

Leaf Litter Decomposition of Mediterranean Tree Species in Relation to Temperature and Initial Water Imbibition under Microcosm Experiments

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Abstracts: Four leaf litter types belonging to mediterranean tree species (sweet chestnut, *Castanea sativa*; downy oak, *Quercus pubescens*; holm oak, *Quercus ilex*; and Aleppo pine, *Pinus halepensis*) were incubated in microcosms for 16 weeks. Five treatments were compared: three soaking periods 1, 6 and 24 h before incubation at 22°C, and two different temperatures 18°C and 26°C with soaking for 24 h. Samples were collected after 2, 4, 8 and 16 weeks, and the remaining dry weight measured. After 4 months, the litter had lost between 7 and 44% of its original mass. Litter mass loss of sweet chestnut was the highest, whereas that of Aleppo pine was the lowest and the two oak species were intermediate. Regression lines fitted to the data showed that for the species under study, litter mass loss was a single exponential function of time. Initial water imbibition had little or no effect on the litter mass loss and decomposition rate. On the contrary, temperature affected litter mass loss and decomposition rate, which varied between the plant species.

Key words: Litter decomposition, Microcosm, temperature, water imbibition, Mediterranean tree species.

INTRODUCTION

Litter decomposition process represents an essential phase in the organic matter and nutrient cycle. The litter decay rate is a factor that largely determines forest soil fertility and its regulation plays an important role in ecosystem functioning^[1]. Litter decomposition is influenced by litter quality^[2], decomposer organisms^[3,4] and environmental conditions^[5,6]. The relative importance of these factors varies according to the characteristics of the ecosystems under consideration^[3].

In the Mediterranean region, studies were carried out on relationships between litter decomposition and biotic and abiotic factors. Gallardo & Merino^[7] determined the relationships between thickness of nine Mediterranean leaf types and their rate of decomposition. In our previous paper^[8], we have shown the influence of initial litter properties of 12 Mediterranean litter types on their decay rate. Likewise, Cortez *et al.*^[9] did not find the relationships between litter quality parameter and decomposition rates of freshly-fallen litter, because under a mediterranean climate where sclerophyllous vegetation dominates, physical structure and leaf toughness must be considered^[7]. However they point out that the oldest stage of litter decay were correlated to litter quality

parameter. The soil organism effects on litter decomposition process were also studied in laboratory and field conditions^[6,10].

To provide informations for impact of climate changes on litter decomposition and organic matter cycle such as nitrogen of some terrestrial ecosystems, some studies have been devoted to relationships between litter decomposition and climate factors. Some researchers have shown that climate has direct effect on litter decomposition due to the effect of temperature and moisture, but also has an indirect effect through the climatic impact on litter chemistry^[3,11]. Other climatic index, such as Actual Evapotranspiration (AET) have been used to estimate the relative contribution of climate to litter decomposition rates^[11]. The climatic factors most often accounted for are temperature and moisture content. With respect of these factors, opinions to the importance of their effects on control of litter decomposition was more widely spread because the effect of either was not constant in time and space and they interact in complicated ways^[12]. Moisture is considered as the major factor controlling litter decomposition^[13]. Nevertheless, some studies have shown that temperature has a dominant effect^[14,15]. Other studies have demonstrated that temperature and moisture content are so interdependent that their

interaction is a key point, individual effects being barely relevant^[16,17].

Most studies on climatic effects on litter decomposition were carried out on field conditions along an environmental gradient which can reflect climatic variations (temperature and precipitation)^[18,19]. However these studies cannot be used to determine any cause - effect relationship because many factors such as soil type, rainfall, temperature and the litter quality vary in uncontrolled field conditions. It is thus difficult to determine in natural conditions, which environmental variables are responsible for the biochemical evolution and litter mass loss during decomposition. The nature and importance of each variable cannot be controlled independently of others^[20] and the contribution of each is not easily quantifiable. Whereas in the laboratory, a variable can be controlled while maintaining constant the others, hence quantifying the relative importance of each of them. The most commonly used laboratory method is the microcosm^[20]. Unlike in studies under natural conditions where the decomposition rate is slow, the microcosm accelerates litter decomposition and enables it to be studied in a relatively short time.

