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Pre-dispersive influence of predation on natural regeneration of *Quercus robur* L.

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Abstract: *Quercus robur* L. shows interannual variability in production of acorns. This process is called "masting" and can generate some disadvantages for natural regeneration by reducing seed recruitment. Acorn production not only have shown variability between years but also among trees. Our aim was estimating the percentage of acorn losses for pre-dispersive predation. For this, we have been assessed for three years the acorns reach the ground. Of all the acorns that produces the tree, only a part reaches the soil in viability to germinate and establish itself as seedling. A significant number fall to the soil before completing its development, probably because failures during this process or by self-regulatory mechanisms of the tree itself, which only keeps the seeds that can withstand according to the resources at its disposal. Another part is consumed by predators on the tree, and finally a significant part of acorns is predated by insect larvae. In the oak species, most are coleopteran of the genus *Curculio* and lepidopteran of the genus *Cydia*. In years of copious production, the acorns that reach the ground viable to germinate and establish themselves as seedlings ranging between 5% and 33%. The larvae damage is not only caused by the direct consumption of cotyledons and embryo but, even in cases in which remain intact, the larvae generate cavities and galleries in the seed, which facilitates entry of fungi, bacteria, and other insects. In conclusion, pre-dispersive acorns predation by insects, it could place itself as one of the main constraints for natural regeneration of *Quercus* species.

Keywords: *Quercus* spp., Atlantic oaks, temperate forests, Galicia, Spain

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1. Introduction

The first phase of the regenerative cycle –production of acorns is vital to study the factors that limit natural regeneration of *Quercus robur* L. [1,2,3]. Seed production also directly affects animal populations that consume them and indirectly to predators and parasites of consumers [4]. Some tree species such as *Quercus robur* L., show a significant interannual variation in seed production. This phenomenon, known as "masting" [5], gives rise to a few disadvantages for natural regeneration of the species because it reduces the chances of recruiting acorns in years of low production [6]. Although there is no consensus on what are the main causes responsible for the "masting", it seems that the hypothesis "more efficient pollination" [7] and "predator satiation" [8] are most consistent with the results obtained in the studies of seed production in tree species. Both hypotheses place the "alternate bearing" as evolutionary reproductive strategy of certain species; more recent studies have found a marked effect of weather conditions on production values [9]. For species of the genus *Quercus*, the most significant correlations between the production of acorns and different climatic factors occur during the fruiting period [10]. Within this genus, each species responds to different environmental conditions, and the replies may vary depending on the site [9]. However, although environmental factors are a determining component of production, the tendency of each species to produce large crops of seeds in cyclical intervals supports the idea that natural selection has favoured the evolution of its "alternate bearing" character [5].

Research on seed production in species of the genus *Quercus* not only establish that significant variability between years, but also between trees [9,10]. Therefore, the variability would result from the interaction of environmental conditions with the gene pool of each individual. Moreover, some intrinsic characteristics, such as age or size of the tree [11,12] also influence the production capacity of seeds. Of the total acorns that each tree produces, only a part reaches the ground in perfect conditions of viability to germinate and establish themselves as seedlings. A significant amount falls to the floor before completing its development due to problems during the process of fructification or for regulatory mechanisms tree itself [9,13]. Another part of the harvest is consumed in the tree itself by different predators and, finally, a percentage of acorns perhaps even larger, are attacked and partially predated upon by larvae of certain insect species [14,15]. In the case of Quercine, most are coleopterans of the genus *Curculio* (Curculionidae) and lepidoptera of the genus *Cydia* (Tortricid). These damages are not only caused by the direct consumption of the cotyledons and the embryo. Even when they remain intact, the larvae attack generates a series of voids and galleries in the seed, which facilitates the entry of fungi, bacteria, and other arthropods. Thus, the pre-dispersive predation of acorns by the action of insects is considered one of the main limitations for the sexual regeneration of *Quercus* species [3].

We have calculated, for three consecutive years, the acorns reach the ground, quantifying losses from predation pre-dispersive. Then, the effect of larval attack on the germination process of acorns has been studied to determine its effect on the natural regeneration of the species. The objectives were: i) quantification of the seed bank; ii) seed loss calculation by incomplete development of the embryo and pre-dispersive predation by small vertebrates and insect larvae attacks; iii) determining of the interannual variability, variability between trees, and phenology of falling acorns; iv) quantification of the damage caused by the larvae on the germination process.

