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Impacts of climate change on pedunculate oak (*Quercus robur* L.) and *Phytophthora* activity in north and central Europe

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ABSTRACT

A climate change will affect the forests around the globe; there may be competitions for available resources that are needed for growth and dispersal. Europe is supposed to be more sensitive and may experience a greater influence than many other regions. As an additional effect of climate change extreme weather events will be more frequent e.g. drought and extreme precipitation that will cause flooding. The future weather and climate may affect pedunculate oak (*Quercus robur*) both by weakening and strengthening. Drought and flooding may induce a higher susceptibility among trees to pathogens such as *Phytophthora* due to stress. A higher temperature may extend the growing season and in interaction with good moisture supply and CO2, carbon assimilation for growth might increase. Pedunculate oak, however, seem rather tolerant to a climate change and its additional effects, tough, in events of infection by *Pytophthora* after a period of stress, the outcome might be more severe than if infected when not stressed. The oak may be declining but compared to other trees e.g. beech (*Fagus syvaltica*), it may not be that severe. It seems as if beech is more susceptible to both climatic factors and *Phytophthora* and might be more threatened in the long run, which might imply on a greater distribution of oaks

SAMMANFATTNING

En förändring i det rådande klimatet med en temperaturhöjning på grund av en ökad atmosfärisk CO_2-koncentration kan komma att ha en påverkan på skogar över hela jordgloben. Trädarter som är anpassade till ett visst klimat kan komma att spridas norrut då klimatet kan vara mer passande i framtiden. Detta medför risken att lövträd från central Europa kan konkurrera ut barrträden i norr. Skogseken som är distribuerad över stora delar av centrala Europa och södra delarna av norra Europa kan i framtiden ha en större utbredning eller en lika stor utbredning men på nordligare breddgrader där ett mer passande klimat kommer att råda.

En klimatförändring har många efterföljande effekter så som extrema väderförhållanden, vilka kan komma att skada Skogseken men möjligheten att den härdas finns även. Extrem torka och översvämningar kommer att bli mer vanligt och har redan blivit observerade i Europa och Skogsekens reaktion på dessa händelser kan variera och forskare är något oense om framtiden. Torka ska, enligt den typiska responsen, generera att en större mängd kol allokeras från skott till rot. Detta ska ge trädet en möjlighet att expandera rotsystemet för lokalisering av vatten längre ned i jorden. Dock har studier visat på olika responser, som både ökad och minskad rottillväxt. Även en reglering av vatten som släpps ut via bladen kan ske för att hushålla med vatten. Vid översvämning är Skogseken väl anpassad genom att trädet kan ta tillvara syre som finns i organiskt material. Denna process är dock energikrävande men det visar sig att Skogseken kan underhålla processen genom att reglerar flödet av kol till rötterna.

En temperaturökning generar även en ändring i fenologiska händelser, så som tid för knoppbristning och bladfällning i slutet av växtsäsongen. En tidigarelagd knoppbristning kan öka risk för nya blad att utsättas för vårfrost, detta kan i värsta fall leda till för tidig bladfällning. Temperaturen kommer även att höjas under vintern och detta kan leda till att trädet inte kan komma in i ett nödvändigt vilotillstånd som sker vid en viss temperatur som krävs för att en växtsäsong senare ska starta. Vid en frånvaro av viloperioden kan en onormal knoppbristning med sämre fungerande blad uppstå.

Ökningen av CO_2-koncentrationen i luften skulle kunna bidra till en ökad tillväxt men då i ett fall med en tillräcklig mängd kväve att tillgå. I framtiden verkar dock detta inte vara något större problem. Däremot finns det andra faktorer som kan hämma denna tillväxt t.ex. vattentillgång.

Ett, p. g. a. klimatfaktorer, redan försvagat träd kan vara mer mottagligt för sjukdomar. Patogenen *Phytophthora* som tidigare har återfunnits i USA och då varit förödande mot ekskogar har även spridits till Europa. Symptomen av denna sjukdom är bl. a. rotröta och uttunning av kronverket. *Phytophthora* även komma att finna fördelar med klimatförändringen då den favoriseras av våta förhållanden och kan lättare spridas vid en översvämning.

