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Original article

Seed germination of *Quercus robur, Q. pyrenaica* and *Q. ilex* and the effects of smoke, heat, ash and charcoal

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Abstract – This study is centred on *Quercus robur*, *Q. pyrenaica* and *Q. ilex* that have a distribution area covering all Europe. Fire is a frequent ecological factor in many ecosystems, especially in those with Mediterranean climates. Our working hypothesis is that fire affects the germination process. An experiment was carried out testing the following treatments: Control, Smoke–5 min, Smoke-10min, Smoke–15 min, 60 ºC–5 min, 60 °C–15 min, 90 ºC–5 min, 110 ºC–5 min, 150 ºC–5 min, Ash, Ash Dilution and Charcoal. The seed incubation was spread over a year. The germination rates of the Control are very high, especially in *Q. ilex.* Almost none of the treatments inhibit germination and only the *Q. ilex* seeds, when subjected to 150 ºC–5 min, show a marked inhibition. *Q. robur* and *Q. pyrenaica* take a year to complete their germination, while *Q. ilex* only takes 22 weeks. Probably, this reproductive behaviour is related to the climate characteristics to which the species have become adapted. Finally, fire does not determine the germination process, the recruitment of new individuals being independent of fire.

Quercus **/ germination / fire / reproductive strategies / seeds**

Résumé – Germination de *Quercus robur*, *Q. pyrenaica* et *Q. ilex* et effets de la fumée, de la chaleur, des cendres et des charbons. Cette étude est axée sur : *Quercus robur*, *Q. pyrenaica* et *Q. ilex*, espèces qui sont représentées dans l'ensemble de l'Europe. Le feu est un facteur écologique fréquent dans de nombreux écosystèmes, spécialement ceux bénéficiant d'un climat méditerranéen. Notre présupposé est que le feu affecte le processus de germination. Nous avons réalisé une expérience destinée à tester les traitements suivants : témoin, fumée –5 min, fumée –10 min, fumée –15 min, 60º C–5 min, 60 ºC–15 min, 90 ºC–5 min, 110 ºC–5 min, 150 ºC–5 min, cendres, dilution de cendres et charbons. L'incubation des semences s'est étendue sur une année. Les taux de germination du traitement témoin sont très élevés, particulièrement en ce qui concerne *Q. ilex*. Presque aucun traitement n'inhibe la germination ; seules les semences de *Q. ilex* manifestent une inhibition marquée lorsqu'elles sont soumises à 150 ºC–5 min. Une année est nécessaire pour que les semences de *Q. robur* et *Q. pyrenaica* complètent leur germination, alors que 22 semaines suffisent au *Q. ilex*. Il est probable que ce comportement reproductif se trouve lié aux caractéristiques climatiques auxquelles ces espèces se sont adaptées. En définitive, le feu n'est pas déterminant dans le processus de germination, l'apparition de nouveaux individus étant indépendante de ce phénomène.

Quercus **/ germination / feu / stratégies de reproduction / graines**

1. INTRODUCTION

The genus *Quercus* is one of the most widely distributed throughout the world, fundamentally in the Northern Hemisphere. We have centred this paper on the study of *Quercus robur*, *Quercus pyrenaica* and *Quercus ilex* subspecies *ballota*. The area of distribution of these three species covers all of Europe and from an economic and cultural point of view they are very important species.

According to [8] and [9] *Q. robur* is a species that can be found forming extensive natural forests from the North of Norway (64º N) to the South of Sicily (37º N) and from Ireland to the Balkans, Urals and Caucasus. *Q. pyrenaica* is a Mediterranean species with a reduced area of natural growth, extending through the South of France, Iberian Peninsula, NW of Morocco and has also been cited in the North of Italy. The species *Q. ilex* subspecies *ballota*, also known as *Quercus rotundifolia* will, from now on, be referred to as *Q. ilex* [8]. The populations of *Q. ilex* are a dominant component of many sclerophyllous forests that at one time dominated vast areas of the Mediterranean region. The geographic distribution of this species is centred on the Mediterranean Basin [8].

In Europe, and above all in the Mediterranean region, fire is an ecological factor that has been present in the terrestrial ecosystems for thousands of years [30, 51] and to which an important influence in the evolutionary process of the vegetal species living there is normally attributed [28, 52]. Today, wildfire continues to be frequent in this area and for this reason knowledge of the germinative behaviour of these species in relation to fire is of interest. The most important fire agents are heat, smoke, ash and charcoal. There are many studies that analyse the effect of heat on the germination of different arboreal [20, 39, 40],

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shrub [15, 18, 45, 46, 53] and herbaceous species [11, 15, 18, 20, 22]. There are some studies that analyse the effect of ash, charcoal or smoke [4, 5, 15, 23, 29, 36] and there is a vast ignorance of the germinative behaviour after fire of *Quercus*.

