Effect of climate variability on Quercus rubra phenotype and spread in Lithuanian forests

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Abstract: This study investigates the effect of climate variability on the phenotype, leaf litter decomposition intensity and seedling spread of alien red oak (Quercus rubra L.). Twenty-eight red oak forest stands located in Lithuania were evaluated. Indirect climate change indicators such as continentality were used in the analysis. Simulation of climate warming was achieved using an agro sheet cover. According to the results, the morphological traits of red oak stems in the maritime regions (warmer winters) do not differ significantly from those of red oaks stems in the continental areas of Lithuania (colder winters, more frequent spring frosts). Red oak leaf litter under an agro sheet cover (warmer conditions) decomposes at almost the same intensity as without the cover (natural conditions). The red oak seedlings spread 100 m or more irrespective of continentality. These results showed indirectly that climate change will not affect red oak stem quality or microorganism activity in the process of leaf litter decomposition. Red oak will thus remain as an invasive species, threatening composition change in native forests.

Additional key words: alien plant, maritime region, seedling, litter decomposition, stem quality

Introduction

Alien red oak (Quercus rubra L.) was introduced in Lithuanian forests in about 1875 (Ramanauskas 1963). Large red oak forest stands grow in western and central parts of Lithuania (Straigyté and Žalkauskas 2006). Most are 40–60 years old. Young red oak stands have higher volume increments than native common oak (Quercus robur L.) stands. Red oak has good potential for natural coppice and seed regeneration and shows no marked difference in susceptibility to fungi and insect damage compared to native tree species (Danusevičius et al. 2002). These characteristics encouraged foresters to plant red oak in the past. However, the danger of invasion was underestimated. Invasive species are defined as naturalized alien plants that produce reproductive seedlings in very large numbers at considerable distances from the parent plant (Richardson et al. 1994, 2000; Pyšek et al. 2004).

Zobel et al. (1987) and Mather (1993) note, in reviews of afforestation history in various countries around the world, that not until the twentieth century did planted tree species dangerously surpass the boundaries of natural habitats. In recent years, more intensive spread of red oak seedlings in Lithuanian forests has been noticed, indicating that this species is becoming invasive. However, not all site types are favourable for the spread of these trees. Red oak seedlings colonize most intensively in poorer site types, while no spontaneous spread of seedlings occurs in very fertile soils, where red oak seedlings are unable...
to compete with dense herbaceous vegetation (Riepšas and Straigytė 2008).

Red oak trees belong to the group of allelopathic plants. Red oak releases the allelochemical material coumarin, which has a negative impact on ferns and grasses. This material is released by all parts of the tree: leaves, bark, stem and roots (Coder and Warnell 1999). This characteristic increases the level of invasiveness of red oak.

The primary purpose of our research was to investigate how climate change affects red oak morphology and invasiveness by seedling spread. Indirect climate warming methods were used to create a simulation of climate change. The secondary aim was to determine changes in the intensity of leaf litter decomposition during the climate warming simulation.

Materials and methods

This research was conducted in 28 red oak forest stands located in the western (maritime) and central-southern (continental) regions of Lithuania (Fig. 1). Red oaks predominate in these areas. In total, 270 red oak trees were measured, ranging in age from 40–60 years. Stand stocking levels varied from 0.7–0.8.

Dendrometrical and morphological data collection

Red oak trees were evaluated in terms of age, crown size, crown density, stem straightness, straight trunk height, stem form, and angle between stem and crown branch attachments. The height of the straight trunk was measured using a Håglof electronic clinometer (Långsele, Sweden). Tree age was measured by drilling at breast height with an increment borer and counting the rings from the outside edge of the core to the pith.

Binoculars assisted in collecting data about the crown. Crown density was measured from one tree length away from the base of the tree. Foliage below the crown ball was not included in the measurement (Tallent-Halsell 1994).

Spread of seedlings

Red oak seedling spread was explored in 16 stands growing on site types of medium fertility (6 in the continental region and 10 in the maritime region). Spontaneous seedlings were calculated in 2.5 m × 10 m transects at distances 10, 100, 300 and 500 m from the parent tree stand.

Leaf litter decomposition intensity

The intensity of leaf litter decomposition depends on the physical and chemical characteristics of the soil, microorganism abundance and leaf litter quality (Swift et al. 1979). Physical and chemical characteristics of the soil and microorganism abundance were the same for all samples in our experiment because they were all located in the same site. Half of the samples (n = 21) were kept under an agro sheet for the duration of the experiment, and thus were influenced by higher temperatures, simulating the effect of climate change.

