the two third obtained in certain sites by Gillon *et al.* [30] in 26 months for *P. halepensis* and three quarters (3/4) for *Q. pubescens*.

It has generally been shown that leaf litter of broad-leaved species loss more masses than those of coniferous species [23]. There is in conformity with our results at Cambo, Liouc and Montpellier since in these 3 sites, annual LML of broad-leaved species (*C. sativa*, *Q. ilex* and *Q. pubescens*) were higher than that of coniferous species (*P. halepensis*). On the other hand, at Pech-Rouge, the driest site, where dominates *P. halepensis* forest, the LML of *Q. pubescens* was lower than that of *P. halepensis*. But, from studies on Pine and aspen leaf litter, Taylor and Parkinson [31] suggested that, under favorable conditions of temperature and humidity, aspen litter decomposes faster than that of Pine, whereas under unfavorable conditions (dryness and cool), pine litter decomposed faster than aspen. This explanation is partial with regard to our study, because at Pech-Rouge, if *Q. pubescens* leaf litter decomposed slower than that of pine, *C. sativa* leaf litter continued to be faster than that of *P. halepensis*.

Effects of Sites on Litter Mass Loss: During the period of experiment, annual rainfall was largely better than average annual rainfall for 30 years, which was

about 1150 mm at Cambo and less than 500 mm at Pech-Rouge. However, during the period of experiment (93/94), rainfall was about 1500 mm at Cambo and about 1200 mm at Pech-Rouge. Compared to the average, excess water was particularly marked at Pech-Rouge (725 mm), the most northern and driest site. rainfall contrasts between the four sites were then masked by abundant rainfall during the period 93/94. In the all sites, rainfall was most important in autumn and least in summer. Differences between the four sites appeared in summer: from 49 mm (Pech-Rouge) to 174 mm (Cambo).

For the three broad-leaved species, litter decomposition differed significantly according to sites; annual LML was higher in the most northern 3 sites than at Pech-Rouge. On the other hand, for pine needle litter, differences between sites were less pronounced and, in total, its litter decomposition rather slowed down in the most northern site (Cambo) compared to the 3 other sites. Globally, differences of the LML according to sites appeared in spring and in summer during the first 6 months of litter decomposition *in situ*. Then, during autumn and winter, differences of LML between sites were insignificant. In spring, LML were especially low at Cambo. In summer, LML were directly linked to rainfall and differed according to sites in the same way for the four species. LML decreased from the most wetted site during summer (Cambo) to the driest site (Pech-Rouge). Summer seems then to be the season during which rainfall influenced most litter decomposition in the Mediterranean region.

Some studies have already showed that litter decomposition varied with study sites. Thus, Gallardo and Merino [23] have compared litter decomposition of 9 Mediterranean species in two sites in Spain: Doñana (annual mean rainfall about 500 mm, annual mean temperature about 16.7°C and 20 m of altitude) and La Saucedá (annual mean rainfall about 1600 mm, mean annual temperature about 16.2°C and 432 m of altitude); they have found that annual LML in Doñana site was lower than in La Saucedá site for all species. Likewise, Martín *et al.* [32] have compared LML of *Q. pyrenaica* and of *Q. lanuginosa* in El Payo site (Spain) and La Vialle site near Montpellier (France); annual LML of the 2 species were higher in La Vialle site than in El Payo site. According to them, climatic factors, especially moist under Mediterranean climate characterized by a great summer-like dryness, plays an essential role in litter decomposition, by their direct effect on microflora and soil mesofauna. It has also been observed the variation of LML between sites under other climates [33]. All these studies showed that climatic conditions, particularly moisture, play an important role in litter decomposition because climate exerts direct effects on mesofaunal and microfloral activities of soil [34-36].