Very few researches have been devoted to comparative study of various litter types in mediterranean region^[7,8,19]. Nevertheless, we do not know any study concerning the individual influence of temperature and water holding capacity on litter decomposition. Owing to biogeographical and environmental conditions, the vegetation in the Mediterranean region includes species with contrasting morphological and life-history traits: species strictly limited to Mediterranean-climate ecosystems vs species with wider ranges. In the present study, we therefore undertook a laboratory experiment involving 4 contrasting species in an attempt to determine the relative contribution of temperature and initial water imbibition to the litter mass remaining and decomposition rate.

MATERIALS AND METHODS

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 on which withered leaves remain on the tree for several months, *Quercus pubescens* L.) and an evergreen one (*Quercus ilex* L.). The distribution of *C. sativa* is wider than that of the Mediterranean climate. In contrast, two species (*Q. ilex* and *P. halepensis*) are strictly limited to the mediterranean climate. *Q. pubescens* represents an intermediate case, being widely distributed, but much

more abundant in Mediterranean zones.

Litter was collected at the season of maximum leaf fall that is in autumn for *C. sativa* and *Q. pubescens*, in spring for *Q. ilex* and in summer for *P. halepensis*. Litter was stored in the laboratory after air-drying before using.

Microcosms: Microcosms were of the type described by Taylor & Parkinson^[20], modified in our previous paper^[7]. They consisted of plastic cylinders 15 cm in diameter and 15 cm high, fitted with a lid and a bottom with a 1 cm diameter hole allowing excess water to drain off. One kilogram of a previously prepared soil mixture consisting of mineral soil (12% of sand, 36% of lime and 50% of clay, ph =7.6) and surface organic horizon (3:1) from a nearby forest plot (Camp Redon CEFÉ-CNRS) was placed on a grid situated 2 cm above the bottom of each microcosm. The litter, previously soaked for 24 h in 0.1 l of water, was placed on the soil in the microcosms and enclosed in a thin litter bag of 1 mm mesh to recover all the material at each sampling time. So as not to deplete the soluble nutrients in the system, the soaking water was poured into the microcosm, and the quantity of water needed to be added to bring the water content of the microcosm soil up to 80% field capacity was calculated by weighing. The quantity of water needed to replace that evaporating and thus maintain a constant soil moisture during incubation was also calculated each week by weighing the microcosms and adding. The microcosms were maintained at 22°C throughout the experiment.

Litter Incubation: In an attempt to determine the effects of temperature and initial water imbibition on litter decomposition rate, five different treatments were realized in similar incubation chambers:

1. One treatment carried out at 22°C with litter previously soaked in water during 24 h.
2. Two treatments carried out, one at 18°C and the other at 26°C, with litter previously soaked in water during 24 h.
3. Two other treatments carried out at 22°C with litter previously soaked in water, one during 1 h and the other during 6 h.

For each treatment, sixteen samples of 7.000 ± 0.001 g of each of four litter types (*C. sativa*, *Q. pubescens*, *Q. ilex* and *P. halepensis*) were weighed and placed in microcosms. Three additional samples were weighed after drying in an oven at 55°C for 48 h to determine the original litter mass. Four samples of each species at each treatment were removed at 2, 4, 8 and 16 weeks, and their dry mass determined after drying in forced draught oven for 48 h at 55°C.

