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European oak decline phenomenon in relation to climatic changes

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ABSTRACT

The complex phenomenon of decline in European oak is currently triggered by changing climatic conditions and their consequences like heavy rains, local floods and pest development. Especially, pathogens from *Phytophthora* genus profit from soil saturation with water. They are alien invasive species, which attack and severely damage fine roots. In drought conditions occurring in the subsequent year, many oaks die as they encounter problem with water uptake. Additionally, insect defoliators followed by oak mildew infections accelerate the level of tree mortality. Secondary insects, butt and root pathogens are usually the final cause of death of many oaks. More research is needed in the direction to determine (i) measurable factors (e.g. chlorophyll florescence) that can indicate that the process of tree decline has already started, (ii) the correlation between the root decay and the crown symptoms (scanners, software), (iii) which combination of stressors stimulate the best development of pathogens that lead to the high plant mortality and (iv) the difference between the mortality caused by the native and the invasive *Phytophthora* species.

KEY WORDS

Quercus spp., Phytophthora, Armillaria spp., climate change, pathogen, pests

INTRODUCTION

The impact of recent global climate change has been well documented through changes in plant phenology, morphology and abundance (Richardson et al. 2013). Damages to forests caused by the extreme climatic events have also been well documented (Linder et al. 2010). The climate change scenarios for the 21st centu-

ry had predicted changes in the ecosystems, which will cause many difficulties for oaks to adopt and mitigate these new environmental conditions (Corcobado et al. 2014; Linder et al. 2010; Borja et al. 2008). During the 21st century, the temperature will continue to raise (according to different scenarios) between 1.1 and 6.4°C (IPCC, 2007), causing many problems to plants and even more complex ecosystems such as forests.

Plants are continuously affected by below- and above-ground abiotic and biotic stressors (Milanović et al. 2015). Because of the complexity of the forest ecosystems, it is becomes very complicated to hypothesise the effect of climatic changes, especially in an interaction between plants and their dependent communities of organisms (including pathogenic ones). The impact of climate change on plants and their interaction with herbivores and pathogens are usually based on models, because of lack of data or insufficient data about these changes (Poutasso et al. 2012; Milanović et al. 2015). The plant diseases driven by pathogens are expected to be exacerbated by the negative effect of weather extremes on forest ecosystems (Santini et al. 2013). The pathogen ecology is strongly dependent on environmental factors, such as temperature, moisture and changes in winter temperatures as a result of global warming. This can influence their distribution and development or even the pathogenicity. The negative effects have also been reported for herbivore and root-damaging insects (Masters et al. 1993).

This review focuses on the importance of climatic changes and how they directly (changing weather conditions) and indirectly (increased pest and diseases) affect the European oak tree populations. Different causes of the oak decline phenomena are mentioned and discussed in this review.

DROUGHT AND WATER LOGGING

The whole of Europe will be, according to climate model simulation, under pronounced periods of droughts and/or water logging (Linder et al. 2010, Potausso et al. 2012, Portz et al. 2011). These two factors cause stress and increase the vulnerability of oak trees, which are among the most valuable broadleaved trees in Europe. The different stages of oak stands affected by the phenomenon of decline were observed in the last decade throughout Europe. The complexity of oak decline process and spectra of involved biotic agents were reviewed by Oszako and Delatour in "Recent advances in oak health in Europe" (Oszako and Delatour 2000). The main biotic factors involved in oak decline are root pathogens (*Armillaria* and *Phytophthora* species) and insect defoliators.

FACTORS AFFECTING OAK DECLINE

Phytophthora

Plant pathogens of the genus *Phytophthora* have a global distribution and play a crucial role in damaging both agricultural crops and forest ecosystems (Nilsson and Diunker P. 1997; Oβwald et al. 2014; Milenković et al. 2012). Several *Phytophthora* species (*P. quercina, P. cambivora, P. plurivora*, etc.) were linked with the decline phenomenon of oak trees. The level of fine root damage often reaches 90% or more (Fig. 1).

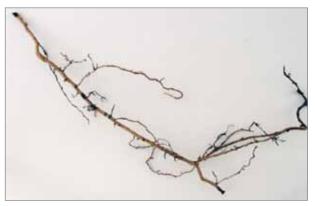


Figure 1. Fine roots of pedunculate oak (over 100-year-old), damaged in 90%

Those species are able to infect both juvenile and mature pedunculate (Quercus robur L.) or sessile oak (Q. petraea Liebl.) trees and affect their vitality by decreasing their photosynthesis, the growth of roots and their functionality (Jönsson et al. 2003, Barajas-Morales et al. 1997). An invasive pathogen such as P. cinnamomi, which can potentially deteriorate the health status of Mediterranean oak trees (Oszako and Orlikowski 2005), has been recently discovered at a high incidence in the study of three native pedunculate oak forests in Poland (unpublished 2015). However, P. cinnamomi was recorded on pedunculate oaks in Poland already in 2005 (Oszako and Orlikowski 2005). As this pathogen is highly dependent on soil water content and mild temperatures, a combination of observed climate warming and frequent weather extremes could enhance the decline process of the abovementioned populations of oaks, which is of much concern for local foresters.