2. Material and Methods

2.1. Experimental design and sampling method

To calculate acorns reaching the ground a total of 40 trees were selected under whose cover circular plots of 1.5 m radius, in which production was quantitated for three years settled (2009, 2010 and 2011). During the period of dissemination of the species, October to December, three measurements were made to determine the phenology of the acorn production, as well as the peaks of the falling acorns. After each count, the acorns were collected and taken to the laboratory to estimate the percentage of losses by different agents. The transport was performed in polyethylene bags and in laboratory were stored in cold room (2-4 °C) until they were processed. In a first selection, acorns with normal development were separated by flotation from those in which the embryo has lost its germination capacity; our idea is to estimate the percentage of acorns loss due to incomplete development of the embryo and pre-dispersive predation by small vertebrates and insect larvae attack. Next, a second visual selection was made with the acorns that did not float and the healthy ones were separated from those with symptoms of larval infestation. Acorns from the latter selection were weighed and their length and diameter were measured.

To study the effect of invertebrate attack on the viability of the seeds, a simple test was performed with acorns normal development, i.e., not floating. These were collected directly of the ground during the peak of its fall (second half of October), from nine trees previously classified as good producers. Once fully healthy acorns were visually separated from those showing symptoms of larval infestation, a sample of 360 acorns was selected. Then, to prevent fungal attack, disinfected by a prior washing with sodium hypochlorite at 2% and later were treated with copper oxychloride to 50% in water. Later, were buried in a mixture of 30% inert material (sand pure silica) and 70% culture substrate to which a small amount of vermiculite was added to prevent the substrate to dry. The containers were taken to the nursery with an average temperature of 18 ºC and a relative humidity of 90%. To keep in optimal humidity, they were watered every 2 or 3 days with 10 ml of distilled water. It was considered that germination had occurred when the radicle protruded 2 mm of the acorn.

2.2. Data analysis

To calculate acorns (total, normal development and potentially viable) per year reaching the ground, a normal analysis was performed using the Kolmogorov-Smirnov test. On the one hand, the interannual variability, in each one of the phases, was analyzed by means of an ANOVA test of repeated measures, using the values obtained in the three consecutive reproductive cycles. On the other hand, the individual variability, for each cycle, was quantified by using coefficients of variation. Once the individual variability was identified, the trees were classified according to the average number of potentially viable acorns (good, medium, and poor producers), adapted from [11], analyzing the interannual variability within each category by the Kruskall-Wallis test. Finally, to determine the relationships between the first phases of the recruitment cycle and the transition percentages between them, as well as the factors that affect the transition from one phase to the next, a linear regression analysis was performed. All statistical analyses were performed using SPSS 11.5 for Windows.

3. Results

Seed bank

Figure 1 shows the average amount of acorns that reach the soil per year. However, of all the acorns that the tree produces, as we mentioned, only a part reaches the ground in viable conditions to germinate and establish themselves as seedlings (Figure 2). There is a strong correlation (r = 0.921) between the number of acorns that reach the soil (SA) to those falls when they have completed their normal development (AND). In fact, the number of acorns that reaches the ground explains 85% (R^2 = 0.849) of the variability of this process: ln (AND) = -0,774 + 1,001 x ln (SA). Which indicates that 48% of the acorns that reach the ground have a normal development. There is also a strong correlation (r = 0.886) between the number of acorns that reach the ground and to those falls without having completed their development. In fact, the number of acorns that reach the ground explains 79% (R^2 = 0.785) of the variability of acorns that reach the ground with incomplete development (AID): ln (AID) = -0,832 + 0,976 x ln (SA), it is indicating that 39% of the acorns that reach the ground are failures.