Data Analysis: The ash content of litter samples was predicted by NIRS^[21], which enabled the ash-free litter mass remaining (LMR). LMR values for each species were fitted to three different models assuming that litter was composed of one or two compartments with different decay rates:

$$\text{- Linear: LMR} = 100e^{-kt} \quad (1)$$

$$\text{- Single exponential: LMR} = 100e^{-kt} \quad (2)$$

$$\text{- Double exponential: LMR} = Ae^{-kt} + Be^{-ht} \quad (3)$$

where LMR is expressed as a percentage of the original mass, t is the time in years, A and B=100-A, are respectively the labile and resistant component, k is a rate constant over time in equations (1) and (2) or for the labile component (A) only in equation (3), and h is a rate constant over time for the resistant component (B) in equation (3).

Various regression lines obtained for each species were compared, using the F- test. Multiple comparisons between the model parameters were carried out using the "T-method"^[22] to compare, for each species, the effects of temperature and initial water imbibition on litter decomposition rate.

Using a one-way ANOVA (temperature or time of initial water imbibition) we tested the effects of temperature and initial water imbibition on litter mass loss at each sampling time (2, 4, 8 and 16 weeks).

RESULTS AND DISCUSSION

Comparison of the Mathematical Models for the Study of Mass Loss Dynamics: The double exponential model (3) had the highest significant coefficient of determination (Table 1). However, the three parameters of this model (A, k and h) were estimated with standard error greater than the estimates because of the limited number of sampling dates and the low number of degrees of freedom. In other respects, the coefficients of determination of the single exponential decay model (2) were lower than the double exponential decay model, but nevertheless remained highly significant. The parameters of this model were estimated with reasonable standard error. The coefficients of determination of the linear model (1) were still much lower than those of the exponential model. Thus the single exponential model was selected for further comparisons.

Effects of Incubation Temperature: From the first sampling time, after fifteen days of incubation, the mass lost by the four litter types differed according to temperature (Table 2). These differences remained

visible after one month. But, after eight weeks of incubation, they disappeared for *C. sativa* and smoothed for *Q. pubescens*. For *P. halepensis*, the litter mass loss at the highest temperature (26°C) was always more than those observed at 18°C and 22°C, which did not differ significantly between them. For *Q. ilex*, the litter mass loss at the lowest temperature (18°C) was always less than those observed at 22°C and 26°C which did not differ between themselves (Table 2).

Comparison of regression constants showed that k increased significantly according to "T-method" between 18°C and 22°C for *Q. ilex*, between 22°C and 26°C for *P. halepensis* (Figure 1). The litter mass loss of *P. halepensis* was the slowest and that of *C. sativa* the most rapid at any temperature. Differences among decomposition rates of the four species studied became smoother when temperature increased.

Effects of Initial Water Imbibition: The initial water imbibition of litter can be defined as a quantity of water, expressed in percentage of dry mass, absorbed by leaves previously soaked in water for 1h, 6h or 24h before incubation.

The effect of initial water imbibition on litter mass loss in the course of incubation time differed according to species (Table 3). For *P. halepensis*, we did not observe any significant difference all along the incubation time. For *Q. pubescens*, we observed an increase in mass loss between 1h and 6h imbibition time at 4 weeks only. For *C. sativa* and *Q. ilex*, the observed increase in mass loss with incubation time did not last more than 8 weeks. At the end of the experiment, the increase in mass loss with initial imbibition time was no longer detectable in any of the four litter types.

Comparison of decomposition rates (k) by the "T-method" showed that throughout the incubation time, decomposition rate was not increased significantly by initial water imbibition, but varied between litter types (Figure 2). Whatever the initial water content, the decomposition rate remained the slowest for *P. halepensis* and the highest for *C. sativa*, the two others decomposing at intermediate rates.

Discussion:

Influence of Temperature on Litter Decomposition: The litter studied came from deciduous species with a wide geographical range and from strictly Mediterranean evergreen species. They were incubated in microcosms in laboratory during 16 weeks. The patterns of litter decomposition and leaching of these species, their initial characteristics and the relationships between their initial litter properties and decay rates were carried out in our previous studies^[8,23].