I en kombination av klimatförändring och *Phytophthora*, kan Skogseken drabbas av en betydande nedgång och i svåra fall även ökad dödlighet. I jämförelse med andra lövträd, t.ex. bok, tycks dock Skogseken vara tolerant mot detta då boken verkar mer mottaglig för dessa faktorer.

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TABLE OF CONTENT

INTRODUCTION

Climate change will affect the entire globe and every living organism in one way or the other. In Europe there may e.g. be a vegetation shift northward where deciduous tree species, mostly occurring in central Europe, might integrate with coniferous forests in the Boreal zone. The effect of this might be that deciduous trees will outrival the coniferous trees due to that future climate will be more suitable for the invasive species (Hickler et al., 2012).

As being a deciduous tree, pedunculate oak (*Quercus robur L.*) is distributed in central Europe and up to southernmost Scandinavia but have, in the past, been covering a much larger area than today due to agriculture and other anthropogenic activities (Smith & Smith, 2003). Today, a great number of oak stands in Europe have been reported as declining, with symptoms such as crown thinning, leaf defoliation & root damage etc. (Jung, 2000) and there are various reasons explaining the decline. Both abiotic and biotic sources of stress have been reported, such as extreme weather events and attacks by pathogens and insects (Thomas, 2002).

Oaks have an optimal physiological environment which includes several factors e.g. temperature, water availability and atmospheric CO_2 concentration etc. These abiotic factors will be changing according to future climate projections, which also may result in a change in the frequency and intensity of weather extremes such as drought, flooding, storms and heat waves (Rowell, 2005). Important components when subjected to different stress factors are duration and intensity of such extremes. If the trees/plants are only stressed during a short interval the effect may not be significant. If they are stressed under a shorter interval during several events, it may harden the trees so that the species eventually adapt to a specific stressor. Though, in terms of climate change, the changes are occurring in a faster rate than succession is (Schultze et al., 2002). A different climate will change a variety of processes in oak forests e.g. growth, competitive abilities and cycling of nutrients (Smith & Smith, 2003).

The changing climate is not only causing direct stress on oaks but also indirect effects due to pathogenic development. The pathogen *Pythophthora* have been found in many deciduous forests through Europe and might be one contributing reason to the complex decline that is already observed (Jung et al., 2000) and there is a possibility that global warming and its additional effects may enhance the activity of the pathogen and so also the amount of trees infected (Bergot et al., 2004).

The pedunculate oak belongs to the Beech family (*Fagaceae*) and is a large, slow growing deciduous tree (Nixon, 2006) and is, together with sessile oak (*Quercus petreae*) and beech (*Fagus sylvatica*), the most common deciduous tree species in northern and central Europe. Oaks have a high economic value and the forests inhabits a high species diversity making them valuable in Europe (Nixon, 2006) and it is therefore important to try to predict the future.

The aim of this literature study is to describe both direct and indirect effects that climate change may have upon the deciduous pedunculate oak in central and northern Europe. The predicted climate change, due to a rising CO_2 concentration in the atmosphere, will raise the global temperature. A resulting effect from the higher temperatures may be more frequent extreme weather events, such as drought and flooding. Another indirect effect may also be a spread of the pathogen *Phytophthora* that might benefit from this warmer climate and the possible weakening of its host due to weather extremes. In this review, there will be a focus in the three following questions but also a discussion concerning the future of pedunculate oak and in comparison to other deciduous trees e.g. beech.

1. What factors are affecting oak in present time?
2. How will a change in climate affect the oak?
3. Will the pathogen *Phytophthora* be affected by a climate change?

As restrictions, due to the broad sentence of climate change, only climatic factors such as drought, flooding, CO_2 and temperature will be addressed. These factors are affecting both growth and adaptability to stress and also the activity of *Phytophthora*. Temperate forests inhabit pedunculate oak and are mostly distributed in central and southern parts of northern Europe, which is why this review is concentrated on this area.