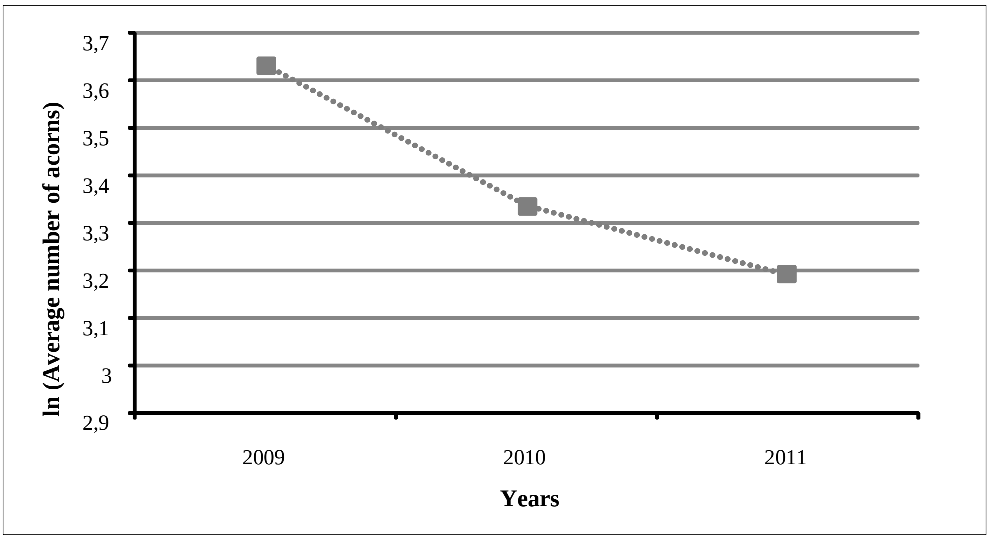

Figure 1. Annual average bank of acorns on the ground.

Of the total production of acorns, only a part of them reaches the ground without completing their development (Figure 2).

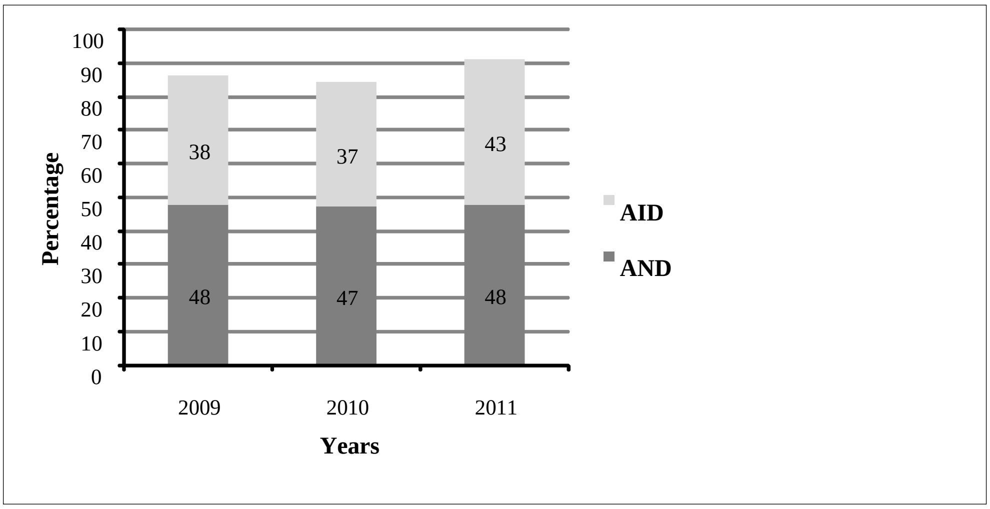

Figure 2. Percentage of acorns per year of *Quercus robur* according to its development (AID: acorns of incomplete development; AND: acorns of normal development).

In this way we can determine the average number of acorns that annually reach the ground after having completed their development (Figure 3).