Table 1: Coefficients of determination (r²) of the three models tested with four tree species at five treatments: (1) linear, (2) single exponential and (3) double exponential. All coefficients were significant at p<0.001. Equation (Eq).

Species	Treatments	Eq.1	Eq.2	Eq.3	n
<i>C. sativa</i>	18°C and 24h	0.916	0.960	0.982	17
	22°C and 24h	0.538	0.723	0.992	17
	26°C and 24h	0.660	0.790	0.963	18
	22°C and 1h	0.939	0.973	0.997	18
	22°C and 6h	0.882	0.937	0.976	19
<i>Q. pubescens</i>	18°C and 24h	0.843	0.903	0.979	19
	22°C and 24h	0.814	0.885	0.990	19
	26°C and 24h	0.675	0.791	0.989	18
	22°C and 1h	0.938	0.965	0.979	18
	22°C and 6h	0.833	0.896	0.983	19
<i>Q. ilex</i>	18°C and 24h	0.902	0.937	0.994	18
	22°C and 24h	0.813	0.902	0.995	19
	26°C and 24h	0.826	0.904	0.983	19
	22°C and 1h	0.887	0.938	0.998	19
	22°C and 6h	0.919	0.962	0.994	18
<i>P. halepensis</i>	18°C and 24h	0.823	0.872	0.988	19
	22°C and 24h	0.805	0.858	0.990	19
	26°C and 24h	0.852	0.918	0.989	18
	22°C and 1h	0.697	0.748	0.930	18
	22°C and 6h	0.681	0.736	0.968	19

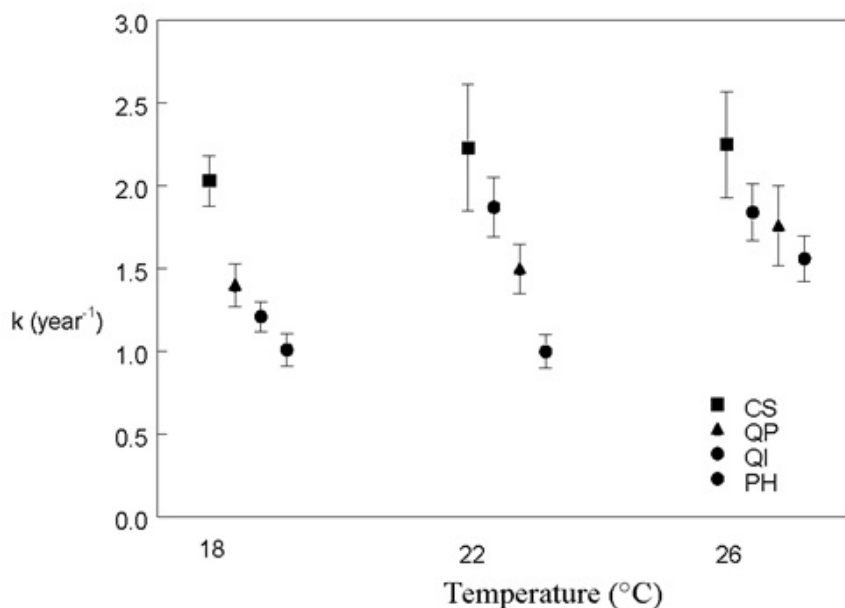


Fig. 1: Influence of temperature on litter decomposition rate (k) using comparison intervals by T¹-method. The k whose intervals do not overlap are significantly different.

CS: *Castanea sativa*, PH: *Pinus halepensis*, QI: *Quercus ilex* and QP: *Quercus pubescens*.

