The Effect of Combined Herbivory by Wild Boar and Small Ruminants on the Regeneration of a Deciduous Oak Forest

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Abstract: The multiple agroforestry land uses of oak forests are of great ecological and economic interest as they contribute to the improvement of animal husbandry, wildlife, and environment. However, herbivory by wildlife and livestock highly affects the structure and the dynamic of forest ecosystems including its regeneration. The aim of this study was to investigate the comparative effect of wild boar and small ruminants herbivory on the regeneration of a deciduous oak forest in northern Greece. Eight sites were selected in an even aged stand of similar canopy cover and forest site quality: four sites with long-time use mainly by wild boar and four sites with long-time grazing by sheep and browsing by goats. A plot of 150 m² in each of the sites was fenced in order to be protected from herbivory. The plant cover and number of oak seedlings and acorns was measured in both grazed and protected plots for four consecutive years. The plant cover increased in the protected plots independent of the type of animals. The seedling cover decreased about 29% and 9% in sites where small ruminants and wild boars foraged respectively. Similarly, the number and the weight of acorns significantly decreased in the sites grazed by small ruminants mainly during the mast year of the oaks. Forest management has to control the small ruminants grazing in terms of intensity, timing, and duration in order to ensure the sustainability of the ecosystem.

Keywords: agroforestry; acorns; sheep and goats; Sus scrofa

1. Introduction

Oak forests and woodlands (Quercus spp.) are widely spread in Mediterranean regions around the world and are of high ecological and socio-economic importance. They are source of wood for timber and fuel [1], forage for wildlife and livestock [2], edible and culinary food products, as well medicine and dietary supplements [3]. Moreover, they provide a variety of ecosystem services [4], and have important aesthetic, cultural, and recreational value. These forests are one of the greatest carbon reservoirs [1] thus contributing to the mitigation of climatic change effects. Moreover, they are very biodiverse ecosystems [5] and therefore in many cases are protected areas (Natura 2000) [6].

Oak woodlands have a long history of grazing with most of them being developed with the presence of livestock, especially in the Mediterranean region. Additionally, they are an important habitat and forage source for wildlife. Herbivory by wildlife and livestock could positively contribute to the increase of species and landscape diversity [7,8], reduction of fire hazards and fire risks [9], improvement of soil properties and nutrient cycling within the system [10], as well as to the
enhancement of the environmental and recreational value of forests [11]. On the other hand, grazing in forested areas could damage trees by browsing and trampling [12,13] and reduce species richness and diversity [14]. However, the main threat of herbivory for forest ecosystems is the negative impact on natural regeneration especially of broadleaved tree species [15]. Nevertheless, there is evidence that the level of damage does not alter tree regeneration [16,17].

The regeneration of oak forests is of great importance for the sustainability of these ecosystems and the maintenance of their ability to provide services. The regeneration of trees is a process influenced by many biotic and abiotic factors at every stage i.e., flower, seed, seedlings, saplings [18]. It is generally assumed that the “seedling emergence and establishment stage” [19] is the most vulnerable to herbivory during the regeneration cycle of oak trees. Herbivory could damage the new seedlings by browsing, rooting or trampling. The oak’s regeneration could also be damaged at the “post-dispersal acorn predation” stage, while the importance of “pre-dispersal acorn predation” stage is much lower [19].

Deciduous oak forests have been used more than other types of forests for livestock grazing due to their soft and relatively large leaves that are of higher nutritive value than the small and leathery leaves of sclerophyllous species. Nevertheless, limited information is available regarding the effect of grazing on their regeneration, as most of the research has focused on the evergreen Quercus ilex L. [21]. Comparative studies of the effect of foraging on oaks’ regeneration between livestock and wildlife are generally lacking. In this regard, the aim of the present study was to detect the comparative effect of wild boar and small ruminants foraging on the regeneration of a deciduous oak forest (Quercus frainetto Ten.) in Northern Greece. The study focused on young seedlings (height < 0.15 m) and acorns abundance in foraged and protected areas of the forest as indicators of regeneration.

2. Materials and Methods

The study area was an oak forest (Quercus frainetto Ten.) on Mt. Cholomontas, N Greece (40°23’ N, 23°28’ E) at 800 m asl. The climate is characterized as sub-humid Mediterranean, with a mean annual air temperature of 11.1 °C and an annual rainfall of 767 mm. The mean monthly air temperature and precipitation during the experimental years is presented in Table 1. The drier season was the spring and summer of 2008 and the wetter the spring and autumn of 2010. The pure Quercus frainetto forest covered an area of approximately 1400 ha with almost ≈300 wild boars foraging at parts of it. No other large herbivores used the study area. The whole area is communally grazed by 1200 goats and 900 sheep for seven months per year in a continuous stocking system, except for the winter months [22]. The research area is described in detail by Parissi et al. [23].