Red oak leaf litter was collected at the beginning of November 2007. All leaves were collected from leaf litter carpets on the ground in 1 m squares randomly arranged at a distance of 2 m from the tree trunks. Forty-two litter bags (1.4-mm nylon mesh) were filled with 5.0 g of air-dried leaves. All litter bags were placed on the mineral topsoil surface of Luvisol in December 2007. Twenty-one litter bags were covered with the agro sheet to simulate higher environmental temperature. Soil surface under the agro sheet cover was 2°C higher than in the open area. Litter bags were collected from each site after 3, 6, 9, 12 and 24 months. Air-dried litter bags were weighed to determine leaf mass losses over time.

Statistical analysis

Possible reactions of red oak morphology to continentality were evaluated by indicator species analysis using PC-ORD software (MjM Software, Gleneden Beach, OR, USA; Dufrene and Legendre 1997). Relative abundance and frequency of tree-specific morphological traits were evaluated in red oak stands in both the continental and marine areas. Differences in the percentage of indicator values in both regions for morphometric traits were determined by combining values of relative abundance and frequency. Monte Carlo testing was applied to determine the significance of observed maximum indicator values after 999 permutations.

Partial Redundancy Analysis (RDA) was performed using Canoco software (Ter Braak and Šmilauer 2002) to determine the continentality effect on red oak phe-
notype. Partial RDA allowed elimination of the effect of covariables (e.g., stand site fertility, stocking volume and tree age) from the ordination. Intermorphological trait correlation scaling was used to display correlations among morphological traits and environmental variables. Generalized log transformation was used for normalization of morphological data. Morphological data were centred and standardized so that the centre of the ordination diagram (zero) was the mean of the data. The ordination diagram was created as follows.

The arrows point in the direction of the steepest increase in values for the corresponding morphological trait. The approximated correlation of one morphological trait with another can be predicted by projecting the arrowheads representing the traits onto overlapping imaginary lines. The length of the arrows represents multiple correlations of morphological traits with the ordination axes. The centroids of the environmental variables (regions) are interpreted as individual classes of samples (trees). The distance between the regional symbols approximates the average dissimilarity in composition between the two sample classes (regions) being compared, as measured by their Euclidean distance. However, this approximation is not optimal, because the scaling of scores is not focused on intersample distances. The projection of regional symbols onto the line overlying the arrow of a particular morphological trait is used to approximate the average abundance of that morphological trait in individual classes of the samples. Projection points appear in order of the predicted increase of the abundance of a particular morphological trait across the classes. The increase is predicted to occur in the direction indicated by the arrow. The classes projecting onto the original coordinate are predicted to have average values for that morphological trait similar to the average values for that trait in the overall data. The Monte Carlo test of significance (999 permutations) of all canonical axes was used in the reduced model.

The Mann–Whitney U test was used for comparing two independent groups (9 samples per group) to measure the influence of temperature differences on leaf litter decomposition intensity after 24 months.

Results

Morphological traits

The phenotypic diversity of tree forms during individual growth depends on many environmental factors. According to the morphological indicators examined in this study, the medium phenotype of red oak in Lithuanian forests is characterized by bifurcate stems with a straight trunk height of only 8 m, ribbed trunk cross-section, lower branches attached to the trunks at angles of 50–70°, crown of moderate size and crown density of about 40%. The highest variation was observed in crown density [standard deviation (SD) ±7.5] and trunk height (SD ±4.4).

No significant difference was observed in morphological traits of red oak growing in different site types. Curved red oak stems predominate in unfertile and high-fertility site types, while bifurcate stems predominate in fertile site type (Table 1). Average straight trunk height is similar in all site types, reaching 7–9 m. This parameter showed no relation to site type fertility. Lower straight trunk height was observed at red oak stands with low tree density (5–6 m). Ribbed trunk cross-sections were common for red oak trees in all site types. The lower branches of trees were attached to the trunks at angles of 50–70° in most cases. Tree crowns in high-fertility site types were narrower than those of trees growing in unfertile and fertile site types. Crown density did not differ across site types.

The results showed that the average red oak trunk examined in this study has poor stem quality. Evaluation of different climatic conditions (continentality, simulated climate change) indicated that changes in these conditions had an impact on red oak stems and other morphological traits. Indicator values analysis showed that the highest effect of continentality was a perfect indicator of crown density (Table 2). In general, however, no significant differences in morphological traits were noted between different climatic conditions.