Table 2: Influence of temperature on litter mass loss during incubation. Results of one-way analysis of variance (temperature) at each sampling time (2, 4, 8 et 16 weeks) and for each species. A posteriori comparisons between means by Scheffer's test at p=0.05. Two different letters indicate that means obtained are significantly different. ():SE;

Factors	<i>C. sativa</i>	<i>Q. pubescens</i>	<i>Q. ilex</i>	<i>P. halepensis</i>
2 weeks				
18°C	11.31 (0.44)b	8.42 (0.37)b	8.32 (0.44)b	6.94 (0.10)b
22°C	14.85 (0.91)ab	10.10(0.40)ab	11.54(0.52)a	6.62 (0.32)b
26°C	15.78 (1.47)a	12.49 (1.31)a	11.15(0.24)a	9.74 (0.43)a
F	7.29*	6.21*	17.55***	30.04***
4 weeks				
18°C	16.71 (0.70)b	12.72 (0.86)c	11.30 (0.04)b	11.19 (0.43)b
22°C	24.02 (0.64)a	15.65 (0.30)b	18.60 (0.73)a	11.26 (0.43)b
26°C	22.87 (1.35)a	19.47 (0.54)a	18.62 (1.10)a	14.35 (0.83)a
F	9.50*	40.58***	22.09***	10.36**
8 weeks				
18°C	26.16 (1.33)a	22.97 (0.85)b	18.04 (0.22)b	16.35 (0.99)b
22°C	32.90 (0.36)a	22.45 (1.27)b	27.37 (0.43)a	16.79 (0.45)b
26°C	29.23 (1.16)a	28.31 (0.85)a	26.05 (1.69)a	22.94 (0.40)a
F	0.88ns	30.29***	24.73***	8.97**
16 weeks				
18°C	43.27 (1.91)a	30.50(1.66)b	29.17(1.05)b	23.84 (0.25)b
22°C	38.83 (0.98)a	33.30(0.27)ab	39.20(0.51)a	23.42 (0.69)b
26°C	44.24 (2.6)a	35.85(0.52)a	39.42(0.49)a	34.18 (1.14)a
F	0.29ns	23.04***	64.20***	6.27*

ns: not significant; * p<0.05; ** p<0.01 and *** p<0.001.

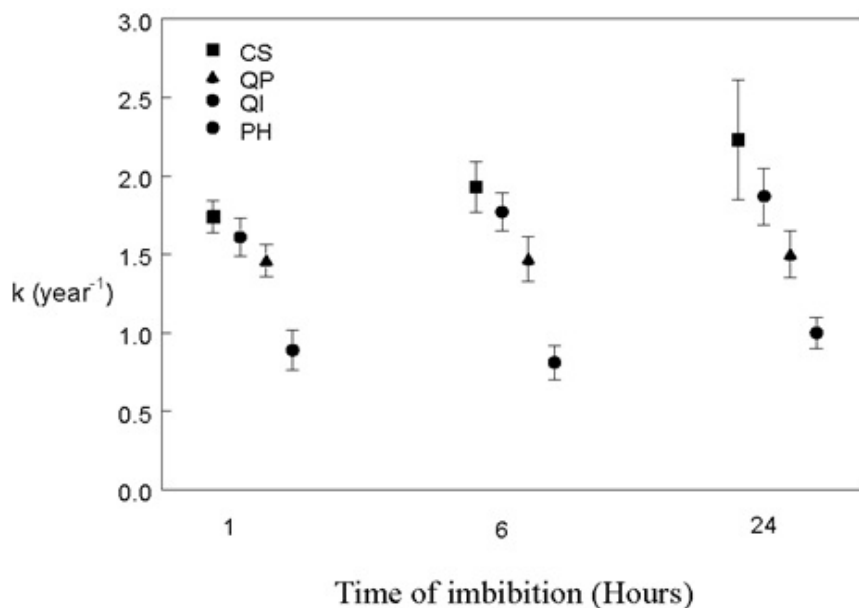


Fig. 2: Influence of initial water imbibition on litter decomposition rate (k) using comparison intervals by T'-method. The k whose intervals do not overlap are significantly different.