Table 1. Mean monthly temperature (T, °C) and precipitation (P, mm) during the experimental years.

<table>
<thead>
<tr>
<th>Year</th>
<th>2007</th>
<th>2008</th>
<th>2009</th>
<th>2010</th>
<th>2011</th>
</tr>
</thead>
<tbody>
<tr>
<td>Month</td>
<td>T °C</td>
<td>P mm</td>
<td>T °C</td>
<td>P mm</td>
<td>T °C</td>
</tr>
<tr>
<td>April</td>
<td>7.8</td>
<td>57</td>
<td>8.5</td>
<td>45</td>
<td>7.6</td>
</tr>
<tr>
<td>May</td>
<td>13.8</td>
<td>59</td>
<td>14.3</td>
<td>13</td>
<td>14.0</td>
</tr>
<tr>
<td>June</td>
<td>18.0</td>
<td>121</td>
<td>17.5</td>
<td>28</td>
<td>16.5</td>
</tr>
<tr>
<td>July</td>
<td>21.0</td>
<td>0</td>
<td>20.1</td>
<td>0</td>
<td>11.8</td>
</tr>
<tr>
<td>August</td>
<td>20.5</td>
<td>44</td>
<td>20.9</td>
<td>0</td>
<td>18.0</td>
</tr>
<tr>
<td>September</td>
<td>14.2</td>
<td>47</td>
<td>14.1</td>
<td>110</td>
<td>13.3</td>
</tr>
<tr>
<td>October</td>
<td>10.2</td>
<td>155</td>
<td>10.3</td>
<td>78</td>
<td>10.4</td>
</tr>
</tbody>
</table>

The research was conducted in an even-aged (about 50 years) coppice stand under conversion. The research was conducted in an even-aged (about 50 years) coppice stand under conversion into high forest. Four sites of similar canopy cover (around 65%) and forest site quality were selected in an area of approximately 169 ha with long-time foraging mainly by wild boar (WB) and occasional...
grazing by sheep and goats, and other four sites in an area of approximately 143 ha with long-time grazing by small ruminants (sheep and goats) (SR). An experimental plot of 150 m² in each of the sites was fenced for foraging exclusion and a similarly sized plot open to foraging was assigned next to the fenced one in autumn of 2006. The topography (altitude, aspect, slope inclination) as well C and N soil content of each stand are presented in Table 2. Four permanent 10 m long transects were established in every foraged and fenced plot. In every plot, the plant and seedling (height < 0.15 m) cover were measured along the permanent transects using the line-point method [24] in June and the number of acorns by using two 0.5 × 0.5 m quadrats placed at 3 and 7 m points of each transect (i.e., eight quadrats per plot) in November for four consecutive years (2008 to 2011). The acorns found in each quadrat were picked up, dried in the oven at 105 °C and weighted. The utilization intensity of the stands was expressed by the forage utilization percentage (FUP) [23] (Table 2).

### Table 2. General description of the plots in the study area.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Plots</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Wild Board</td>
</tr>
<tr>
<td>Altitude (m)</td>
<td>1 2 3 4</td>
</tr>
<tr>
<td>Aspect</td>
<td>W W E W</td>
</tr>
<tr>
<td>Slope inclination (%)</td>
<td>8 13 38 45</td>
</tr>
<tr>
<td>Soil organic carbon content (C)</td>
<td>4.0 3.3 2.8</td>
</tr>
<tr>
<td>Total N/%</td>
<td>0.45 0.34 0.25</td>
</tr>
<tr>
<td>Forage utilization percentage (FUP %) *</td>
<td>50 18 35 27</td>
</tr>
</tbody>
</table>

* It is the average of four years.

The repeated-measures Analysis of Variance (ANOVA) in IBM SPSS statistics 23 (SPSS Inc., Chicago, IL, USA) with Generalized Linear Model (GLM) model was used for detecting the effect of foraging (foraged vs. fenced) and the effect of different users (small ruminant vs. wild boar) on seedling cover and on the number and weight of acorns. The within-subject factors were the years and the foraging and the between-subject factor the users. The Least Significant Difference (LSD) test at the 0.05 probability level was used to detect the differences among means [25].