Results of partial RDA showed that the covariables (stand stocking level, site type fertility, tree age) explained 5.4% of the total variability in morphological traits data. Regional differences explained 4.9% of the

<table>
<thead>
<tr>
<th>Site type fertility</th>
<th>Unfertile</th>
<th>Fertile</th>
<th>Very fertile</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stem quality</td>
<td>curved</td>
<td>bifurcate (two-stemmed)</td>
<td>curved</td>
</tr>
<tr>
<td>Straight trunk height (m)</td>
<td>8</td>
<td>9</td>
<td>7</td>
</tr>
<tr>
<td>Crown branch angle</td>
<td>50–70°</td>
<td>50–70°</td>
<td>50–70°</td>
</tr>
<tr>
<td>Crown shape</td>
<td>medium</td>
<td>medium</td>
<td>narrow</td>
</tr>
<tr>
<td>Crown density, %</td>
<td>42</td>
<td>41</td>
<td>41</td>
</tr>
<tr>
<td>Number of trees in the analysis</td>
<td>26</td>
<td>153</td>
<td>91</td>
</tr>
</tbody>
</table>
total variability in the morphological traits data, which cannot be explained by covariables (Monte Carlo test, 999 permutations). Significant values were observed on all canonical axes (sum of all eigenvalues = 0.946, sum of all canonical eigenvalues after fitting covariables = 0.049, F-ratio = 14.351, p-value = 0.001). However, 89.7% of the variability in the data remains unexplained.

Red oak stem quality was better in the maritime climate (western region) than in the continental climate (colder winters), where lower stem quality, that is, more curved, bifurcated stems, was observed (Fig. 2). Red oak stems with branches were more often attached at an angle of about 90°, indicating better quality (single) stems. Denser crowns were more common in the continental region. Stem quality did not correlate with crown density. Therefore, climate warming may not influence red oak stem quality.

### Seedling spread

The density of germinated red oak seedlings at a distance of 10 m from the parent tree in moderate fertile site types was higher (8300 seedlings ha⁻¹) in the continental region than in the area with a marine climate (4600 seedlings ha⁻¹) (Table 3). Results for spontaneous seedling density at distances of 100 or 300 m were similar, while more densely germinated seedlings at 500 m were found in the maritime region.

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**Table 2. Red oak morphological traits in relation to continentality**

<table>
<thead>
<tr>
<th>Morphological traits Phenotype difference</th>
<th>Maximal indicator value in the group</th>
<th>Continental (central-southern) part of Lithuania</th>
<th>Maritime (western) part of Lithuania</th>
<th>Monte Carlo test, p*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crown size</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Narrow</td>
<td>31</td>
<td>20</td>
<td>31</td>
<td>0.708</td>
</tr>
<tr>
<td>Medium</td>
<td>46</td>
<td>46</td>
<td>45</td>
<td>0.994</td>
</tr>
<tr>
<td>Wide</td>
<td>50</td>
<td>50</td>
<td>23</td>
<td>0.155</td>
</tr>
<tr>
<td>Crown density</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>20–29%</td>
<td>28</td>
<td>19</td>
<td>28</td>
<td>0.650</td>
</tr>
<tr>
<td>30–39%</td>
<td>63</td>
<td>35</td>
<td>63</td>
<td>0.013</td>
</tr>
<tr>
<td>40–49%</td>
<td>54</td>
<td>54</td>
<td>33</td>
<td>0.221</td>
</tr>
<tr>
<td>50–59%</td>
<td>60</td>
<td>60</td>
<td>0</td>
<td>0.001</td>
</tr>
<tr>
<td>Stem</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Straight</td>
<td>48</td>
<td>35</td>
<td>48</td>
<td>0.556</td>
</tr>
<tr>
<td>Curved</td>
<td>57</td>
<td>38</td>
<td>57</td>
<td>0.186</td>
</tr>
<tr>
<td>Double</td>
<td>54</td>
<td>54</td>
<td>26</td>
<td>0.106</td>
</tr>
<tr>
<td>Triple</td>
<td>37</td>
<td>37</td>
<td>9</td>
<td>0.175</td>
</tr>
<tr>
<td>Multiple</td>
<td>13</td>
<td>13</td>
<td>0</td>
<td>0.489</td>
</tr>
<tr>
<td>Crown branch angle</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&gt;70°</td>
<td>52</td>
<td>29</td>
<td>52</td>
<td>0.203</td>
</tr>
<tr>
<td>50–70°</td>
<td>56</td>
<td>56</td>
<td>16</td>
<td>0.056</td>
</tr>
<tr>
<td>30–50°</td>
<td>48</td>
<td>48</td>
<td>34</td>
<td>0.442</td>
</tr>
<tr>
<td>&lt;30°</td>
<td>25</td>
<td>17</td>
<td>25</td>
<td>0.758</td>
</tr>
</tbody>
</table>

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**Fig. 2. Partial RDA (covariables: stand stocking levels, site type fertility, tree age) Ordination diagram: correlations among red oak morphological traits by continentality.**

Crown width increases from narrow to wide crown. Stem quality increases from multiple-stemmed tree to one straight stem tree. Crown branch attachment angle increases from 20° to 100°. Length of straight stem increases from 0 to 25 m. Crown density increases from 20% to 65%
In general, red oak seedlings spread successfully 100 m from the parent tree in sites with moderate fertility.