Our hypothesis is that the fire acts on seed germination process and for this reason we have centred this investigation on the study of the germinative response of *Q. robur, Q. pyrenaica* and *Q. ilex* to the principal fire agents: smoke, heat, ash and charcoal.

2. MATERIALS AND METHODS

The biological material used for this study were acorns from *Q. robur* harvested on the outskirts of Santiago de Compostela (42º 52', 7º 58', province of A Coruña), from *Q. pyrenaica* harvested on the outskirts of Sanabria (42º 04', 6º 52', province of Zamora) and from *Q. ilex* harvested in Ricobayo (41º 63', 5º 73', province of Zamora). The mature acorns were collected either directly from the mother tree or from the ground. The type of soil on which the population of *Q. robur* is established is an acid Cambisol soil formed from acid metamorphic rocks (Prieto, pers. comm.). The climate is humid Atlantic, with an average annual rainfall of 1 886 mm. The driest months are July and August, with an average monthly rainfall of 39 and 57 mm, respectively (National Institute of Meteorology, 2001, [19]). The soil over which the population of *Q. pyrenaica* has developed is an acid Ranker soil on granite bedrock [14]. The climate in this zone is Mediterranean, with an average annual rainfall of 1000 mm and, during the summer, an average rainfall of 100 mm [12]. In the *Q. ilex* population, the soil is basic Luvisol close to neutrality [13, 14]. The average annual rainfall is 363 mm and a steep descent is produced in summer, as between the months of July to September it only rains 50 mm [12].

The seeds were held at a temperature of 4 ºC from harvesting until the beginning of the experiment. The treatments applied were Control, 60 ºC–5 min, 60 ºC–15 min, 90 ºC–5 min, 110 ºC–5 min 150 ºC–5 min, Ash, Ash Dilution, Charcoal, Smoke–5 min, Smoke–10 min and Smoke–15 min [15, 18, 20, 45, 53, 55]. The Heat treatments were applied by introducing the seeds into a forced-air stove for the fixed time indicated. In the Dilution of Ash treatment, 120 mL of a solution of ash in distilled water (at 5 g/L) was added to the seeds. The Ash treatment was performed by adding 0.168 g of ash to each of the incubation trays. This amount of ash was selected after taking into account the surface area of the trays and that Soto et al. [41] registered 8 g of ash/m^2 in a real wildfire, as well as other studies on the effect of ash carried out by the authors [36, 38]. The Charcoal treatment was performed by incubating the seeds of each tray in the presence of 1 g of fragmented charcoal. The Smoke treatments were obtained by exposing the seeds during 5, 10 or 15 min to an atmosphere saturated with smoke. The ash, charcoal and smoke used in these treatments were obtained from the combustion of thin branches from individuals of each species and each of the species was treated only with its own ash, charcoal and smoke. The methodology followed for applying the smoke treatments was that of Casal et al. [7] based on De Lange and Boucher [10] and Baxter et al. [2]. The seeds were incubated in plastic trays with a surface area of 210 cm^2, adding perlite to favour humidification. Six replicas of 25 seeds each were used for each treatment. Throughout the experimental period the seeds were maintained in total darkness, to simulate conditions underground, and were only illuminated with a tenuous green light (25 W) during recounting.

After this period of 22 weeks some of the treatments of *Q. robur* and *Q. pyrenaica* continued in incubation until a full year was completed. It was noticeable that in *Q. ilex*, after 22 weeks of incubation, almost all of the acorns sown had germinated and most of the rest showed clear symptoms of rot. The treatments in which incubation of

