Temporal Dynamics and size effects of Mistletoe (Loranthus europaeus Jacq.) Infection in an Oak Forest

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Keywords: Growth decline; Host-Hemiparasite interaction; Loranthus europaeus Jacq., Quercus petraea (Matt) Liebl.

Abstract

Establishing a better understanding of changes in mistletoe abundance over time could prove useful in the development of future conservation and management strategies for mistletoe-host complexes. The purpose of this study was to describe and examine how time influenced host trees sessile oak (Quercus petraea (Matt) Liebl.) and the abundance dynamics of their hemiparasites yellow mistletoe (Loranthus europaeus Jacq.). The research was conducted in Podyjí National Park, Czech Republic, from 2011–2015. Each oak stem (1599) was visually checked for the presence of he-
miparasites during the bud growth period. We investigated the temporal dynamics of *L. europaeus* abundance (number of *L. europaeus* shrubs per *Q. petraea* stem) and volume (total volume of *L. europaeus* shrubs per stem) on individual host stems using linear mixed effects models. The abundance of *L. europaeus* increased with larger host diameter at breast height (DBH), time and their interaction. The abundance of *L. europaeus* slightly increased over time on hosts with smaller DBH, but this phenomenon slowed down as host DBH increased. Mistletoe abundance started decreasing over time on hosts with large DBH. The study showed that time plays an important role in determining the distribution of mistletoes in the stand. Thanks to the inclusion of the time component, it was possible to create a model that showed the most vulnerable groups of host trees to which forest management should focus on.

**Zusammenfassung**


**1. Introduction**

Mistletoes are a taxonomically diverse group of angiosperms that rely partially or completely on host plants (Watson 2011). Mistletoes can be found in a wide range of ecosystems around the world, from boreal forests to tropical rain forests to arid
woodlands (Norton and Carpenter 1998). The occurrence of individual species is limited by specific climatic conditions (Černý 1976, Sangüesa-Barreda 2018). Mistletoes establish xylem connections with their hosts to obtain water and other xylem-borne nutrients (Ehleringer et al. 1985). Most stem mistletoes produce their own metabolites whenever they have access to light and carbon dioxide (Watson 2001). They increase drought stress and compromise the carbon balance of the host tree (Glatzel and Geils 2008), which negatively affect the condition of the host plant (Kołodziejek et al. 2013). Trees with mistletoe have significantly higher crown transparency (Dobbertin and Rigling 2006) which may lead to serious damage or death of infected trees (McDowell et al. 2011). However, mistletoes also play important roles as nutritional resources within canopies (Watson 2001).

The presence and abundance of mistletoe plants in a given area are usually spatially non-random and are regulated by various abiotic and biotic factors (Gairola et al. 2013). The majority of mistletoe seeds are dispersed by birds (e.g., Turdidae family and Loranthus europaeus Jacq.); many birds are highly specialized to consume mistletoe berries and are entirely dependent on mistletoe fruit at certain times of the year (Janssen and Wulf 1999).

At the habitat-scale, mistletoes are influenced by the distribution of suitable host species (Rödl and Ward 2002) and dispersers and pollinators (Ladley et al. 1997, Norton and Reid 1997), the behaviour of avian dispersers (Aukema and Martínez del Río 2002), habitat fragmentation (Lavorel et al. 1999), and topographical features such as elevation, slope and aspect (Hawksworth 1961, Smith 1972, Ganguly and Kumar 1976, Merrill et al. 1987, Aukema 2004).

On the individual-tree scale, mistletoe infection is correlated with tree height (Downey et al. 1997) and diameter (Siegel 1980, Bannister and Strong 2001, Aukema and Martínez del Río 2002, Carlo and Aukema 2005, Idžojtić et al. 2008, Gougherty 2013, Kołodziejek et al. 2013, Teodoro et al. 2013). Trees closer to the edge of a stand are more susceptible to hosting mistletoe (Lopez de Buen et al. 2002). Competition among trees has a negative effect on mistletoe occurrence (Matula et al. 2015). The establishment of mistletoes species is also influenced by previous infestations of a tree or a site (Aukema and Martínez del Río 2002).