Table 3: Influence of initial water imbibition on litter mass loss during incubation. Results of one-way analysis of variance (initial water imbibition) at each sampling time (2, 4, 8 et 16 weeks) and for each species. A posteriori comparisons between means by Scheffer's test at p=0.05. Two different letters indicate that means obtained are significantly different. ():SE.

Factors	<i>C. sativa</i>	<i>Q. pubescens</i>	<i>Q. ilex</i>	<i>P. halepensis</i>
		2 weeks		
1h	10.50 (1.01)b	8.37 (0.86)	9.66 (0.21)	6.67 (0.36)
6h	10.22 (1.61)ab	9.16 (0.89)	10.30 (0.56)	7.23 (0.68)
24h	14.85 (0.91)a	10.10 (0.40)	11.54 (0.52)	6.62 (0.32)
F	7.23*	1.74ns	4.31ns	0.49ns
		4 weeks		
1h	13.52 (0.13)b	11.45 (0.28)b	14.99 (0.35)b	10.79 (1.56)
6h	18.25 (1.65)ab	15.69 (0.88)a	15.81 (0.38)b	9.76 (0.66)
24h	24.02 (0.64)a	15.65 (0.30)a	18.60 (0.73)a	11.26 (0.43)
F	11.92***	6.54*	13.18**	0.85ns
		8 weeks		
1h	23.59 (0.15)c	20.39 (1.07)	23.03(0.21)b	15.79 (1.50)
6h	25.60 (1.16)b	20.85 (1.23)	23.67(0.67)b	13.73 (0.28)
24h	32.90 (0.36)a	22.45 (1.27)	27.37(0.43)a	16.79 (0.45)
F	26.31***	0.71ns	31.28***	2.89ns
		16 weeks		
1h	40.17 (0.42)	34.83 (0.92)	36.49 (1.85)	20.63 (1.42)
6h	42.36 (1.11)	33.08 (0.69)	40.06 (0.87)	19.10 (0.96)
24h	38.83 (0.98)	33.30 (0.27)	39.20 (0.51)	23.42 (0.69)
F	0.39ns	1.96ns	2.36ns	4.04

ns: not significant; * p<0.05; ** p<0.01 and *** p<0.001.

The effect of temperature differed according to species. The decomposition rate of the two species which were strictly Mediterranean (*P. halepensis* and *Q. ilex*) was markedly influenced by temperature. Litter mass loss was significantly different at each sampling time and the decomposition rate increased significantly with increase of temperature. For the *Q. ilex* litter, an increase in rate of decomposition occurred between 18°C and 22°C, in contrast to *P. halepensis*, where this increase occurred between 22°C and 26°C. For *Q. Pubescens* the decomposition rate was only slightly influenced by temperature, but at each sampling time. For *C. sativa* (the least Mediterranean type) decomposition rate increased with increase in temperature only during the first four weeks of the experiment.

In general, studies carried out in the laboratory as well as in the field, showed that litter decomposition was faster at higher temperature. Thus Mikola^[24] compared the natural decomposition rate of different litter types at 4 latitudes and found that the decomposition rate increased with the mean temperature in summer. Carreiro & Koske^[25] determined the influence of temperature on the decomposition rate of

incubating deciduous leaf litter of oak (*Quercus spp*), red maple (*Acer rubrum*), sassafras (*Sassafras albidum*) and cinnamon fern (*Osmunda cinnamomea*) in microcosms placed at 0°C, 10°C and 20°C. Litter mass loss, after 90 weeks, was respectively 13.5, 19.0 and 30.7%. In the same way, Taylor & Parkinson^[20] found that temperature was an important variable for litter decomposition.

Other studies showed that the influence of temperature varied with incubation time. Thus Waksman & Gerretsen^[26] studied decomposition of oat straw at temperatures varying from 7°C to 37°C. They found that the decomposition rate increased with temperature during the first 16 days and that this influence was negligible after 105 days. Our results confirm theirs only for *C. sativa*, since the decomposition of the litter of this species was influenced by temperature only during the first 4 weeks of incubation. On the other hand, there is a discrepancy between their results and ours concerning the three other litter types, *P. halepensis*, *Q. ilex* and *Q. pubescens*.