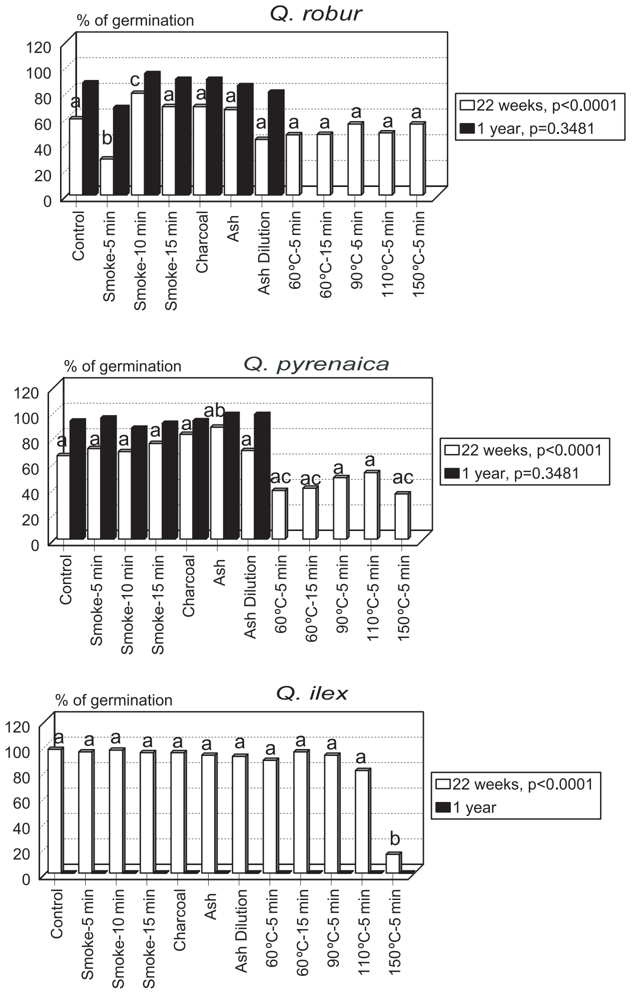

Figure 1. Germination rates reached by *Q. robur*, *Q. pyrenaica* and *Q. ilex* at 22 weeks and after one year of incubation. In each incubation time, the treatments which displayed significant differences have different letters.

the acorns was continued until the end of the full year were the following: Control, Smoke–5 min, Smoke–10 min, Smoke–15 min, Charcoal, Ash and Ash Dilution. At the end of the year, the germination rate and resulting T_{50} was calculated and the data on the temporal distribution of germination was completed.

Both the data on germination rates and T_{50} data (the time required to reach 50% of germination) were analysed using Analysis of Variance to check whether there are significant differences between treatments. In those cases in which significant differences were detected an LSD Test a posteriori was applied to detect the treatments responsible for these differences.

3. RESULTS

3.1. Germination rates at 22 weeks of incubation

The germination rates of these three species are notably different (Fig. 1). *Q. robur* usually shows the lowest germination rates in all the treatments carried out and *Q. ilex* is the species that usually shows the highest rates, with *Q. pyrenaica* in an intermediate position.

Q. robur reaches 59.2% of germination in the Control treatment. In this species, with treatments of Smoke–5 min, Ash Dilution, 60 ºC–5 min, 60 ºC–15 min and 110 ºC–5 min, much lower values than Control were observed, with Smoke–5 min having the lowest germination rate.

Q. pyrenaica showed a natural germination rate (value of Control) of 65.6%. On the contrary to what occurs in *Q. robur*, in *Q. pyrenaica* the treatments of Smoke, Ash Dilution, Ash and Charcoal show germination rates that are higher than those registered in the Control treatment. The highest rates correspond to Ash and Charcoal. The heat treatments are the ones that most inhibit germination. In this sense, the most important decrease is produced in the treatments of 150 ºC–5 min (35.5%), 60 ºC–5 min (38.2%) and 60 ºC–15 min (40.0%).

In general the germination rates obtained in *Q. ilex* are very high, close to 100%. In the Control treatment a germination rate of 97.33% was obtained and values of above 90% were obtained in the treatments of 60 ºC–15 min, 90 ºC–5 min, Charcoal, Ash, Ash Dilution, Smoke–5 min, Smoke–10 min and Smoke–15 min. There is another group of treatments with germination rates of between 80 and 90%. These are 60 ºC–5 min and 110 ºC–5 min. Finally, the treatment of 150 ºC–5 min obtained the lowest value with a germination rate of only 14.66%.

The ANOVA applied to the data of the three species analysed together detected significant interactions between the factors species and treatment ($p < 0.0001$). The ANOVA applied to the data of *Q. robur* revealed significant differences between the treatments ($p < 0.0001$) and the LSD Test found that these differences were due to the fact that the treatments of Smoke–5 min and Smoke–10 min differed significantly to Control.

When the ANOVA was applied to the data of *Q. pyrenaica* significant differences between the treatments were also detected ($p < 0.0001$). The LSD Test found that the treatment Ash differed significantly from 60 ºC–5 min, 60 ºC–15 min and from 150 ºC–5 min. In this species the Control is not significantly different from any of the fire treatments.

The ANOVA applied to *Q. ilex* showed highly significant differences between the treatments ($p < 0.0001$) and the LSD test determined that these differences are due to the fact that the treatment of 150 ºC–5 min is different from all the others. The differences that were observed between treatments that had germination rates above 90% and those with germination rates above 80% are not significant. Only in the heat treatments and only when very high temperatures are applied, is germination of the seeds of *Q. ilex* significantly affected, in this case by inhibition.

3.2. Germination rates at the end of a year of incubation

The germination rates of *Q. robur* and *Q. pyrenaica* after a year of incubation are very high: around 85% in *Q. robur* and at 93% in *Q. pyrenaica* (Fig. 1).

Q. robur shows a natural germination rate of 87.2%. The treatments in which the highest values were registered were Smoke–10 min, Smoke–15 min and Charcoal, obtaining rates of between 90 and 94%. The rest of the treatments (Smoke–5 min, Ash and Dilution) showed lower values than Control of between 68 and 85%.