The presence and abundance of mistletoe plants are well described, mainly as a result of short-term studies (Idžojtić et al 2005, Idžojtić et al. 2008, Lushaj and Lushaj 2009, Sayad 2017). Mistletoe population dynamics, i.e., the rate at which mistletoe populations build up or subside within trees, has only rarely been the subject of research. Mistletoe recruitment depends on a number of life cycle steps associated with pollination, including seed set, successful dispersal, and establishment on a suitable host (Reid et al. 1995). The life cycles of mistletoes are short compared to the life cycles of host trees. The average mistletoe population can double in 16 years (Scharpf and Parmeter 1982). This is because mistletoes produce fruit at a young age. L. europaeus
can produce fruits at an age of 3 years (Kubiček and Martinková 2010). Therefore, mistletoes in different stages of their life cycle can be found in the same habitat.

The purpose of this study was to describe and examine how time influenced host trees (*Quercus petraea* (Matt) Liebl.) and the abundance dynamics of their hemiparasites (*Loranthus europaeus* Jacq.). We think that a better understanding of changes in mistletoe abundance over time could prove useful in the development of future conservation and management strategies for mistletoes, which contribute to high biological diversity.

As far as we know, only a few studies have focused on the dependencies of host-hemiparasite abundance dynamics. Teodoro et al. (2013) demonstrated that suitable habitats for mistletoes occurred in discrete patches; additionally, local populations went extinct during the study and the colonization rate of previously non-occupied patches increased. Noetzli, Müller and Sieber (2003) found that a high degree of mistletoe attack had a negative effect on the growth of the host trees because the growth increments of the infested trees decreased compared to those of the uninfected trees.

In this study, we monitored the changes in infestation during 2011-2015 and compared the effects of host growth parameters on the intensity of infection and the differences in hemiparasite dimensions (volume).

We sought to answer the following questions:

- **I:** Do time dynamics influence the number of infected trees and shrub volume?
- **II:** Are there differences in hemiparasite dynamics between large and small DBH trees?

**Hypothesis I:** Larger trees have a higher occurrence of hemiparasites (Siegel 1980), which can inflict greater damage on their hosts (Kołodziejek et al. 2013). Mistletoe has a higher transpiration rate than the host plant (Glatzel and Geils 2008), so it extracts water and minerals from the host, even during drought, and reduces the number of resources available to the host (Garkoti et al. 2002). Over time, this can lower the abundance of hemiparasites as the attacked branches and crown of the tree die (Scharpf and Parmeter 1982). Therefore, we expect, that time would have a negative effect on the number of infected trees. The volume of mistletoe shrubs on a single stem will increase or decrease with changes in the abundance of individual mistletoes per stem.

**Hypothesis II:** The die-off of infected branches shortens the average lifespan and slows the rate of population growth (Scharpf and Parmeter 1982). Therefore, we expect, that mistletoe abundance would decrease with the age of the tree, i.e., there would be less mistletoe on old trees. Successful mistletoe establishment requires
host trees have branches 3–20 mm in diameter (Sargent 1995). Therefore, old trees will have a lower probability of new infection, because they lack branches that are suitable in size for mistletoe establishment.

Low DBH trees, which are younger and faster-growing trees, can potentially withstand the infection because of their better regeneration capability. On the other hand, these trees have faster-growing tissues with bigger and thinner cells and thinner bark; thus, when stressed, these trees might be more easily penetrated by mistletoe haustoria - root like attachments that obtain nutrients from its host (Thoday 1961). We expected that smaller trees would have a lower rate of infection, but infection rate would increase over time.

2. Materials and methods

2.1 Study site

The study site is situated in the Šobes area of Podyjí National Park, which is located in the southern part of the Czech Republic (48°49'32"N; 15°58'21"E), approximately 4 km southeast of the village of Podmoli. The study site is 390 m above sea level. The average slope of the plot is 3°. Land area is 2.37 ha. The border is irregularly shaped. The mean annual temperature is 8.5°C, and the length of the growing period is between 155–165 days. The long-term mean annual total precipitation is 486 mm (Kuchařovice Weather Station 2011). Bedrock is formed by granite.

