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Title: COMPARATIVE LEAF DECOMPOSITION WITHIN THE HOLM OAK COMPLEX

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COMPARATIVE LEAF DECOMPOSITION WITHIN THE HOLM OAK COMPLEX

DECOMPOSITION COMPARATIVE DES FEUILLES AU SEIN DU COMPLEXE CHENE VERT

SADAKA-LAULAN N., and PONGE J.F.

Abstract: The decomposition of holm oak leaves was compared using material embracing the genetical range of the holm oak complex. Collection sites were located in Morocco (*Quercus rotundifolia*), in the French Provence (*Q. ilex*), and in the French Languedocian Coast (*Q. ilex* x *rotundifolia*). Leaves (living and senescent) were taken directly on the tree and in the litter at five decomposition stages. The areal weight was used to follow the loss in weight of leaves in the course of their senescence then of their decomposition, in order to overcome limitations of the litterbag method. Leaves of *Quercus rotundifolia* had a higher areal weight in their living stage but they lost more weight in the course of decomposition than leaves of *Q. ilex*. Leaves from hybrid populations had an intermediary behaviour. All three populations of leaves exhibited an increase in weight during senescence. At the white-rot stage (stage V), leaves of every origin reached a similar areal weight. Reasons for the observed resemblances and discrepancies have been discussed to the light of existing knowledge. Our results give additional strength to the separation of *Q. ilex* and *Q. rotundifolia* as two distinct species, with possible introgression and hybridization in contact zones.

Key words : *Quercus ilex*/ *Quercus rotundifolia*/ *Q. ilex* x *rotundifolia*/ leaf areal weight/ litter/ decomposition.

Résumé: L'étude comparée de la décomposition des feuilles de chêne vert a été réalisée sur du matériel provenant du complexe "chêne vert. Les sites d'étude sont localisés au Maroc pour *Quercus rotundifolia* et en France, d'une part en Provence pour *Q. ilex*, et d'autre part au Languedoc pour *Q. ilex x rotundifolia*. Le poids surfacique a été utilisé pour suivre la perte pondérale des feuilles aussi bien au cours de leur sénescence qu'au cours de leur décomposition, dans le but de surmonter les limites de la méthode des sacs de litière. Les feuilles vivantes de *Q. rotundifolia*, bien qu'ayant un poids surfacique plus élevé que celui de *Q. ilex*, perdent plus de poids au cours de la décomposition. Les feuilles issues des populations hybrides occupent une position intermédiaire. Au stade V (feuilles blanchies) les feuilles des trois provenances atteignent le même poids surfacique. Les similitudes et les différences observées sont discutées à la lumière des connaissances existantes. Nos résultats apportent un élément supplémentaire à la distinction des deux espèces, *Q. ilex* et *Q. rotundifolia*, avec un génotype intermédiaire provenant d'une zone d'introgession et d'hybridation entre les deux taxons.

Mots clés : *Quercus ilex*/ *Quercus rotundifolia*/ *Q. ilex x rotundifolia*/ poids surfacique/ litière/ décomposition.

1. INTRODUCTION

Holm oak is an evergreen Mediterranean oak species known for the complexity of its taxonomic status, due to high genetical and ecological plasticity [2, 3, 13, 21, 27, 35]. Its variability has been studied at the scale of populations, of individuals, and even at the scale of a ramus [13].

Lamarck [10], followed by Schwartz [30], described two distinct species, namely *Quercus ilex* L. and *Q. rotundifolia* Lam. Differential anatomical features of *Q. ilex* are oblong, slender leaves, with few spines, and bitter acorns. Leaves of *Q. rotundifolia* are round-shaped, with numerous spines, its acorns are bigger and they have a soft taste. Saenz De Rivas [27, 28] states that these taxa should be considered only as sub-species, on the basis of statistical analysis of leaf hair and shape, thus reinforcing Morais [18] opinion. Conversely Saenz De Rivas [29] considers them as true distinct species, on the basis of pollen morphology. Madjidieh [13, 14] compared leaf anatomical features using both TEM and light microscopy and concluded them to be synonymous.