After one year of incubation the natural germination rate of *Q. pyrenaica* increased to 92.8%, which was excelled by the treatments of Smoke–5 min, Ash and Ash Dilution, with rates of between 95 and 98%. Smoke–10 min was the treatment with the lowest value (87.2%).

The ANOVA applied to the germination data after one year of incubation confirmed the existence of significant differences between *Q. robur* and *Q. pyrenaica* ($p = 0.0012$) and that there were no differences between the treatments ($p = 0.3481$).

The values obtained at the end of a year represent a considerable increase with respect to the values corresponding to 22 weeks of incubation. The final values are very close to those shown by *Q. ilex* at 22 weeks (Fig. 1), above all those of *Q. pyrenaica*. The increase is greater in *Q. robur*, were in one of the treatments an increase of 40% was registered, against a maximum of 28% in *Q. pyrenaica*.

Comparing the germination values of *Q. robur* at the end of a year with those registered at 22 weeks, it can be seen that Control considerably increases its germination, from 59% to 87.2%. The treatments that show the highest increase are Smoke–5 min, with an increase of 40% and Ash Dilution, with an increase of 36.8%. In the rest of the treatments the increase is not as great, but is still important, being close to 20%.

On making the same comparison in *Q. pyrenaica* it can be seen that the treatments in which the germination rate increases most are Ash Dilution (increase of 28%), Control (increase of 27%) and Smoke–5 min (increase of 24%). In the treatments Smoke–10 min and Smoke–15 min the increases are more moderate, 18.4 and 16%, respectively. Finally, with the other two treatments, the germination rate increases by 10%.

The results obtained for each species at 22 weeks and at the end of one year were compared and no significant differences were detected between the germination rates of *Q. robur*, but were detected between those of *Q. pyrenaica* ($p < 0.0001$).

3.3. T_{50} at 22 weeks

The three species of *Quercus* show average T_{50} values that are relatively close to each other. *Q. robur* is the species that is most delayed with 9.8 weeks, followed by *Q. pyrenaica* with 8.4 weeks and *Q. ilex* with 6.6 weeks (Fig. 2).

In *Q. robur*, the T_{50} value corresponding to Control is 11.2 weeks. This value is only exceeded by the treatment Ash Dilution with 13.6 weeks. The rest of the treatments advance germination, the most notable being Smoke–5 min, 110 ºC–5 min and 150 ºC–5 min (3 weeks earlier).

Under natural conditions, *Q. pyrenaica* is the species that has the most rapid germination. The T_{50} value of the treatment Control (7.8 weeks) is the lowest obtained in the three species. In *Q. pyrenaica*, the treatments of Smoke–5 min, Smoke–10 min, Smoke–15 min, Charcoal and Ash Dilution reduce the T_{50} value even more, although only by 1 or 2 weeks.

For its part, *Q. ilex*, with the Control treatment, shows a T_{50} value of 9.7 weeks, the highest registered in any of the treatments. The treatments that most advance germination in this species are Smoke–10 min and Smoke–15 min, reducing the T_{50} values to less than half.