Background

CLIMATE CHANGE MAY INDUCE STRESS

Present climate is changing due to increasing CO_2, which in turn will raise temperatures around the globe. Though, the magnitude of change over the globe has different projections (IPCC, 2007). According to the Rowell et al. (2005), Europe will experience a higher anomaly than the global average with a higher increase in temperatures and a north to south gradient in precipitation change with a decrease in southern Europe and an increase in northern. One reason to the more pronounced warming expected in Europe is due to seasonal snow cover deficit which has the effect of lowering the albedo making the temperature contrast even greater (Giorgi et al., 2004). Environmental factors such as climate can become stressful to trees when their optimal environment turns into a non-suitable environment. All vegetation is stressed under some time in their lifecycle, although, the degree of stress is mostly a determining factor when considering survival. When exposed to a long term stress, competition between species begins, due to the shift from reproductive survival to a more maintenance survival strategy, some species don't have the ability to sustain in its origin if the needs are not fulfilled (Larcher, 2001).

When trees are subjected to stress there may be different stages to go through. If the stress event is approaching gradually the tree will probably be able to recover. However, if the stress factor is appearing rapidly and is intense, there may be a more complicated outcome. One stress reaction is catabolism, which means that the tree rather breaks down proteins and carbohydrates than build them up, although, if stress last, the tree will try to repair the damage that is done. When subjected to stress the tree may be hardened and it may go into a resistance phase that may last for some time afterward. Though, there will not be a lifelong protection against new stress events (Larcher, 2001).

All carbon that is assimilated in the photosynthesis process is not directly used for growth and reproduction. Trees also have to store carbon for events such as bud burst and later growth. The stored carbon is used in events of stress, when usually assimilation decreases due to stress maintenance. Deciduous trees are highly dependent on seasonal storage due to their variation in demands between growth and dormancy periods (Chapin et al., 1990). The capacity to buffer carbon is time limited and the stored carbon used for e.g. bud burst is only 0.7 years old and for root growth 0.4 years when not stressed in contrast to coniferous trees that can store carbon for several years. This fact indicates that, if trees are stressed they might not assimilate enough carbon for their annual growth and reproduction processes in coming years (Gaudinski et al., 2009).

There are several ways to investigate the health of trees. By studying tree rings, it is possible to determine if any stress have occurred in the past. An annual tree ring is divided into early- and latewood, the early wood production is to a large extent influenced by previous environmental events and is also dependent on the same factors as bud burst and new shoots. In turn, those factors that retards the shoot growth and enhances senescence, makes up the differentiation in the latewood. A smaller tree ring may indicate on stress due to the need of using more carbon to sustain other organs or the fact that there is lower carbon assimilation. Also, a stressed tree that decreases in stem growth etc. may lose its stability and be more susceptible to other stresses, both biotic and abiotic (Spies et al., 2012).

INCREASING TEMPERATURES

In the future, according to Rowell, (2005), seasonal temperature changes will differ between locations and it will most likely be an increase in winter temperatures in northern Europe. The expected temperature rise will range from 3 to 5^{o}C over most of Europe during winter. Eastern Europe may though experience a greater change than the western, up to 7^{o}C due to loss of seasonal snow cover. The albedo will be lowered due to absence of snow cover which enhances warming in northern and eastern Europe. Most of the present snow covered areas will experience reduces in up to 80% and as a result of lost snow cover, flooding will be more common (ibid). The winters may be experiencing a higher temperature anomaly in the future, however, summer temperatures will also be higher and in combination with drought temperatures might reach even higher. According to Beniston et al. (2007), inter-annual variations in temperature will also be more prominent in the future and there is a probability that central Europe will experience the same number of excessive heat days by 2100 that southern Europe experiences today. Also, the number of hot days will increase more rapidly than the average temperature. When trees are subjected to extremely high temperatures one of the first reactions is to slow down photosynthetic activity, with a later result of an unbalanced carbon metabolism. This stop in photosynthesis may lead to cell death and at some point, the damage is no longer reversible (Larcher, 2001). Changes in phenology are also effects caused by warming, bud burst occurring earlier and senescence later and higher winter temperatures may lead to a lack in winter dormancy which is highly important for e.g. bud break.