ARMILLARIA

The Armillaria species are opportunistic pathogens that cause damage to a wide range of woody hosts (Shaw and Kile 1991; Fox et al. 2000). Usually, they attack the already stressed oaks and cause decay in the main roots and the sapwood. These fungal species demonstrate different levels of their pathogenicity, which is highly correlated with the production of rhizomorphs (Morrison 2004). The shift in the pathogenicity of opportunistic pathogens, Armillaria gallica (Fig. 2) and A. cepistipes, was observed in Europe during the oak decline incidents in the past (Keča et al. 2006; 2009; Lushaj et al. 2010; Keča and Solheim 2011; Cleary eta l. 2012, Cleary and Holmes 2011). They also often follow damage that Phytophthora causes to fine roots infecting the vicinity of cankers occurring on mother roots (Fig. 3).

Insect defoliators

The insect defoliators regularly cause damage to oaks and other broadleaf forest tree species, particularly in the Northern Hemisphere. A recent study showed that the leaves of *Quercus rubra* L., naturally infected by *Phytophthora plurivora* are more susceptible to an attack by *Lymantria dispar* L., than leaves of healthy trees (Milanović et al. 2015).

OAK DECLINE PHENOMENA AND RESEARCH GAPS

There are considerable knowledge gaps about the oak decline phenomenon; especially processes leading to the deterioration of tree health and possible death are barely investigated. The visible symptoms of disorders are often too general and therefore it becomes difficult to find practical solutions to mitigate its consequences. In particular, there is little understanding of how the extreme weather conditions influence the subtle interaction between the local population of tree-hosts, pathogens and insect pests. How do host-pathogen interactions change if abiotic stress disrupts physiological processes in oaks? It is of major importance to recognise the decline process in the initial phase, because once the decline syndrome starts, it is hard to stop its further development. Also the involvement of contributing factors such as secondary insect pests (Cerambyx spp., Agrillus spp., Scolytus intricatus (Ratz.) (Coleoptera: Scolyti-



Figure 2. Mycelial fans of *Armillaria gallica* developing under the bark od declining oak trees



Figure 3. Lateral roots completely damaged by pathogens of *Phytophthora* genus. The canker (in the middle) is being healed by callus tissues (from both sides) but rhizomorphs of *Armillaria* sp., which are attached to the root surface, (above) started secondary infection

nae), etc. or stem-decaying fungi (Fomes fomentarius (L.) J.J. Kickx, Kretzschmaria deusta (Hoffm.) P.M.D. Martin (Fig. 4), Stereum spp., Trametes spp., Phellinus igniarius (L.) Quél. and P. robustus (P. Karst.) Bourdot & Galzin, etc) is usually hard to prevent.



Figure 4. Mycelium of *Kretzschmaria deusta* destroying bark and wood of stressed oak trees

Oak decline phenomena are complex, multi-factor disease, resulting in a progressive weakening of trees and leading to the dieback of their crowns (Manion and Lachance 1992). In their study, they observed the loss of vitality of oaks and the reduction in their growth rate, as well as an increase in their susceptibility to abiotic and biotic stressors. The decline syndromes generally affect trees of all age classes and ultimately cause their death, unless the stress is removed (Woo 2009). Though many researchers had studied forest decline from different points of view, the main cause of this widespread phenomenon is still not well understood. In the light of effects of climatic factors (single or combined), such as summer drought or heavy rains, the decline of trees, in particular oaks, could be even more readable in the course of

the 21st century. Knowledge of physiological processes accompanying different disorders, ultimately leading to the mortality of oaks, is crucial to understand their susceptibility to predisposing (soil properties, drought, stand structure, etc.), inciting (primary insects, oak mildew, winter frost, etc.) and contributing (root rot diseases, stem decay fungi, secondary insect pests, etc.) factors (Figs. 3) and 4) (Ceisla and Donauber 1994). To understand this complex process, the factors contributing to the decline process and their interactions under controlled conditions need to be separately tested. The susceptibility of pedunculate oak (O. robur) to climate extremes like drought/ flood, followed by the root infection with the native pathogens like Armillaria gallica, P. plurivora or the invasive one as *P. cinnamomi*, is still unclear. The decline process is strongly correlated with the destruction or decay of the root system and crown defoliation (Figs. 1 and 2). However, in the case of mature trees, it is very hard to find any correlation between the amount of decayed roots and symptoms observed in their crowns.

Armillaria gallica is the native pathogen to oak stands representing an opportunistic species that attacks stressed trees and coarse roots, while P. plurivora is a biotroph that colonises mainly fine roots. It is still unknown if the loss of the fine roots will have a stronger influence on the decline of stressed trees, e.g. by insect defoliators, than the loss of the coarse roots. Also, there is evidence that the synergistic activity of both pathogens may occur during the decline of oaks (Jung et al. 2016; Oßwald et al. 2014; Keča et al. 2015). The invasive P. cinnamomi could cause much more serious problems if it is introduced in a new ecosystem, similar to as it was observed in oak stands (Quercus coccifera L., O. ilex L. and O. suber L.) in the Mediterranean region (Brasier 1996; Brasier and Scott 1994; Corcobado et al. 2014; Linaldeddu et al. 2014).