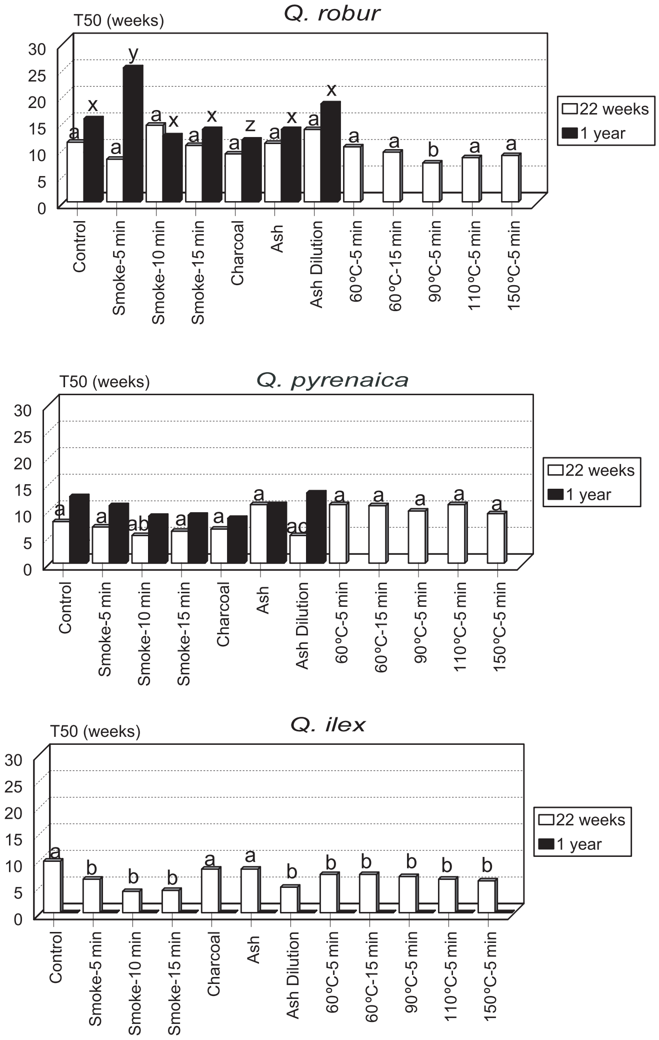

Figure 2. Average time required to reach 50% of germination with respect to total germination (T_{50}) at the 22th week and at the year of incubation corresponding to each of the treatments applied to *Q. robur*, *Q. pyrenaica* and *Q. ilex*. In each incubation time, the treatments which displayed significant differences have different letters.

The multivariant ANOVA applied to the T_{50} values of the 3 species detected a significant interaction between the factors species and treatment and the one-way ANOVAs applied to the data of each species detected significant differences between the treatments in all three species. In *Q. robur* the LSD test showed that only the treatment of 90 ºC–5 min was significantly different from the Control. In *Q. pyrenaica* none of the treatments were significantly different from the Control. The differences detected by the ANOVA are due to the differences found between Smoke–10 min and Ash Dilution. Lastly, in *Q. ilex*, the differences found are due to Control being different to all the treatments, excepting Charcoal and Ash.

3.4. T_{50} at the end of one year

The T_{50} values of the seeds reached after one year of incubation are found to be around 13 weeks (Fig. 2). *Q. robur* registered average T_{50} values of 15.8 weeks and *Q. pyrenaica* of 10.5 weeks. In *Q. robur* the T_{50} value reached in Control at the end of the year was 15.6 weeks. The treatments that produced the lowest values were, in increasing order, Charcoal, Smoke–10 min, Smoke–15 min and Ash. The rest of the treatments registered higher values than Control, above all Smoke–5 min with a T_{50} value of 25 weeks. For its part, in *Q. pyrenaica*, Control showed a T_{50} value of 12.5 weeks, a value that was only exceeded by the treatment Ash Dilution.

The ANOVA corresponding to the data of 1 year of incubation indicated the existence of significant differences between *Q. robur* and *Q. pyrenaica* ($p < 0.0001$); moreover, it also showed significant differences between treatments ($p < 0.01$). In *Q. robur* Smoke–5 min and charcoal treatments are significantly different from the other treatments ($p < 0.01$). In *Q. pyrenaica* significant differences were not detected among treatments ($p = 0.6385$).

Comparing the values obtained for both species at 22 weeks and at the end of a year, we can see that the greatest increases are produced in *Q. robur*. The treatment that produces the greatest increase is Smoke–5 min with 17 weeks difference, followed by Ash Dilution and Control with an increase of 4 weeks. In the rest of the treatments the respective increases are of 2 or 3 weeks.

In *Q. pyrenaica*, the treatment that most increases the T_{50} value is Ash Dilution with an increase of 8 weeks, followed by Control and Smoke–5 min with an increase of 4 weeks each. With respect to the value obtained in the first experiment, the treatments of Smoke–10 min and Smoke–5 min caused a delay of 3 weeks, Charcoal caused a delay of 2 weeks and Ash obtained exactly the same value.

The ANOVAs used to compare the data obtained for both species at the end of a year and at 22 weeks, detected significant differences both in *Q. robur* and in *Q. pyrenaica* ($p < 0.0001$ and $p < 0.001$ respectively).

3.5. Temporal distribution of germination over time

Broadly speaking, the temporal distribution of the germination of these three species of the genus *Quercus* is similar, despite the fact that *Q. ilex* completes its germination cycle in 22 weeks and the other two species can germinate during the whole year.

The temporal distribution of the germination of *Q. robur* is irregular and spread over time (Fig. 3). The control treatment shows a more or less uniform distribution of germination until the 41st week, after which germination is much reduced. This same behaviour is repeated in the treatments Smoke–5 min, Smoke–15 min and Ash Dilution. In the Charcoal treatment, germination is concentrated mainly during the first 13 weeks and there is almost no germination after the 41st week. In the Ash and Smoke–10 min treatments, the most important reduction of the peaks occurs after the 33rd week. In this species, the heat treatments show a more concentrated distribution of germination, presenting the more important peaks between the 5th and 17th week of the experiment.