Ecological research added some interesting differential characters. Achhal et al. [1] observed that *Q. ilex* was much less climate tolerant than *Q. rotundifolia*. In Morocco, *Q. ilex* is limited to mild, moist places under Mediterranean climate, while *Q. rotundifolia* tolerates colder, dryer climate conditions. This may partly explain differences in their geographical distribution, *Q. rotundifolia* being common in western Mediterranean countries (Morocco, Algeria, Tunisia, Central Spain), mostly in mountains, while *Q. ilex* is restricted to a coastal fringe, and remains alone in eastern Mediterranean countries. There exists a wide overlapping zone in the South of France, mostly along the Languedocian Coast where both taxa live in mixed populations [3].

Recognition of nearby species only on the basis of morphological, phenological and ecological features is not very easy, being often disputed. This encouraged scientists to select other, more ecologically stable criteria, such as enzymes [2, 17] and plant secondary metabolites [21], which enabled to separate definitely *Q. rotundifolia* from *Q.*

ilex. Nevertheless hybridization between these two species still occurs, as along the Languedocian Coast [3, 17, 35].

Our contribution to this still debated question has been to follow the decomposition of their leaves in field conditions, comparing true *Q. ilex* and *Q. rotundifolia* with individuals living in mixed populations. Rather than using litterbags, which are known to largely influence the decomposer activity [31], we preferred to compare still attached leaves and fallen leaves belonging to five stages of decomposition, by measuring changes in their leaf areal weight [26]. A previous study dealt with *Q. ilex* [26]. In the present study a comparison was made with new data concerning *Q. rotundifolia* from Morocco and *Q. ilex* x *rotundifolia* from the Languedocian Coast.

2. METHODS

2.1. Sites

Leaf collection was done in June 1998, at the time of the optimum litter fall [11]. Sites were located in Morocco (Toufliht, northern slope of Higher Atlas) and France (Gardiole de Rians, Provence, and Montpellier, Languedoc). *Table I* indicates main environmental conditions prevailing at the collection sites.

2.2. Material

Leaves were collected directly on the tree and in litter horizons. Still attached leaves were separated into living (green) and senescent (yellow) leaves, notwithstanding their age. The mean duration of life of holm oak leaves (Languedocian Coast) has been estimated as two years, but leaf fall may occur during their 1st as well as during their 3rd year of life [25]. Leaves from litter horizons were divided into 5 stages of decomposition according to morphological criteria (*table II*). We studied 200 leaves for each of the seven stages and for each species, only means and standard errors being presented here.

2.3. Measurements

Leaves were washed then brushed in order to remove adhering mineral particles. The distal part of leaf blades was stamped once with a 6 mm diameter copper punch, avoiding the main nerve. Leaf disks were oven-dried at 105°C during 48 h, then weighed. The individual mass of leaf disks was used to derive the leaf areal weight (mg.cm^{-2}), i.e. the weight per unit surface of leaf (one side only being accounted for).

3. RESULTS

Two phases can be distinguished in the comparable patterns of aerial weight changes of *Q. ilex*, *Q. rotundifolia* and hybrid holm oak leaves (*figure 1*). There is an increase in the leaf areal weight from living to stage I leaves (12%, 9%, and 14% for *Q. ilex*, *Q. rotundifolia* and hybrid, respectively), followed by a decrease until stage IV (19%, 37%, and 28% for *Q. ilex*, *Q. rotundifolia* and hybrid, respectively). The weight of senescent leaves (not measured in *Q. ilex*) does not greatly differ from that of stage I leaves. Stage V was collected only for *Q. rotundifolia* and hybrid holm oak. From stage IV to stage V leaves still lose weight (43% and 25 % for *Q. rotundifolia* and hybrid, respectively).