DROUGHT

Dry summers in central Europe have been observed frequently in the last years. According to Briffa et al. (2009), this is due to the increasing summer temperatures. The typical drought stress reaction in trees is to allocate more of the energy to the root system. By expanding its root system it may be able to reach deeper soil layers were moisture content is higher. In particular, the fine roots are very important to trees due to uptake of water and nutrients. The allocation is, however, in expense of other organs, such as shoot growth, and also reproduction efficiency may be lowered with lowered fertility in pollens. During drought, there are probably no organs that don't get affected by the stress (Larcher, 2001).

PRECIPITATION

Beniston et al., (2007) also predicts that the precipitation pattern will change, with an increase in winter in northern and central Europe. The winter precipitation increase occurs north of latitude 42°N (Giorgi et al., 2004) and only slightly south of 50 °N (Rowell, 2005) and the annual projection may exceed a threefold increase. Summer precipitation in northern and northeastern Europe will probably increase but not to the same extent as in winter time (Beniston et al., 2007). Though, central Europe may experience less precipitation than northern but with an increase in frequency of high intensity rainfall events during shorter periods (Beniston et al., 2007; Christensen & Christensen, 2004). Variability in precipitation may also increase with a higher frequency of rainfall and with a greater magnitude causing flooding and destruction. Southern Sweden and Central Europe for an example will have a lower mean summer precipitation but the daily extreme precipitation seems to increase (IPCC, 2007). Flooding events may for some tree species be a source of stress with hypoxia as a result. On the contrary, oak trees are often grown by river banks and it seems as if they are tolerant to this kind of event. Although, as earlier mentioned, much of the tolerance ability is dependent on duration and intensity (Larcher, 2001).

In case of e.g. drought or flooding that exceeds a threshold in time which the tree can sustain, the stress may lead to a state of exhaustion which may weaken the tree and make it more vulnerable to e.g. infections and parasites. The tree may be able to recover, but if the duration and intensity exceeds the tolerance level the tree may be permanently damaged or it may even be mortal (Larcher, 2001).

PHYTOPHTHORA - AN AGGRESSIVE PATHOGEN

The pathogenic family *Phytophthora* includes various species and has a wide host range. The most severe damage, that also is the most common, is that it can cause root rot, though in some cases, it infects the stem of trees as well. In addition, in stands with the pathogen, there have often been observations of thinner crown, which may be a part of the infection pattern (Jung et al., 2000, 2009). *Phytophthora* is fungus-like but is more closely related to brown algae. There are several species in this family that infects oak trees, such as *P. ramorum* that seems to have caused Sudden Oak Death in the U.S. (McPherson et al., 2005) and *P. cinnamomi* that infect trees mostly in temperate and subtropical areas (Sturrock et al., 2011). However, the one species that are most common in soils of oak trees in north and central Europe is *P. quercina* that seems to be more host specific than other *Phytophthoras* and is infecting mostly oak species. This species have been found frequently in pedunculate oaks rizosphere. It is aggressive towards the roots and is one of the most damaging of all the *Phytophthora* species to oaks in Europe (Jung, 1999).

Pythophthora is a soil born pathogen that uses moisture for dispersal and reproduction and is rather sensitive to pH in soils. E.g. in more acidic soils, no findings have been done (Camy et al., 2003). If the future will lead to a more common extreme weather, like drought and flooding, epidemics may be triggered (Sturrock et al., 2011). Soil type seems to be a significant factor in the spread of the pathogen. Sandy-loamy to loamy, silty and clayey soils with pH between 3.5 and 6.6 seems to be more preferable (Jung et al., 1999). Also, due to the fact that it favors moisture it is most likely to be infecting trees grown in more clayey soil. However, soils can inhabit *Phytophthora* species, though not very active due to present unfavorable conditions (Thomas et al., 2002).

Results

What factors are affecting oak in present time?

There are several factors influencing the oak in present day. The tree responds to all of them, though, in different ways to each factor. These responses are often caused by stress and can either harden or weaken the tree which may be important when, or if, subjected to the stressor recurrently.

Recurrent Flooding

Mature oaks are rather tolerant to flooding (Kramer et al., 2008). When inundated and subjected to oxygen deficit, they have the capability to switch from mitochondrial respiration to fermentation metabolism which uses oxygen from organic compounds. This is however, an energy consuming process and uses stored carbohydrate, tough, especially oaks have the ability to regulate the energy flow to the roots so it may be able to be inundated for a longer period (Ferner et al., 2012). Also, to survive during these conditions the mature oak has the possibility to form lenticels that can supply roots with oxygen. This would indicate on a rather high tolerance to flooding (Parelle et al., 2007).