The study site is located in the core zone of Podyjí National Park where forest ecosystems are left to spontaneous development. The forest stand comprising the research plot has a canopy structure of a single layer, but many trees are multi-stemmed due to coppice origin. However, the forest stand has not been actively coppiced since the end of 19th century and has become over mature (currently, approximately 120 years), undergoing a natural transformation into the high forest (Vrška et al. 2017). The stand is identified as acidophilous oak woodlands. The area is dominated by Quercus petraea (Matt) Liebl. with 1599 individuals (97.7%). The other tree species found on the plot included 34 individuals (2.1%) of Pinus sylvestris L., 2 individuals (0.1%) of Carpinus betulus L. and 1 individual (0.1%) of Larix decidua Mill. The average density of live stems was 634 stems ha⁻¹ (Vrška et al., 2017). Stand density index (Reineke, 1933) was 623.

Mistletoes range from extremely host-specific (e.g., Arceuthobium apachecum) to host-generalist (e.g. Dendrophthoe falcata) (Norton and Carpenter 1998). Mistletoe seedlings may establish more successfully on some host species rather than others (Reid et al. 1995). We avoided this problem by choosing a study plot with the presence of only one hemiparasite – Loranthus europaeus that had only one suitable host – Quercus petraea.
2.2 Data collection

All tree stems with DBH ≥ 7 cm were stem-mapped using Field-Map technology (www.fieldmap.cz), measured and identified to species. The number of stems that belonged to each individual tree was counted (stool). The investigation of the tree infestation by *L. europaeus* at the site was launched (2011) cooperatively with other research by Matula et al. (2015), which primarily focused on the impact of host competition on the intensity of the yellow mistletoe incidence. On the other hand, our investigation continued and rather concentrated on the changes in infestation monitored during a time series (2011–2015). Therefore, each oak stem (1599) was visually checked for the presence of *L. europaeus* in the years 2011, 2013, 2014 and 2015 and the effect of host growth parameters on the intensity of infestation and the differences in dimensions (volume) of the hemiparasite. Observations were made at the beginning of bud growth, so it was easier to spot the hemiparasites in tree crowns. The determination whether the mistletoe is dead or alive was performed on the basis of observations of growing buds and leaves. The number of *L. europaeus* shrubs per stem was counted (abundance) and the diameter of each shrub was estimated with laser rangefinder with a precision of 10 cm. Shrub diameters were used to calculate volume with the formula: $V = \frac{1}{6} \pi d^3$, where $d$ is *L. europaeus* shrub diameter. *L. europaeus* individuals that grew on the same stem were added together to obtain the total volume of *L. europaeus* per stem (volume).

2.3 Data analysis

All analyses were performed in the R environment (R Development Core Team 2015). We investigated the temporal dynamics of abundance and volume of *L. europaeus* infection on individual stems using linear mixed effects models (LME) using the “nlme” package (Pinheiro et al. 2016) in R. The abundance and volume of *L. europaeus* shrubs per stem acted as response variables. The fixed effects of LMEs were DBH, number of stems in a tree, year, and their pairwise interactions. Therefore, the linear predictors had the form of multiple regression and were structured as follows: DBH + Stool + Year + DBH * Stool + DBH * Year + Stool * Year. The terms were removed from the models according to their significance and the rule of marginality (Pekár and Brabec 2016). The volume and abundance values were log transformed, as LME requires a normal distribution of errors (Pekár and Brabec 2012). The *Q. petraea* stem IDs acted as random effects. In addition to the random effects, we included the spatial exponential correlation or the linear correlation of the true residuals using the function ‘corExp’ or ‘corLin’, respectively, to address the spatial autocorrelation problem (Pinheiro et al. 2016).
3. Results

Mean DBH of host trees was 28.8 cm (± 0.401), while mean DBH of uninfected trees was 23.0 cm (± 0.173). The number of infected trees decreased through the monitored years, with the exception of 2013. The rate of infected stems decreased from 9.3% in 2011 to 6.9% in 2015 (Tab. 2). The number of newly disinfected trees was higher than the number of newly infected trees (Tab. 2). The greatest difference was noted in 2014 when 36 trees were disinfected and no newly infected trees were recorded. The number of *L. europaeus* shrubs on sessile oak tree hosts decreased through the monitored years, from 248 in 2011 to 152 in 2015 (Tab. 3). There was a break year in 2014, where 86 hemiparasites died, and only two new individuals were found (Tab. 3).