The three studied populations greatly differ in their leaf area weight. Living leaves of *Q. rotundifolia* are heavier ($15.98 \pm 0.21 \text{ mg.cm}^{-2}$), than those of *Q. ilex* ($9.57 \pm 0.15 \text{ mg.cm}^{-2}$), hybrid individuals being intermediary ($12.63 \pm 0.14 \text{ mg.cm}^{-2}$). They differ also in their decomposition dynamics. The weight loss rate from living leaves to stage IV is 10%, 31%, and 19% for *Q. ilex*, *Q. rotundifolia*, and hybrid, respectively. If stage V is included in our calculations the weight loss rate reaches 61% and 39% for *Q. rotundifolia* and hybrid holm oak, respectively. It can be pointed out that, despite strong differences in leaf areal weight between the three studied populations, areal weight values converge towards 7 mg.cm^{-2} at stage V. This value seems convenient for *Q. ilex*, too, suppose we lengthen its decomposition curve (*figure 1*).

4. DISCUSSION

The increase in weight observed from living to senescent leaves could have been attributed to the sampling procedure used. The collection of living leaves included 1st to 3rd yr or even still older leaves, thus leaves which are far from fall (too young) as well as leaves prone to senesce then fall within a few months. In fact, as this has been demonstrated by Sadaka [26], holm oak (*Q. ilex*) leaves lose areal weight during their development. Thus the observed increase in weight from living to senescent leaves has been probably underestimated and cannot be explained by a sampling bias. Rather it is hypothesized that tannins, which oak leaves have accumulated during their entire life [24, 26], will become totally or partly oxidized during the senescence of foliage [8], which will increase the areal weight of leaves before they fall.

Although climate conditions do not differ markedly between the three study sites (*table 1*), strong differences have been registered in the decomposition curves of members of the holm oak complex (*figure 1*). Several reasons could be invoked to explain this phenomenon. The decomposition of leaf litter is controlled, not only by physical factors such as temperature and moisture, which may act upon decomposer communities [15], but also by litter quality, defined by its C:N ratio [33], its lignin and tannin content [6, 7, 16, 19], as well as its content in nutrients such as N, Ca and P [7, 16, 32]. In addition, the toughness of leaves may affect their decomposition rate [9], and this should be considered when trying to explain the observed differences. Living leaves of *Q. rotundifolia* are slightly thicker in average than those of hybrid individuals. This could be explained by drier summer conditions in Toufliht (Morocco), where the period without rain exceeds that in Montpellier (France) by several months. The xerophytic character of *Q. rotundifolia* may be related to this difference in blade thickness.

Despite a higher initial areal weight, leaves of *Q. rotundifolia* decay at a higher rate than that of *Q. ilex*, reaching a similar areal weight at stages IV and V (*figure 1*). This could be explained by more total precipitation in Toufliht, mostly distributed from October to February, which could be favourable for decomposer activity (microbes,

fauna) in winter periods, directly and by increasing the leaching of distasteful or toxic substances [20, 22].

It is considered that differences in leaf areal weight between French (Provence) and Morocco populations allow the consideration of *Q. ilex* and *Q. rotundifolia* as two distinct species. Languedocian populations are living in a zone of hybridization and introgression between these two species.

The advantage of the method used for measuring litter decomposition, compared to the widely used litterbag method [4, 5], lies on the absence of perturbation of the decaying material. Nothing else than weighing different leaf categories collected once is necessary for assessing differences in decomposing ability between plant species and/or between sites. In addition, the exclusion of macrofauna from small-mesh nets prevents results from litterbag studies to be used when comparing sites of varying quality [23]. Witkamp & Olson [34] found two to three times more loss in weight in unconfined compared to confined litter. St John [31] observed that the number of fungal propagules colonizing the confined substrate was lower than when the substrate was unconfined. Microclimate conditions may be also strongly affected by the confinement of litter, for instance litterbags increase the moisture content of leaves [12]. All these shortcomings argue for the abandonment of the use of litterbags, more especially for decomposition studies in Mediterranean countries where i) macroinvertebrates are abundant, ii) decomposition is mainly limited by dryness of the litter during summer months.