However, there is a probability that flooding may lead to more damage to trees when inundation persist over a longer time or occur at several occasions during growth period. In floodplains with recurrent flooding, the presence of hardwood tree species such as oak decreases as fewer saplings can survive. Annual time of inundation seems to be the factor keeping them from growing in such a site. Especially, saplings seem to be sensible to flooding and they suffer severe damage at only a low inundation period (Vreugdenhil et al., 2006), which may be a reason to the absence of oak trees. According to Alaoui-Sossé et al. (2005), who subjected saplings to inundation for 14 days, the root system was severely affected. Both length and biomass decreased and also a decline in stem width and total leaf area was observed. Due to hypoxia in the root system, which most probably was the reason to the decrease, there was a delay in bud break which may explain the decrease in leaf area. However, after the 14 days of inundation the saplings were subjected to drainage. 26 days later both root length and root biomass increased (ibid). Pedunculate oak sapling seems, although, to recover from inundation quite well as in contrary to sessile oak that, according to Parelle et al. (2006), suffered to a greater extent by shoot dieback and had less chlorophyll in leafs.

However, Vreugdenhil et al., (2006) suggested that on a 10 year average, approximately three days of flooding per year should be enough time to cause damage to the oak saplings and, if longer time of inundations occurs, there will be fewer saplings present. Also, the effect of inundation occurring in their growing season (june-july) is also mostly negative. Flooding during this time of year is the worst scenario and is a highly disadvantage. Lack of oxygen and overall physical damage prohibits the growth. (ibid)

TEMPERATURE EXTREMES

The environmental temperature is controlling trees phenology e.g. bud burst and leaf senescence. To proceed from the event of winter dormancy a specific temperature has to be reached and this threshold for oaks is at circa 5°C for bud break and senescence demands at least 10°C. If frost occurs after bud break the tree may suffer from damage in newly unfolded leaves by causing embolism in vessels and reducing water transport and it could generate a complete defoliation if the frost is severe enough. This kind of event was observed in Germany during 1990's with the result of defoliation and loss in tree vigor (Thomas et al., 2002).

SUMMER DROUGHT

According to Friedrichs et al. (2008), Gieger & Thomas (2001) and Epron & Dreyer (1993), oaks adapt to drought by reducing the amount of water lost by leaves i.e. higher water use efficiency as result of reduced stomatal conductance and carbon assimilation. Even though these processes alter when subjected to drought, a severe drought, that would imply even more reduced processes, does not seem to affect trees to such a great extent, carbon assimilation still function substantially (ibid).

The summer of 2003 was extremely dry and warm with drought issues through Europe. Van der Werf et al. (2007) studied the tree rings of mature pedunculate oak in the Netherlands with the conclusion that the oaks were not greatly affected by the severe drought during this summer. Actually, in 2004, tree rings were rather wide and with no substantial difference on width during 2003 (ibid). This apparent non-existing long term water deficit may be due to already long fine roots that had access to deep water (Leuschner, 2000). Longevity of leaf should decrease in an event of drought, tough in a study by Leuzinger et al. (2005), no effects in leaf duration was detected. However, a reduction in leaf duration also depends on the length of time and intensity of the drought event.

PHYTOPHTHORA INFECTION

One of the more active *Phytophthora* species in North and central Europe is *P. Quercina* which have been found in several oak stands in e.g. Germany, France, United Kingdom, Luxembourg, Sweden, Poland, Hungary, Switzerland (Jung, 2000) and Austria (Balci & Halmschlager, 2003). According to Jung et al., (2000), who studied oak stands in Germany, a higher crown transparency is more frequently observed in stands were *Phytophthoras* is found and that root rot was correlated to transparency, although, roots were sometimes healthier in declining stands. Due to these findings there is a suggestion that crown thinning may have occurred earlier than root decline. However, during a severe infection the tree may not be able to produce new roots to replace those that are infected, this is often more common in mature oaks due to a lower plasticity and regeneration capacity. This unbalanced scenario continuing over several years may lead to a destruction of the whole fine root system and make the tree more vulnerable to other biotic or abiotic stress factors e.g. drought. This has been observed not only in Germany but also in other European countries (ibid).