A detrended correspondence analysis (DCA) was performed in order to select the appropriate canonical ordination. The linear method was selected as the gradient of the 1st axis in (DCA) was <3 standard deviation units [26]. The variance partitioning procedure [27] was used in order to distinguish the effect of foraging variables (type of user, utilization percentage) from the effect of topography variables (altitude, aspect, slope inclination, C soil content, N soil content) on seedling cover and acorns number. A Redundancy Analysis (RDA) was performed using both groups of variables (foraging and topography) as explanatory followed by two partial analyses, one with topography variables as explanatory (pRDA1) and foraging as co-variables, and another one with foraging as explanatory (pRDA2) and topography as co-variables. Type of users and aspect were included in the analyses as dummy variables. Prior to analyses, all the data were logarithmically transformed, except N soil content and FUP. An automatic forward selection procedure using the Monte Carlo test with 999 permutations was used to test the significance of the explanatory variables. The CANOCO v4.5 for Windows [26] was used for DCA and RDA analysis.

### 3. Results

Year significantly affected all the measured parameters (Table 3). Foraging significantly affected only the plant and seedling cover, while the type of users influenced all the parameters with the exception of plant cover (Table 3). The lower plant and seedling cover were recorded in 2009 and 2008, respectively. The number and the weight of acorns were much higher in 2010, mast year of the oaks, compared to the other years. The percentage of plant and seedling cover were significantly higher in
the protected sites than in the foraged ones, while the percentage of seedling cover as well the number and weight of acorns were higher in the sites foraged by wild boar. The seedling cover was reduced on average 29% in the foraged areas compared to the protected ones (Table 3). This reduction was much higher in the sites with small ruminants reaching 49%. Similarly, the number of acorns was 83% lower in sites grazed by small ruminants than those foraged by wild boars.

Significant interaction was observed between the year and the type of user for seedling cover as well as for the number and weight of acorns (Table 2). In particular, the seedling cover gradually increased in sites foraged by wild boars especially after the mast year of the oaks (Figure 1a), whereas decreased in these with small ruminants. Additionally, the number (Figure 1b) and weight of acorns (Figure 1c) were significantly lower in sites grazed by small ruminants compared to those that foraged by wild boar, during the mast year of the oaks, while no significant differences were detected in the other years.

Table 3. The effect of year, foraging, and type of users on plant cover, seedling cover, number of acorns and weight of acorns (mean ± SE).

<table>
<thead>
<tr>
<th>Year (A)</th>
<th>Plant Cover (%)</th>
<th>Seedling Cover (%)</th>
<th>Acorns (No plot⁻¹)</th>
<th>Weight Acorns (gr)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2008</td>
<td>65 ± 2.1 a *</td>
<td>4.5 ± 0.4 c</td>
<td>2.2 ± 0.4 b</td>
<td>0.26 ± 0.05 b</td>
</tr>
<tr>
<td>2009</td>
<td>49 ± 2.6 c</td>
<td>8.3 ± 0.7 b</td>
<td>0.5 ± 0.1 c</td>
<td>0.15 ± 0.04 b</td>
</tr>
<tr>
<td>2010</td>
<td>54 ± 3.2 ab</td>
<td>9.0 ± 0.8 ab</td>
<td>25.4 ± 2.9 a</td>
<td>23.7 ± 2.4 a</td>
</tr>
<tr>
<td>2011</td>
<td>53 ± 2.9 b</td>
<td>10.8 ± 0.9 a</td>
<td>0.4 ± 0.1 c</td>
<td>0.19 ± 0.05 b</td>
</tr>
</tbody>
</table>

Foraging (B)
- Protected:
  | Plant Cover (%) | Seedling Cover (%) | Acorns (No plot⁻¹) | Weight Acorns (gr) |
  | 58 ± 2.2 a      | 9.3 ± 0.5 a        | 7.7 ± 1.0          | 6.0 ± 0.7          |

- Foraged:
  | Plant Cover (%) | Seedling Cover (%) | Acorns (No plot⁻¹) | Weight Acorns (gr) |
  | 52 ± 2.7 b      | 6.9 ± 0.6 b        | 6.6 ± 0.9          | 6.2 ± 0.8          |