Influence of Season on Litter Mass Loss: For all species, in all sites, the most important LML occurred during autumn and it was still low in winter. On the other hand, the importance of LML during the two other seasons, spring and summer, varied much more according to sites. In summer, LML was especially lower as rainfall was low and in spring like in winter, it was especially lower at Cambo. It was then at Cambo, the highest, the most northern, most fresh and most wetted plot, that LML in spring was lower than in summer whereas the opposite was observed in the 3 other sites.

The important litter mass loss in autumn in the all plots may be explained by rainfall. It is the most wet season in all the plots and the rainfall was still more than 40% of the total annual. The lack of water during summer would slow litter decomposition, especially in the 2 most southern sites, Montpellier and Pech-Rouge. The low LML in winter in all sites could be attributed to cold, because during this season the measured rainfall differed little from that of the former spring.

In spring as winter at Cambo the particularly low LML, would be due to cold. In fact, meteorological station at Sumene, which we use for reference for Cambo site, is located at an altitude of 200 m. This station supplies probably climatic data which roughly indicates only those

of Cambo site, located up to 700 m. It was probable that in winter and spring, temperatures were lower in this site than in meteorological station of Sumene. So, in spring at Sumene, minimum mean temperature was lower than in other site and, during the first 10 days of March, daily average minimum temperature was under zero (-1.3°C) whereas, it was positive in the 3 other sites.

Influence of season on litter decomposition in Mediterranean region has been reported. Thus, Jackson *et al.* [37] have shown that, under Mediterranean type climate, nutrient cycle appears more active during autumn and spring when the soil is moist and warm. Likewise, Stamou *et al.* [33] have shown that, in semi-arid system in Greece, the rhythm of litter decomposition of *Asphodelus* was synchronous with the climatic variations; the highest rate of litter disappearance intervenes in autumn (27%) and in spring (22%), but it was only 4% in summer as in winter. Martín *et al.* [32] have determined the LML of *Q. pyrenaica* and *Q. lanuginosa*, which were much lower in summer than in other seasons; they have attributed this seasonal slowing down to dryness in general and to strong summer-like temperatures. Escudero *et al.* [38] have also shown that, after one month of litter decomposition in field conditions at Salamanca (Spain), the LML of *Q. rotundifolia* was highest in spring (from 16.1 to 20.6%) and in autumn (from 10.4 to 14.2%) than in summer (from 5.1 to 5.8%) and in winter (from 5.1 to 5.8%). However, from the eleventh month of litter decomposition, this LML was more important in spring (from 2.3 to 2.8%) and in summer (from 3.0 to 5.2%) than in autumn (from 0.9 to 1.8%) and in winter (from 0.4 to 1.3%). Billes *et al.* [39] have shown that the release of CO₂ revealed appreciable decrease during summer in *Q. ilex* forest; the rainfall which occurs in autumn and spring has then a stimulating role because it was followed invariably by great soil biological activity. On the contrary, Mitchell *et al.* [40] have apparently found no seasonal effects on litter decomposition of *Leucospermum parile* in Fynbos shrubs of South Africa.

Comparison Between Species: After one year of litter incubation *in situ*, the litter decomposition of *C. sativa* which is not a strictly Mediterranean species was the highest in all sites. On the contrary, that of *P. halepensis* was the lowest except at Pech-Rouge in summer. The litter mass loss of both oaks was intermediate, except at Pech-Rouge where it was low, much lower than that of *P. halepensis*. These results agree with those of Schlesinger and Hasey [41], with the exceptions of Pech-Rouge site.

At Pech-Rouge, in spite of the abundant rainfall during period of studies, the annual LML (31-32%) of both oaks were in the same high order than in the other investigated Mediterranean species. On the other hand, in other sites, the LML values (45-49%) of *Q. ilex* and those (45-52%) of *Q. pubescens* were remained higher than those reported by other studies on oaks species. Because, the annual LML was from 23 to 27% for *Q. ilex* [42], from 35 to 42% for *Q. rotundifolia* [38], of 37% for *Q. cerris* [43], from 32 to 37% for *Q. pyrenaica* and from 26 to 34% for *Q. lanuginosa* [32].