The largest number of *L. europaeus* individuals recorded on one host stem was between 3-7 (Tab. 3). The average diameter of *L. europaeus* decreased to 63.7 cm (± 3.01) in 2015. The maximum recorded *L. europaeus* diameter was 170 cm. The average number of hemiparasites on one contested stem decreased through the years, from 1.68 in 2011 to 1.38 in 2015 (Tab. 3).

We found no significant relationship between the abundance of *L. europaeus* per stem and the number of stems per tree (LME, F1,176 = 0.2, P = 0.654). The abundance of *L. europaeus* increased with an increase in DBH (LME, F1,177 = 13.3, P < 0.001, Fig. 1, Tab. 1, Tab. 4), year (LME, F1,352 = 8.7, P = 0.004, Fig. 1, Tab. 1), and their interaction (LME, F1,352 = 6.1, P = 0.014, Fig. 1, Tab. 1). At smaller DBH, the abundance of *L. europaeus* slightly increased through the years, but this phenomenon slowed down with increasing DBH. Mistletoe abundance started decreasing over time when the host trees had high DBH (Fig. 1).

There was no significant effect of the number of stems per tree on the volume of *L. europaeus* (LME, F1,176 = 0.9, P = 0.348). The volume of *L. europaeus* decreased over time (LME, F1,353 = 11.6, P < 0.001, Tab. 1) and increased with the DBH of their hosts (LME, F1,177 = 6.3, P = 0.013, Tab. 1, Tab. 4). The total volume of *L. europaeus* shrubs decreased, from 79.79 m³ in 2011 to 43.13 m³ in 2015 (Tab. 3).
Table 1: The estimated coefficients (SE) of the fixed effects of the linear mixed effects models on the abundance and volume of L. europaeus. The dash means that the term was not significant in the model. The estimates are for log-transformed abundance and volume.

Tabelle 1: Koeffizienten (Standardabweichung) der fixen Effekte der Linearen Gemischten Modelle für die Abschätzung von Häufigkeit (Abundance) und Volumen (Volume) von L. europaeus. Der Strich bedeutet, dass dieser Term nicht signifikant ist. Für die Ermittlung der Koeffizienten wurden Häufigkeit und Volumen log-transformiert.

<table>
<thead>
<tr>
<th></th>
<th>Intercept</th>
<th>DBH</th>
<th>Year</th>
<th>DBH-Year interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abundance</td>
<td>-0.56 (0.23)</td>
<td>0.03 (0.01)</td>
<td>0.10 (0.06)</td>
<td>-0.005 (0.002)</td>
</tr>
<tr>
<td>Volume</td>
<td>-2.90 (0.61)</td>
<td>0.05 (0.03)</td>
<td>-0.12 (0.04)</td>
<td>-</td>
</tr>
</tbody>
</table>

Table 2: Fluctuation of host stem infestation of L. europaeus. Number of newly infected stems represents the newly infected host stems compared to findings from the previous year. Number of disinfected stems represents stems with no mistletoes in a given year but were infected in a previous year. Number of surveyed Q. petraea individuals was 1599.

Tabelle 2: Variation des Befalls durch L. europaeus über die Zeit. Wir zeigen die Anzahl befallener Bäume sowie deren prozentueller Anteil an allen erhobenen Eichen (1599). Die Anzahl der neu befallenen Bäume beschreibt die Anzahl Bäume die im Vorjahr keinen Mistelbefall aufwiesen aber im aktuellen Jahr befallen waren. Zum Schluss zeigen wir noch die Anzahl vormals befallener Bäume, die aktuell keinen Befall mehr aufwiesen.