Type of Users (C)
- Wild boar:
  | Plant Cover (%) | Seedling Cover (%) | Acorns (No plot⁻¹) | Weight Acorns (gr) |
  | 55 ± 3.0        | 10.6 ± 0.6 a       | 10.4 ± 0.9 a       | 9.2 ± 0.7 a        |

- Small ruminant:
  | Plant Cover (%) | Seedling Cover (%) | Acorns (No plot⁻¹) | Weight Acorns (gr) |
  | 56 ± 3.4        | 5.6 ± 0.4 b        | 3.8 ± 0.9 b        | 3.0 ± 0.7 b        |

Source of Variation
<table>
<thead>
<tr>
<th>Year (A)</th>
<th>Plant Cover (%)</th>
<th>Seedling Cover (%)</th>
<th>Acorns (No plot⁻¹)</th>
<th>Weight Acorns (gr)</th>
</tr>
</thead>
<tbody>
<tr>
<td>p &lt; 0.05</td>
<td>p &lt; 0.05</td>
<td>p &lt; 0.05</td>
<td>p &lt; 0.05</td>
<td>p &lt; 0.05</td>
</tr>
</tbody>
</table>

- Foraging (B) p < 0.05 ns ns
- Type of Users (C) ns **
- A × B (Interaction) ns ns
- A × C (Interaction) ns
- B × C (Interaction) ns
- A × B × C (Interaction) p < 0.05 ns

* Means followed by the same letter in the column did not significantly differ (p > 0.05) according to Bonferroni test.
** ns: not significant (p > 0.05).

The foraging and topography variables explained 64% of variation in seedling cover each year (RDA2; F-value = 2.012, p = 0.1060). Topography variables (management as co-variables) explained 29% of variation (pRDA1; F-value = 1.297, p = 0.3110), while foraging variables (topography as co-variables) explained 14% of it (pRDA2; F-value = 1.501, p = 0.2070). Amongst the six explanatory variables, only the C content of the soil (Figure 2a) was significant for pRDA1 (F-value = 3.20, p = 0.0490) explaining the 14% of the variance, while for the management variables (Figure 2b) only the type of users (F-value = 2.91, p = 0.0480). The seedling cover tended to increase in sites with lower C content and in sites foraged by wild boar.

The foraging and topography variables explained 51% of variation in the number of acorns each year (RDA1; F-value = 1.189, p = 0.2960). Topography variables (management as co-variables) explained 30% of variation (pRDA1; F-value = 0.964, p = 0.5300), while foraging variables (topography as co-variables) explained 12% of it (pRDA2; F-value = 1.011, p = 0.4400). Amongst the six topography explanatory variables (Figure 3), only slope inclination was significant for pRDA1 (F-value = 2.76, p = 0.0450) explaining 15% of the variance, while none of the management variables were significant.
Figure 1. Interaction between years and type of users for (a) seedling cover, (b) number of acorns, and (c) weight of acorns.
precipitation. Indeed, changes in precipitation and/or temperature influence the regeneration dynamic of Mediterranean oak forests; the soil water availability to which the emerged seedlings are very sensitive is directly affected [28]. In the present study, the lowest seedling’s cover was recorded in 2008, the year with the lower precipitation and higher temperatures during spring and summer compared to the other experimental years. On the other hand, the highest seedling’s cover was observed one year with the lower precipitation and higher temperatures during spring and summer compared to the year with the higher precipitation and lower temperatures during spring and summer.

Figure 2. (a) Biplot from the pRDA1 showing the position of the following: (1) number of acorns each year (solid arrows), (2) significant (dashed black arrows) and not significant (dashed grey arrows) foraging variables. Eigenvalues: axis 1 = 0.122, axis 2 = 0.014, axis 3 = 0.255. (b) Biplot from the pRDA2 showing the position of the following: (1) seedling cover each year (solid arrows), (2) significant (dashed black arrows) and not significant (dashed grey arrows) topography variables. Eigenvalues: axis 1 = 0.227, axis 2 = 0.049, axis 3 = 0.017. Dummy variables are represented by solid black (significant) and grey (not significant) triangles. E: east, W: west, SR: small ruminant, WB: wild boar, FUP: forage utilization percentage, Slope: slope inclination (%), N: N soil content (%), C: C soil content (%).

Figure 3. Biplot from the pRDA showing the position of the following: (1) number of acorns each year (solid arrows), (2) significant (dashed black arrows) and not significant (dashed grey arrows) topography variables. Eigenvalues: axis 1 = 0.162, axis 2 = 0.105, axis 3 = 0.024. Dummy variables are represented by solid black (significant) and grey (not significant) triangles. E: east, W: west, Slope: slope inclination (%), N: N soil content (%), C: C soil content (%).