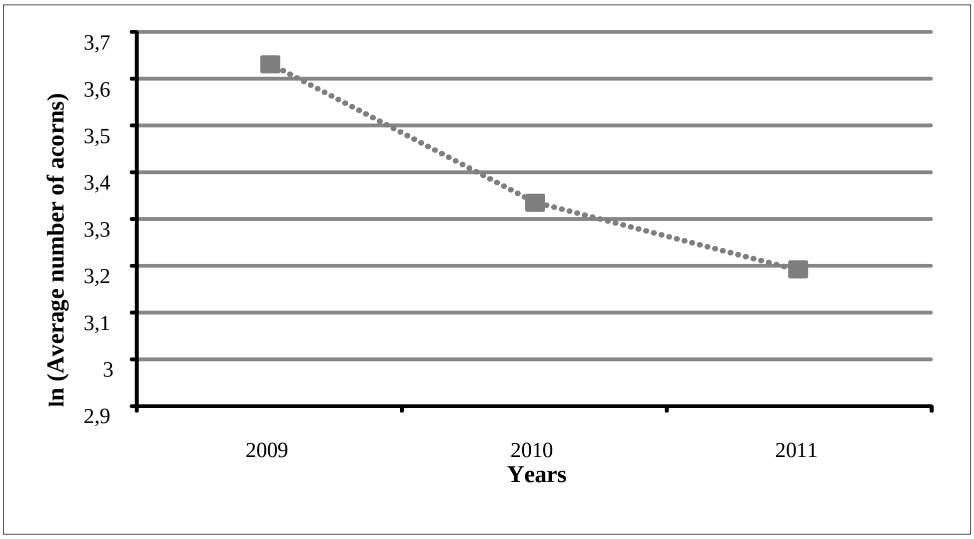

Figure 3. Annual average bank of acorns with normal development.

Finally, we can determine the average amount of acorns that reach the soil per year in perfect viability to germinate and establish as seedlings. Statistically significant differences were found in the number of acorns that reach the ground in perfect conditions of viability ($F = 3.565$; $p = 0.031$) during the three reproductive cycles (2009, 2010 and 2011) in which the sampling was carried out. It should be noted that the years that showed the greatest differences between them were 2009 and 2011.

4. Discussion

In the first phase of the reproductive cycle, acorn production, it was found different limiting factors. On the one hand, an important part of acorns that reach the ground are underdeveloped, i.e., 39% were failures. Among the causes of premature abscission of the acorns involved physiological processes, genetic and climate, differently and in different amounts [13,16]. In any case, it appears that a high rate of failures may reflect an excess of fruiting [17]; there is a positive correlation coefficient (r = 0.886) between the number of acorns that reach the ground and those which do without having completed their development. On the other hand, of the acorns that have completed their development, a part has been predated by small vertebrates or attacked by larvae, thus losing their viability to germinate and establish themselves as seedlings. For individuals classified as "bad" producers, 80% of normal development acorns were consumed by different types of predators. However, this data is reduced for individuals classified as "good" and "medium" producers. Accordingly, it appears that there is a positive correlation even stronger (r = 0.809), between the number of acorns with normal development and the number of these predated, i.e., a greater number of acorns available with normal development implies they will be attacked by small vertebrate, predators of acorns, and insect larvae in a higher percentage. The results are consistent with the hypothesis "predator satiation" [8].

It should be remembered that the number of acorns that reach the ground in optimal conditions to germinate and grow as seedlings varies with individuals and year, i.e., there is a high individual and interannual variability. At the population level, 89% of the analyzed individuals give rise to potentially viable acorns. However, the probability of recruitment cumulative, i.e., the probability of acorns that reach the ground do so in conditions of viability to germinate and establish themselves as seedlings, it is higher in the trees considered "medium" and "good" producers. These represent 79% of the trees that result in potentially viable acorns. This probability is 28% and 33%, respectively, in the years of good production. What is constant are the peaks in which the greatest fall of acorns to the ground occurs, since during the three reproductive cycles studied, they occurred in the second half of October [18].

5. Conclusion

A significant number of undeveloped acorns, about of 40%, falls to the ground because failures during the fructification period or by self-regulatory processes of the tree itself, which only keeps the seeds that can withstand according to the available resources. Another fraction is consumed by predators on the tree, and finally a significant part of acorns is predated by insect larvae, most are coleopteran of the genus *Curculio* and lepidopteran of the genus *Cydia*. In years of abundant production, the seeds that reach the ground viable to germinate and establish themselves as seedlings ranging between 5% and 33%. *Quercus robur* L. shows a significant interannual variation in seed production because it is an "alternate bearing" species. Thus, statistically significant differences were found in the acorns that reach the ground in viability conditions (F = 3.565; p = 0.031) during the three reproductive cycles (2009, 2010 and 2011), in which the sampling was carried out. It should be remarked that the years that showed the largest differences between them were 2009 and 2011. During the acorn production phase there are different limiting factors. Among the causes of premature abscission of the acorns involved physiological processes, genetic and climate, differently and in different proportion. The results are partially consistent with the hypothesis of "predator satiation".

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