**Leaf litter decomposition intensity**

The results of this study show that leaf litter decomposition intensity for red oak in natural conditions is almost the same as in higher temperature conditions, as when samples were under an agro sheet cover (Fig. 3).

Figure 4 shows that leaf litter mass loss after 2 years (24 months) was almost the same in both conditions. No significant difference was observed ($Z = -0.13; p = 0.89$).

### Discussion

Red oak is native to the American continent. Mean annual temperatures vary from 4°C (northern regions) to 16°C (southern regions) in its native habitat. Growing season duration ranges from 100–220 days (Core 1971). Lithuanian territory lies at the northern border of red oak habitat, according to the USDA plant hardiness zone map (Cathey 1990, Kelley 1998, Sander 1990). In the western part of Lithuania, mean annual temperature was 6.30°C, mean temperature in January was −4.16°C, mean temperature in July was 16.52°C and the growing season was 197 days from 1980–1990 (Anonymous 1999). In the central-southern part of the country, mean annual temperature was 6.27°C, mean temperature in January was −5.56°C, mean temperature in July was 16.90°C and the growing season was 194 days in the same period (Anonymous 1999). Minor differences in climatic data are evident between these regions, but in the maritime area the winter is milder and spring frosts are less dangerous than in the continental region.

Cold winters and spring frosts restrict good tree growth and healthy stem development. However, climate warming may improve red oak stem quality, providing harvesters of this tree with an economically rewarding future in Lithuania. However, no obvious differences in red oak stem quality were noted after comparison of the milder marine and colder continental habitat conditions in this study.

Red oak acorns are primarily dispersed by birds and mammals. Mice and chipmunks are short-distance dispersers that usually move acorns 10–30 m from the parent tree (Crow 1988). Squirrels distribute acorns over longer distances. Blue jays are effective long-distance dispersal agents; acorns can be transported from several hundred meters to 4–5 km away (Kittelredge et al. 1990).

Results of investigations of seedling spread show indirectly that climate warming will not reduce invasiveness of this alien species. Thus, the threat of native forest tree species composition change remains. Red oak seedling spreads at sufficiently long distance for adequate growth in both mild and harsh climate zones. Seedling spread is limited by soil fertility rather than temperature difference. The abundant herbaceous cover restricts the competition limit of alien oak spread (Riepšas and Straigytė 2008).
In an investigation of leaf decomposition, Hansen (1999) noticed that red oak leaves decompose better only after their second fall. Thus, the remaining leaves create a litter carpet in dense stands. Our results showed that after 2 years, red oak leaf litter mass losses were 42.4% (under the agrosheet cover) and 41.8% (without the cover). These results are very close to those of another study conducted on Q. robur, where mean mass loss after 24 months was 40.4% (Sariyildiz and Anderson 2003). However, most intensive leaf litter decomposition occurs after the first fall (31% of mass loss). During the second year of this study, the intensity of leaf litter decomposition decreased and mass losses reduced to 11% (Figs 3, 4).

Plant leaf litter indirectly affects neighbour plants in various ways. One of the most important is that it changes the biotic, physical and chemical characteristics of the soil. Our results show that in a simulated climate warming situation, increased temperature did not influence microorganism activity and resulting decomposition of red oak leaf litter. The explanation for these results is unclear. Results of other studies show an impact of increased temperature on microorganism activity.

Temperature plays an important role in soil quality, affecting both the microbial biomass content and soil processes mediated by enzymatic catalysis (Li et al. 2011). Only in recent years have experiments shown that plant populations can be affected by the complex relations between plants and soil microorganisms in a biocenosis (Bever et al. 1997, Clay and Van der Putten 1999, Packer and Clay 2000).

Vegetation structure of alien red oak stands and natural common oak stands differ in Lithuanian forests. Species numbers are significantly lower in red oak stands (Marozas et al. 2009). Nevertheless, alien oak changes vegetation cover and decreases diversity in domestic plant communities. If climate warming occurs, this tendency will remain, as microorganism activity will not change and the conditions will remain favourable for alien oak seedlings to spread.

According to the results of this study using indirect climate warming indicators, the effect of climate change on red oak development in Lithuanian forests will be minimal. Red oak stem quality will not be influenced. The environmental conditions for red oak spontaneous seedling spread will remain favourable. Intervention is needed to prevent composition changes, promote native stand tree species and protect diversity in domestic plant communities.

Acknowledgments

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References