The temporal distribution pattern of germination of *Q. pyrenaica* is very similar to that of *Q. robur* (Fig. 3). Control, Smoke, Charcoal, Ash and Ash Dilution treatments all coincide in showing the most important peaks of germination

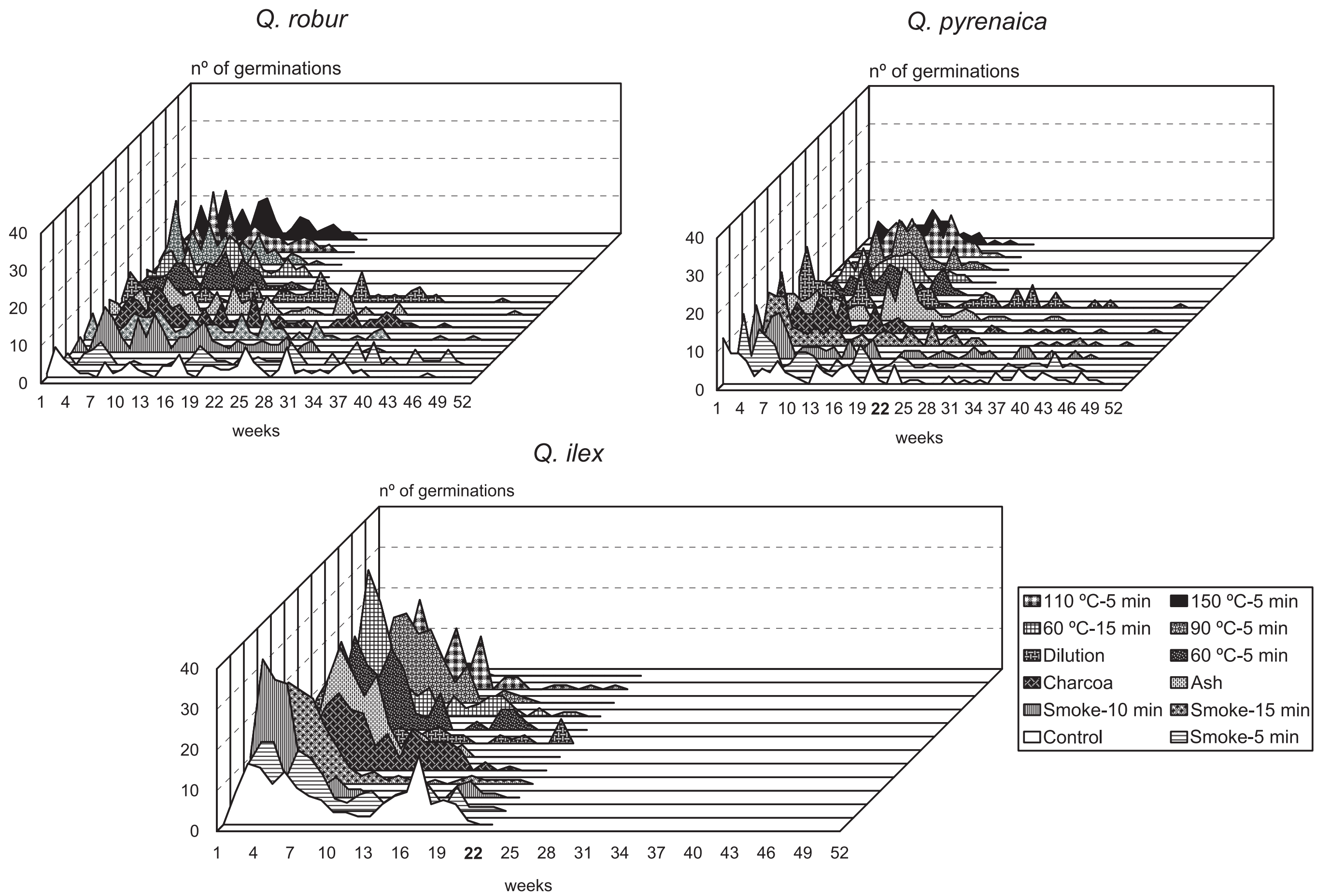

Figure 3. Temporal distribution of *Q. robur*, *Q. pyrenaica* and *Q. ilex* germination for each of the treatments studied.

during the first weeks, followed by smaller peaks up to the 45th week in the case of the Smoke treatment and up to the 41st week in the rest of the treatments. The heat treatments slightly delay the beginning of germination, but in exchange, germination is slightly higher and more concentrated in time. The temporal distribution of germination in *Q. ilex* varies according to the treatment applied (Fig. 3). In the Control treatment, germination was distributed over the 5 month incubation period of the seeds, but not uniformly. Two important peaks were observed, the first during the 1st and 2nd months and the second during the 4th month. The treatments of Smoke–10 min, Smoke–15 min, Ash and 60 ºC–15 min all showed an abrupt peak during the first two months, but the germinations produced in the other three months contributed very little to the final germination rate. The Charcoal and Smoke–5 min treatments showed a more or less constant distribution of germination, without notorious peaks. In the 60 ºC–5 min treatment, two peaks were produced, the second being much less important than the first. In the 90 ºC–5 min and 110 ºC–5 min treatments, germination was concentrated in the first four months and almost no new germinations were registered in the last month. Lastly, the treatment of 150 ºC produced very little germination and even this was reduced to the 2nd and 3rd month of incubation.