PHYSIOLOGICAL ASPECTS OF TREE REACTION TO DROUGHT AND PEST ATTACK

The high carbon availability during the root growth should increase an oak's defence capacity against the root pathogens (Jönsson 2006). Another study showed that the ability of trees to mobilise non-structural carbohydrates against root-rot pathogens enhances its susceptibility and speeds up the decline process (Angay

et al. 2014). So, there is no consensus reached on the influence of photosynthetic assimilates (simple sugars) on the activity of harmful organisms (insect defoliators, fungi, Oomycetes).

The root pathogens strongly influence the water relations in the woody plants, which particularly implies the transpiration and photosynthesis of leaves. The measurements of gas exchange and the fluorescence of leaves may be used to calculate the electron transport rate (Laisk and Loreto 1996). The differences between the electron transport rate calculated from the fluorescence ratio and that calculated from the gas-exchange measurements have been used to estimate the mesophyll diffusion resistance and chloroplast CO₂ concentration and non-photosynthetic carboxylation and decarboxylation rates. These parameters could be used for an assessment of the process of photosynthesis and the health condition of oaks.

Furthermore, plant hormones, like abscisic acid (ABA), play an important role in many aspects of plant growth. The adaptation to drought and low temperatures is regulated by the combinatorial activity of interconnected ABA-dependent and ABA-independent signalling pathways (Mauch-Mani and Mauch 2005). By contrast, the plant hormones like salicylic acid (SA), the jasmonate acid (JA) and the ethylene (ET) play a major role in the trees' resistance to pathogens and insects (Flors et al. 2008). The combination of these hormones could be crucial in the assessment of the stress in trees as well as in the resistance/susceptibility of trees to later pest attacks (Thaler and Bostock 2004).

GENETIC VARIATION VS HEALTH STATE OF OAK STANDS

Thirteen oak (*Q. robur*) populations from the Krotoszyn and Elbląg Forest Districts, located in central and northern Poland (51°68' N, 17°44' E and 54°20' N, 19°73' E, respectively), were analysed in order to determine genetic variation and similarity in relation to health and resistance to stress factors (Nowakowska et al. 2007). Chloroplast DNA was investigated using PCR-RFLP markers. Different frequencies of six haplotypes variants ('1', '4', '5', '7', '10' and '12') of 'DT' and 'CD' loci primers were determined. All oak populations studied were characterised by high genetic variation ($G_{ST} = 0.818$), which

indicate higher genetic variation observed within the stand than among them (Nowakowska et al. 2007). Going into details, higher genetic variation was observed in trees from central Poland (Krotoszyn; $H_T = 0.809$) in comparison to the northern part (Elblag; $H_T = 0.785$). Oaks stands from Krotoszyn mostly originated from the Balkan and Iberian oak refugees, as demonstrated by the presence of prevalent haplotype pattern composed of variants '5', '10' and '12', respectively. Within this region, noticeably Jarocin stand was composed by trees with one Balkanian haplotype '7' to the extent of 87%. Conversely, most stands of the Elblag Forest Region presented the haplotype pattern typical of the Apennines post-glacial oak refuge (with predominating variants '10' and '12'). One population from this region, Młynary, exhibited slightly different pattern with a high proportion of Balkanian haplotype '4' (40%) and Iberian haplotype '12' (38%).

Within these oak populations, Jarocin (Krotoszyn FD) and Młynary (Elblag FD), stand health was monitored from 1999. Different levels of injury symptoms were observed between stands but mortality was higher in Jarocin, less genetically variable (with predominant frequency of one Balkanian haplotype '7'). Severe damage affected 60% of the trees in Jarocin stand after 2003, which was probably due to a combination of unfavourable climatic conditions and infection by pathogens, e.g. Phytophthora and Pythium. It has been shown that in Poland, oak trees have been colonised mainly by P. quercina, P. cactorum, P. plurivora, P. cambivora and P. cinnamomi (Oszako and Orlikowski 2005; Jankowiak et al. 2014; Nowakowska et al. 2016). Comparing chloroplast DNA variation data obtained for Młynary from central Poland and Jarocin from northern Poland, the population with higher cpDNA differentiation (Młynary) appeared better adapted to the changing environmental conditions (drought, high temperature) than Jarocin with lower genetic variation (Nowakowska et al. 2007).

RECOMMENDATIONS FOR FURTHER RESEARCH

Further research has to be done in order to determine (i) measurable factors that can indicate that the process of tree decline has already started, (ii) the correlation between the root decay and the crown symptoms,

(iii) which combination of stressors stimulate the best development of pathogens leading to high plant mortality, (iv) the difference between the mortality caused by the native and the invasive pest species.

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