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Table I. Main ecological conditions in the three collection sites.

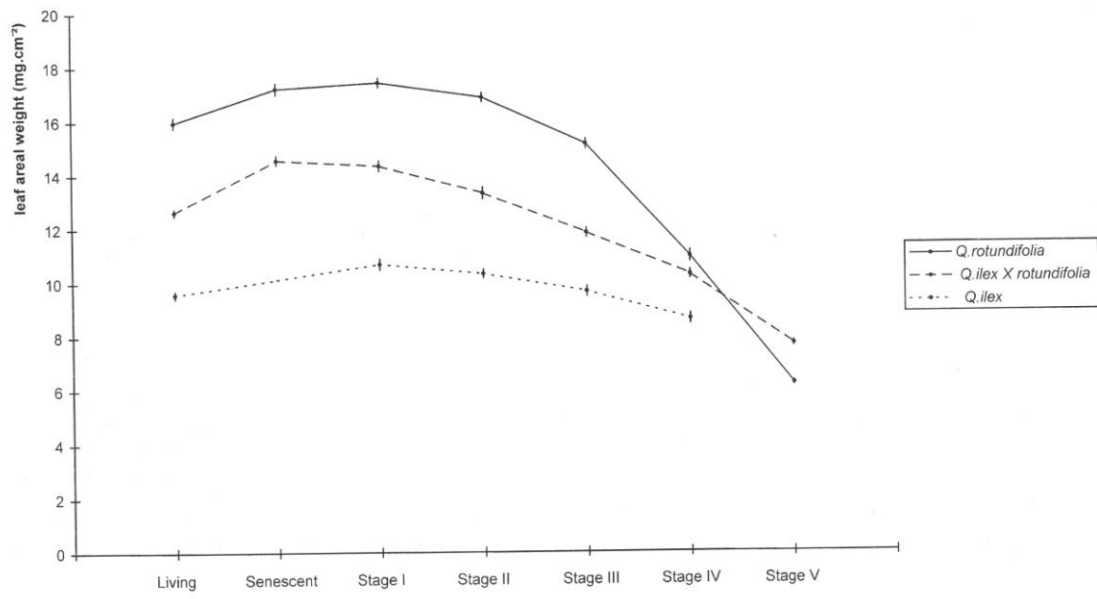
	Q. rotundifolia Toufliht, Morocco	Q. ilex Gardiole de Rians, France (Sadaka, 1986)	<i>Q. ilex</i> x <i>rotundifolia</i> Montpellier, France
Altitude (m)	1540	620	56
Aspect	N-NE	NE	S
Mean annual rainfall (mm)	840	747	793
Relief	Very rough	Rough	Level
Substrate	Sandstone and clay	Compact limestone	Clay
pH	5,7	6,7	7,3
Vegetation	Dense forest	Dense forest	Clump of trees
Bioclimate	Subhumid to semiarid	Humid to subhumid	Humid to subhumid

Table II. Morphological features of the five decomposition stages for holm oak leaf litter.

Stage I	Yellow, externally intact, thick, hard, lower side densely covered with green hairs
Stage II	Yellow, slightly decayed but still thick and hard, hairs cover on the lower side invaded by fungi
Stage III	Brown, thin, soft, decayed, a few hairs still present
Stage IV	Brown, thin, very soft, strongly decayed but still recognizable, no hair present
Stage V	Bleached, very thin, brittle and more or less aggregated by fungal mycelium

Legend of figure

Fig. 1. Leaf areal weight (mean \pm standard error) of holm oak leaves at varying senescence and decomposition stages



1
2 Fig. 1