<table>
<thead>
<tr>
<th>Year</th>
<th>No. of infected stems</th>
<th>% of infected stems</th>
<th>No. of newly infected stems</th>
<th>No. of disinfected stems</th>
</tr>
</thead>
<tbody>
<tr>
<td>2011</td>
<td>148</td>
<td>9.3</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>2013</td>
<td>155</td>
<td>9.7</td>
<td>26</td>
<td>19</td>
</tr>
<tr>
<td>2014</td>
<td>119</td>
<td>7.4</td>
<td>0</td>
<td>36</td>
</tr>
<tr>
<td>2015</td>
<td>111</td>
<td>6.9</td>
<td>10</td>
<td>18</td>
</tr>
</tbody>
</table>
Table 3: Fluctuation of *L. europaeus* shrubs in the entire plot

<table>
<thead>
<tr>
<th>Year</th>
<th>No. of shrubs</th>
<th>Newly grown shrubs</th>
<th>Newly dead shrubs</th>
<th>Max. no. of shrubs per stem</th>
<th>Average no. of shrubs per stem</th>
<th>Average diameter (cm)</th>
<th>Sum of shrub vol. (m³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2011</td>
<td>248</td>
<td>-</td>
<td>-</td>
<td>7</td>
<td>1.68 (±0.1)</td>
<td>72.40 (±2.10)</td>
<td>79.78</td>
</tr>
<tr>
<td>2013</td>
<td>249</td>
<td>45</td>
<td>44</td>
<td>5</td>
<td>1.61 (±0.08)</td>
<td>70.60 (±2.04)</td>
<td>70.98</td>
</tr>
<tr>
<td>2014</td>
<td>165</td>
<td>2</td>
<td>86</td>
<td>3</td>
<td>1.39 (±0.06)</td>
<td>72.90 (±2.54)</td>
<td>53.54</td>
</tr>
<tr>
<td>2015</td>
<td>152</td>
<td>28</td>
<td>41</td>
<td>5</td>
<td>1.37 (±0.07)</td>
<td>63.70 (±3.01)</td>
<td>43.13</td>
</tr>
</tbody>
</table>

Tabelle 3: Zusammenfassung der Eigenschaften der *L. europaeus* Pflanzen (Büsche) im Untersuchungsgebiet
Table 4: Fluctuation of host stem infestation of *L. europaeus* by DBH classes. The interval of DBH classes was created based on Doležal (1965) design and was adapted to local conditions.


<table>
<thead>
<tr>
<th>DBH class</th>
<th>Range of DBH classes (cm)</th>
<th>% of infested stems</th>
<th>Average no. of shrubs per stem</th>
<th>Average vol. of shrubs per stem (m³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>7–8</td>
<td>0.00</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>2</td>
<td>8.1–16</td>
<td>0.54</td>
<td>1.33 (±0.33)</td>
<td>0.02 (±0.01)</td>
</tr>
<tr>
<td>3</td>
<td>16.1–24</td>
<td>6.08</td>
<td>1.23 (±0.05)</td>
<td>0.40 (±0.05)</td>
</tr>
<tr>
<td>4</td>
<td>24.1–36</td>
<td>18.06</td>
<td>1.59 (±0.05)</td>
<td>0.47 (±0.03)</td>
</tr>
<tr>
<td>5</td>
<td>36.1–48</td>
<td>37.21</td>
<td>1.76 (±0.18)</td>
<td>0.56 (±0.07)</td>
</tr>
</tbody>
</table>
Figure 1: The Fitted relationship between abundance of C. europaeus and time, with the interaction of host tree DBH. The DBH was discretized for illustrational purposes. The estimated model can be found in Table 1, the DBH classes are structured in Table 4. The small noise was added to the data to see the data structure.


4. Discussion

Generally, our study confirmed that mistletoe occurrence and volume increased with DBH, i.e., with size and age of the hosts. Our estimated model showed differences in mistletoe abundance with time. While a slight increase in the number of C. europaeus over time was recorded in host trees with a very low DBH (Fig. 1), the number of C. europaeus plants declined in trees with a high DBH (Fig. 1) during the study period.
The number of hemiparasites on host trees with intermediate DBH values stagnated over time. The decline in the number of *L. europaeus* on host trees with a greater DBH can be attributed to the natural dieback that occurs as they reach a maximum age, and, as Monteiro (1992), we assumed that larger (older) hosts could be attacked sooner than hosts with a smaller DBH. Some *L. europaeus* individuals died because of the gradual loss of host branches caused by the accelerated ageing of their growth modules. None of the monitored host trees has completely died. The ageing of the modules may be caused by hemiparasite stress on the host, which affects host growth and architecture (Rigling et al. 2010), reduces host photosynthetic efficiency (Dobbertin and Rigling 2006) and alters the respiration rates of the plants (Watling and Press 2001).