4. DISCUSSION

In the three species of *Quercus* studied, the response pattern to fire is similar and constant when faced with any of the fire agents analysed.

None of the three species is stimulated by smoke. Other authors who studied all these factors in other species obtained very different results, which were dependent on the species and fire agent analysed. The effect of smoke on germination was studied in a large number of species in South Africa, Australia and United States. Thus Brown [4], Brown et al. [5], Brown and van Staden [6], Read et al. [31], Enright and Kintrup [11], Keeley and Bond [23] detected very large stimulations of the germination rates of many species, a neutral effect on other species and also an inhibiting effect on some others. At this time it is known that the active compounds responsible for the stimulation are oxidising gases and/or acids [24]. Other authors [27, 48] found that in some plants the smoke acted on the seed-coat, in others on the seed-coat and on the embryo, and there may also be other species in which the smoke also acts on the cotyledons. Tieu et al. [49] concluded that the potential stimulation of the smoke is lower in the shrub species with hard seed coats than in the herbaceous species. The three species of *Quercus* studied have fairly hard coats and do not show that they are stimulated by smoke.

Our data indicates that *Q. robur* is a species resistant to high temperatures and that *Q. pyrenaica* shows a decrease in germination with intensive heat shocks, although this does not become significant. These results are similar to the behaviour detected by Valbuena and Tárrega [55] in another population of *Q. pyrenaica*, who found that intense heat treatments inhibited germination in this species. Other data on the inhibition of germination in trees caused by intense heat are those contributed by Keeley [20] in *Quercus dumosa*, by Reyes and Casal [34, 35] in *Betula pendula* and *Pinus sylvestris* and by Trabaud and Oustric [54] and Martínez-Sánchez et al. [26] in *Pinus halepensis*. May be that the high resistance to thermal shock of *Quercus* seeds is due to its size. The cotyledons and the hard coat can isolate the embryo from the lethal temperatures. This hypothesis was verified for *Pinus* species [35]. In this study it was showed that for three species of *Pinus* with different average size for their seeds, those with bigger seed were more resistant to high temperatures.

With respect to the effect of ash, either applied directly or diluted in water, the response of all three species was the same; there was no modification of the germination rate. With relation to germination, the ash was a factor that was studied least. Even then, most of the investigations that dealt with the question of germination response to ash [15, 29, 36, 38, 40, 47] found that ash either did not affect germination or inhibited it.

The charcoal did not produce important variations in the germination rate of the three species. The effect of charcoal varies according to the species studied. According to Keeley and Bond [23] charcoal can act as an important germination trigger as occurs in *Emmenanthe peduliflora*, or as an important inhibitor, as occurs in various species of *Ceanothus*. In Australia, Enright and Kintrup [11] studied the emergence of seedlings in *Eucalyptus* woodland and found that the charcoal did not stimulate germination relative to the control.

The germination velocity of the three species of *Quercus* is slow when compared to that of other arboreal species [35–37], of shrubs [15, 53] or grasses [15]. Treatments with fire has a neutral effect on the germination velocity of the three species of *Quercus*. This is a common response to fire in many species, such as *Pinus pinaster* and *Pinus radiata* [38], *Cistus psilosepalus*, *Calluna vulgaris*, *Erica umbellata* or *Daboecia cantabrica* [15].

The general distribution pattern of germination is similar in the three species of *Quercus* (Fig. 4). All three have a dilated and irregular germination velocity. The most notable difference between the three species is that *Q. ilex* presents all its germinations in 5 months and the other two species spread their germinations over 12 months. These results coincide with those of Li and Romane [25], who found that a population of *Q. ilex* in the South of France presented a similar distribution of germination. The species of *Quercus*, which do not have dormancy, have transient soil seed banks and one of the features of their reproductive strategies is based on the development of banks of persistent seedlings [16, 17, 32, 44]. For this reason the germination of a cohort of seeds cannot extend further than the moment of the following harvest, i.e. more than one year. *Q. robur* and *Q. pyrenaica* live in environments that are cooler than *Q. ilex*, with a higher rainfall and, what is more important, this is distributed more evenly throughout the year. These climatic conditions could be one of the fundamental reasons for producing germination during almost all the year. The distribution of germination throughout the year allows *Q. robur* and *Q. pyrenaica* to have a group of seedlings available to take advantage of punctual resources or favourable circumstances at any time of the year. For its part, *Q. ilex* lives in a Mediterranean environment with a summer drought, for which reason it has logically developed strategies that enables it to complete germination before the dry season begins. The seeds of *Q. ilex* have to germinate in less time so that when the dry season begins the seedlings are sufficiently developed and can live off their own resources. Moreover, this behaviour can be an advantage in the occupation of the space and resources available. In the genus *Quercus* the development of the seedlings is rapid and in a very short time the young plants acquire a considerable biomass [33].