Taylor & Parkinson^[12] observed that aspen leaves litter decomposed faster than pine needles under

favorable temperature and moisture condition. Conversely, when conditions were unfavorable (drought and coldness), pine litter decomposed faster than that of aspen. These authors suggested that these differences could be attributed to physical and chemical nature of litter, since these two species differed in anatomical features. In our experiments, broad-leaf litter decomposed faster than pine needle litter, in the favourable conditions of our microcosms. We even observed that differences between species changed with changes in temperature. Thus, at 18°C of incubation, the litter decomposition rate of *Q. pubescens* was greater than that of *Q. ilex*, whereas we observed the opposite at 22°C.

Litter decomposition of both strictly mediterranean species (*Q. ilex* and *P. halepensis*) increased with high temperature (from 18°C to 26°C), whereas that of *C. sativa*, having a wide geographical distribution did not. Litter decomposition of *Q. pubescens*, a species having an intermediate geographical distribution, was progressively influenced by temperature.

Influence of Initial Imbibition on Litter Decomposition: Litter mass loss could not be more influenced by initial water imbibition in the course of incubation. For pine litter, no significant effect of initial water imbibition on mass loss was observed. For 3 other species this influence was low and lasted only one month (*Q. pubescens*) or 2 months (*C. Sativa* and *Q. ilex*). At the end of 4 months of incubation, we could not observe any influence of initial water imbibition on litter mass loss. To observe a marked effect of initial water imbibition during 16 weeks of incubation, it was probably necessary to maintain difference of water content of litter throughout the duration of incubation.

Interaction between temperature and moisture was not studied in this experiment, but Taylor & Parkinson^[20] found that temperature was a more important factor than moisture. In tropical^[3] or boreal^[27] forests, litter decomposition does not so much depend on moisture since water is always available. On the other hand, in semi-arid countries^[28], moisture plays a major role, because it limits biological activity. Van Cleve & Sprague^[29] estimated that factors, such as temperature and moisture, are intimately related in the field and that we cannot separate their influence.

Comparisons Between Species and Conclusion: Initial water imbibition has a sudden effect on the water content of leaf litter. It influences temporary or not at all the decomposition rate of the 4 studied species. On the other hand, litter decomposition was influenced by temperature, but this influence differed markedly among these 4 species.

Litter of *C. sativa* differed greatly from the 3 others species. Its decomposition was not affected by increase in temperature from 18°C to 26°C and remained the fastest at whatever temperature. This tree species, which can be found in mesic climate, may have lower temperature thresholds for decomposition than the other species studied. Experiments carried out at temperatures lower than 18°C would have perhaps shown other features. *Q. ilex* and *P. halepensis* are strictly mediterranean species. Decomposition of their litter was more sensitive to increased temperature. The temperature threshold from which the effect is significant ranged between 18°C and 22°C for *Q. ilex* and between 22°C and 26°C for *P. halepensis*. *Q. pubescens* has an intermediate position. Its area of distribution is wider than that of strictly mediterranean species, but less than that of *C. Sativa*. In Mediterranean regions, it is found on cool mountain sides, whereas *Q. ilex* occupies warmer and dryer mountain sides. Litter decomposition of *Q. pubescens* was progressively favoured by temperature increase from 18°C to 26°C. We could observe that at the lowest temperature studied (18°C), the litter decomposition rate of *Q. pubescens* was greater than that of *Q. ilex*. Nevertheless, at 22°C, *Q. ilex* had a greater decomposition rate. This could indicate that optimum temperature for decomposition of *Q. pubescens* leaf litter is lower than *Q. ilex*, which would correspond to their differences in distribution on the field.

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