Mistletoe haustoria need to overcome the thick bark of host branches to successfully establish on trees. This is easier in places where the host stem tissues are in tension, disrupted or replaced by secondary protective tissues in oak branches, this exchange occurs between ages of 4-6 years (Kubiček, Martinková and Špinlerová 2011). Sargent (1995) found that mistletoe seedlings died more frequently on larger branches than on smaller twigs, probably because they were unable to penetrate the thicker bark of the hosts with larger stem diameters. Young branches are more likely to be attacked by hemiparasites. This can be one factor that explains why the abundance of *L. europaeus* increased more on low DBH trees and why is not as abundant on high DBH trees.

The mean DBH of host trees (28.80±0.401 cm) is comparable with findings of Sayad (2017) – 27.10±1.59 cm. These numbers are higher than mean DBH of all trees.

Over the years included in the study period, 6.9%–9.7% of the *Q. petraea* stems (Tab. 2) were infested with 152–248 *L. europaeus* individuals (Tab. 3). This result can be compared with Iđžoñtić et al. (2005), who reported a 14.2% infestation rate of *Quercus* trees over 30 years old in the Forest Administration Požega. Sayad (2017) reported an infection ratio of 23% in Oak Zagros forest.

The average number of *L. europaeus* plants detected on one infested tree was 1.4–1.7 pieces (Tab. 3, Tab. 4), which corresponds to the abovementioned research (Iđžoñtić et al. 2008 report 2 pieces). Sayad (2017) stated that infected trees had an average of 4.08 mistletoes in Oak Zagros forest. The maximum number of individuals (7 pieces per a tree, Tab. 3) was lower than values reported in Croatia (38). There were no sufficient regularities to make a connection between the analysed parameters and the occurrence of mistletoe.

In Albania, Lushaj and Lushaj (2009) conducted two research time series on *L. europaeus* infestation of *Castanea* sp.. Their work mentions an average *L. europaeus* incidence between 3 and 7 (9) individuals per a tree. They determined infestation rates of 4.8% and 5.9% for the first and the second time series, respectively. A gradual in-
crease in infestation was also recorded in our case (Tab. 2), during the first three years of research. However, over the last two years, the percentage dropped quite sharply, and the number of *L. europaeus* individuals decreased by more than 40% (Tab. 3). The reason for this sudden drop and the increased mortality of the *L. europaeus* plants can only be hypothesized. *L. europaeus* death may have occurred naturally, as the individuals reached their maximum age, a hypothesis that is supported by the high volumes of hemiparasites we measured in some cases. According to Úradniček (2009), *L. europaeus* individuals form branches over 80 cm long, which corresponds to the dimensions we measured (biggest shrub was 170 cm in diameter). We noticed that a few young *L. europaeus* shrubs died. The low number of newly established individuals can be attributed to the slower growth of new yellow mistletoe, and it is possible that new individuals could not be seen in the high crowns during the five-year research period. Higher mortality may also be associated with worsening climatic conditions - a prolonged dry period (Bartošová et al., 2015), which can cause photoinhibition and affect intrinsic water-use efficiency (Sangüesa-Barreda 2018).

Throughout 5 years of research, we did not detect a relationship between increased *L. europaeus* incidence and higher within-tree competition caused by the multi-stem growth in the coppice. This supports the short-term results of Matula et al. (2015), who found a small dependency, but noted that the likelihood of *L. europaeus* infection is more dependent on the host thickness than the competition between the stems. It is also true that the authors who monitored *L. europaeus* infections in various types of stands that were managed in different ways (Idžojtić et al. 2005, Lushaj and Lushaj 2009) did not note any within-tree differences in competition.

Our data indicate that the abundance of *L. europaeus* increased with time on host trees with smaller DBH. For this reason, it is important to properly manage in a way that focuses primarily on preventing young trees from drought stress (planting of drought-tolerant species, increasing species diversity, coppicing), which would otherwise accelerate attacks by hemiparasites. The priority harvesting of already infested high DBH trees should help to slow the mistletoe dissemination.

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