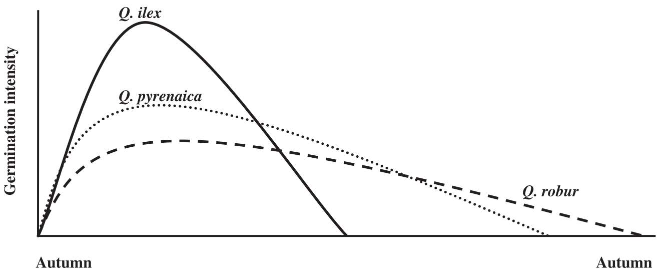

Figure 4. Germination model for the three *Quercus* species. Intensity of germination changes through the first year following seed dispersal.

The pattern of distribution of germination over time in the three species is not modified importantly by any of the fire treatments used. This is also the response detected in other arboreal species [35–39].

According to Keeley [21], the scrubland and Mediterranean Basin species of the genus *Quercus* can be classified as Disturbance-Free Recruitment species, i.e. the recruiting of new seedlings does not depend on the fact that a wildfire has occurred. We have confirmed that wildfire, in no case, directly increases the germination rate of *Q. robur*, *Q. pyrenaica* and *Q. ilex* (through high temperatures, ash, smoke or charcoal) and, thus, the recruitment of new individuals is independent of fire. This is in agreement with the conclusions of Keeley [21] about the regenerative strategies of species from the genus *Quercus*. According to the classification of fire survival forms by Trabaud [50] and taking into account the type of resprout, *Q. robur, Q. pyrenaica* and *Q. ilex* are Pyrogeophyte species. The first of these resprouts from the stump or epicormic buds and the other two resprout from the root as well.

Of the three species studied, two of them (*Q. pyrenaica* and *Q. ilex*) live in fire-prone environments. It can be expected that these species will show pyrophyte tendencies. Moreover, it was demonstrated that human management of this species, through cutting and occasional burning, favoured expansion of its populations [1]. None of the three species directly increases its germination because of fire. Li and Romane [25] and Bran et al. [3] found that *Q. ilex* showed auto-inhibition of germination

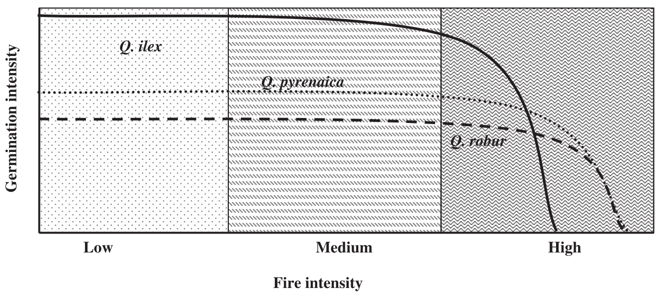

Figure 5. Model of fire response for the three *Quercus* species. High values of temperature, smoke or ash result in a sharp decrease in germination rate.

through a process of allelopathy [42, 43] and of *Q. pyrenaica* there is no bibliographic reference with respect to this factor. The fact that *Q. ilex* shows auto-inhibition of its germination could help to explain the full adaptation of this species to fire-prone environments: wildfires eliminate these allelopathic substances and allow germination of its seeds that, on the other hand, are not damaged by fire and so have a natural germination rate of close to 100%. Therefore, it can be said that the fire exercises an indirect increase in the germination of *Q. ilex*, by eliminating the allelopathic substances. Based on this information, it is necessary to distinguish between the species of *Quercus* that are only resistant to wildfires (*Q. robur*) and the species that in addition are benefited by them (*Q. ilex*). Therefore, it can be said that *Q. robur* is a species with disturbance-free recruitment and that *Q. ilex* is a disturbance-dependent recruitment species: immediate post-fire, according to the classification of Keeley [21]. In order to include *Q. pyrenaica* in one of these two groups it is firstly necessary to determine whether it has auto-allelopathy.

In conclusion it can be said that all the fire agents produce a unique response of non-modification of germination at low doses of the factor (Fig. 5) and a tendency towards an inhibiting response with high doses of the factor. This tendency is more notable in *Q. ilex* than in the other two species. With respect to the reproductive strategies of *Q. ilex*, this species presents features adaptive to fire-prone environments based on its combination of eliminating auto-allelopathy and non-inhibition of germination by fire factors. On the other hand, from the methodological point of view, it can be concluded that the germination of *Q. robur* and *Q. pyrenaica* takes place during the whole year and that of *Q. ilex* during 5 months. These periods of germination should be taken into account in future studies with these species, as experiments that contemplate shorter incubation periods could give partially incomplete results.

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