4. Discussion

The effect of year on oak regeneration regarding the “seedling emergence and establishment stage” could be attributed to the climatic conditions of each year, mainly temperature and precipitation. Indeed, changes in precipitation and/or temperature influence the regeneration dynamic of Mediterranean oak forests; the soil water availability to which the emerged seedlings are very sensitive is directly affected [28]. In the present study, the lowest seedling’s cover was recorded in 2008, the year with the lower precipitation and higher temperatures during spring and summer compared to the other experimental years. On the other hand, the highest seedling’s cover was observed one
year after the mast year of the oaks, i.e., 2011, the year with relatively wet spring. Similarly, Perea and Gil [29] reported that 24.7% and 9% of Quercus pyrenaica Willd.’s seedlings survived during the wet and dry years respectively.

Herbivory by both wild boar and small ruminants negatively affected the regeneration of oak in terms of seedlings establishment and number of acorns. Similarly, reduction of both seedlings and number of acorns in areas foraged by wild boars was reported by Sweitzer and Van Vuren [30] (2002). Moreover, rooting frequency of wild boars was negatively correlated with the regeneration of Quercus robur L., Quercus petraea (Matt.) Liebl., and Quercus rubra L. [31]. However, the reduction of seedlings and number of acorns were less severe in areas foraged by wild boars. This is probably due to their diet selection which is highly dependent on feed availability, including agricultural crops [32] which are available in the study area. Wild boars are omnivores with plant materials dominating their diet [32]. Plant materials include both above ground parts of plants (aerial parts, fruits, seeds) and below ground (bulbs, roots) [33], but the proportion of above and below ground materials in their diet is highly differentiated among habitats [32]. It should be noted that the average utilization percentage in sites foraged by wild boars (approximately 33%) was less than in sites grazed by small ruminants (approximately 48%). Therefore, the specific size of wild boar population in the study area is not as harmful as this of small ruminants for the forest regeneration.

The seedlings, acorn abundance, and weight in the areas grazed by small ruminants were notably reduced indicating the negative effect on the regeneration of Q. frainetto. This is probably because Q. frainetto is an important part of goats’ diet [34]. Additionally, goats consume acorns and especially the larger ones in the Mediterranean region mainly in autumn and winter [34,35] as they are an important source of energy-rich feed [36] during these seasons. On the other hand, sheep are grazers and as such strongly avoid woody species. However, since seedlings are found in the herbaceous layer, they are classified in the herbaceous vegetation [37] and it seems that they are also consumed by sheep.

The seedling cover was increased in stands with less soil C content. Generally, it is assumed that soil C content is an important source for the maintenance of forest productivity. However, the low abundance of oak’s seedlings that was recorded in areas rich in C in the present study is related to the grazing and not to the effect of resource availability on their establishment and growth. In the study area, the soil C increased in sites with heavy grazing [23] probably due to changes in floristic composition [38] which in turn affect the rooting biomass contribution to C inputs [39].

The negative effect of small ruminants grazing on oak’s regeneration has also been reported for Q. ilex L. in Spanish dehesas [40,41] and for Quercus macrolepis Kotschy, Quercus pubescens Willd., and Quercus cerris L. in woodlands of Lesvos Island, Greece [42]. In these cases, the importance of utilization intensity on the severity of this effect was noted. Moreover, the timing of grazing is another important factor related to the impact of grazing on oaks’ regeneration. The seasonality of grazing by transhumance increased the regeneration rate in a dehesa ecosystem [39]. Utilization intensity and grazing timing could be controlled by forest management in order to limit the negative impact of livestock grazing on oak regeneration.

5. Conclusions

The combined herbivory by wild boars and small ruminants had a negative impact on the regeneration of a broadleaved oak forest in terms of seedlings and acorns abundance. The effect of the small ruminants’ grazing proved much more detrimental for the regeneration of oak forest compared to wild boars’ foraging in this study. The number of acorns was highly related to the mast year of the oaks. Other determinants of seedling emergence were environmental factors such as climatic conditions, especially precipitation, and soil nutrients. The forest managers have to take into consideration all the above parameters related to oak regeneration in order to spatially and temporally control livestock grazing and foraging by wild boars.


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**Conflicts of Interest:** The authors declare no conflict of interest.

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