Annual LML (43% - 62%) of *C. sativa* species were among the highest found in literature on the high altitude species or on the more northern region species. For example, Gallardo and Merino [23] have studied litter decomposition of *Fraxinus angustifolia*, widespread species like *C. sativa*, in 2 sites in Spain; they found that annual LML ranged from 42% (Doñana) to 62% (La Saucedá). MacLean and Wein [44] noted that after one year of litter decomposition in the field conditions at New Brunswick (Canada), the LML of four deciduous species (*Acer rubrum*, *Prunus pensylvanica*, *Populus tremuloides* and *Betula papyrifera*) varied between 38 and 58%.

Influence of Initial Litter Quality Parameters on Litter Decomposition:

LML was often correlated with initial litter characteristics. The parameters retained in Literature varied according to ecosystems under consideration. The whole parameters have been recapitulated from literature in the studies of Taylor *et al.* [45], Gallardo and Merino [23] and Gillon *et al.* [30]. In addition, the last 2 authors have shown that, under Mediterranean climate, the rate of litter decomposition was linked to the physical properties of leaves (permeability, thickness, toughness, etc.). Contrary to the results of field studies of Gallardo and Merino [23] and microcosms studies of Gillon *et al.* [30], the litter mass loss was correlated with C/N ratio of original litter in our experiment. This correlation varies with plots; the C/N ratio of original litter was correlated with LML in the most northern 2 sites. At Pech-Rouge, none of these correlations were significant. It then appears that at Pech-Rouge, where litter decomposition of 3 broad-leaved species was especially slow, other more limiting factors than the C/N ratio may be controlling litter decomposition.

Influence of Climatic Factors on Litter Decomposition:

Litter decomposition was generally influenced by climatic factors [46, 10]. However, in our study with the exception

of seasonal influences, no significant correlation exists between litter mass loss and rainfall (annual and three months during experiment or average annual calculated for 30 years). Rainfall measured during our experimental period was above annual standard in all sites; it was probably why selected rainfall gradient slightly influence litter decomposition. Likewise, average data of temperature, vary slightly along a climatic gradient, has not explained the variations of litter decomposition in our experiment except in terms of seasonality.

Berg *et al.* [14] have studied climatic effects on litter mass loss of Pinus at regional scale and their results have shown that climatic factors (temperature, precipitation, AET, PET) correlated significantly with the annual litter mass loss. At regional scale, spatial variability of LML was well described by climate [47], but when studies occurred on some sites where climate was little different, litter decomposition appears better explained by litter quality parameters [20]. The results of last author on the one hand and exceptional rainfall during experiment on the other hand, explained probably why, in our study, site variation of litter decomposition was not related by classical climatic factors.

CONCLUSION

During studies of site variability of litter mass loss, several points came out clearly: The litter mass loss was among the highest values measured under Mediterranean climate, because annual rainfall during experiment was largely above the normal annual rainfall. This confirms the importance of humidity on litter decomposition. Leaf litter of *C. sativa* was the fastest to decompose in all sites and that of *P. halepensis* the lowest, except in the southern and the driest site, dominated by *P. halepensis* forest (Pech-Rouge). The two Quercus had intermediate behavior except at Pech-Rouge where their litter decomposition was slower than that of *P. halepensis*. Litter decomposition was seasonal, maximum in autumn, still low in winter. In summer and spring, it was varied according the sites; it was especially lower as rainfall was low in summer and it was probably limited by cold in spring in the northern and highest site (Cambo).

Globally for broad-leaved species, litter mass loss was lower in the southern and the driest site (Pech-Rouge) than in the 3 other sites. It was at Liouc, one of two wetted plots and where litter decomposition was not slowed down by cold in spring, that litter mass loss was the greatest. For *P. halepensis* species litter

decomposition was slower in the northern and the coldest plot (Cambo) than in the 3 other plots.

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