Also, according to Jönsson-Belyazio & Rosengren (2006), oak stands in southern Sweden are infected by *P. quercina* with symptoms of fine root rot and necrotic spots on the tap root. As a try to restore the damage in the roots, carbon is allocated to roots rather than shoots. This measure reduces the size of tree crown and lowers carbon assimilation. Some trees can recover from such unevenness but some reduces the crown to such a great extent that remaining leaves cannot assimilate enough carbon which in combination with other stress factors may be lethal (ibid).

How may a change in climate affect the oak?

Pedunculate oak often grows in moist soils but may be distributed at dryer soils as well. The change in climate as earlier mentioned may limit the distribution and vigor of trees and complicate their existence in different ways.

Growth in oaks are rather sensitive to climate of earlier years and specially the previous growing season, e. g. cold winters and scarce precipitation during autumn and early winter. Dry autumns affect the early wood production negatively due to low accumulation to the carbon reserve earlier, which is the source to regrowth during spring. Late wood production is mostly dependent on precipitation during June and July rather than temperature, but it is also affected by previous season with less suitable climate conditions. Also this wood production is contributing the most to total tree ring width of the season. The need of precipitation during these months makes the oak particularly sensitive to soil water deficit. So a drought during summer may be a threat to oak growth in the long run with the effect of carbohydrate reserve depletion. (Michelot et al., 2012; Friedrichs et al., 2009)

Drought

As mentioned earlier, the summers are expected to be warmer and during extensive summer drought, soils in Europe may experience deep soil moisture depletion with a result in even warmer surface air temperatures due to less cooling from evaporation. In combination with surface solar warming even higher temperatures will be reached. The depletion may be that severe that not even the predicted increase in winter precipitation can compensate for the loss during summer. This scenario is derived from the higher air temperature that enhances the evaporation rate due to the fact that the warmer air can contain more water molecules which will increase the vapor pressure deficit and water demand and thus increase evaporation. Although, the extensive drought may rather be present in central Europe than in northern/northeastern, due to precipitation derived from cooler northwesterly winds from the Baltic Sea which may provide heavy rains (Giorgi et al., 2004).

Arend et al. (2011) & Spies et al. (2012) found relations between growth and drought when studying saplings from Switzerland and Italy. Shoot length and stem diameter were inhibited by drought but the root system seemed unaffected with neither substantial growth nor decline. Also, the overall tree leaf area seems to decrease in a dry climate which would imply on an adaption with higher water use efficiency. Although, there was a difference in this reaction to drought between saplings collected from the two different countries, which could indicate on a possible site specific adaption to drought. Those collected from more southern sites seemed to be more adapted to drought than saplings from north (Arend et al. 2011). However, Gieger & Thomas, (2001), found that when oaks were subjected to drought there was increased fine root mass which should be the most common reaction to drought due to an increased demand of water.

Increased CO_2 concentration

Future climate scenarios that will have a higher CO_2 concentration may also affect oaks in a direct way. By elevating CO_2 in the atmosphere trees may grow to a larger extent, especially with good supply of water and nitrogen (Vivin et al., 1997; Wamelink et al., 2009). A higher CO_2 concentration in the atmosphere generates a steeper gradient between leaf and air CO_2 concentration and the leaf should therefore in general assimilate more carbon due to higher diffusion rate (Larcher, 2001). However, according to Maillard et al. (2001), who subjected saplings to an enriched CO_2 environment, found that a possible restriction to growth may be nitrogen deficit. This deficit may emerge from a loss through transpiration or there might be because of dilution when more carbon is assimilated (Taub & Wang, 2008). Also, that stomatal conductance is lowered may be an explanation, this also generates a higher water use effiency (Leuzinger, 2008). Those grown in both elevated CO_2 and was well supplied with nitrogen grew significantly more than those with a deficit. The saplings with nitrogen deficit had lower shoot growth and most growth in the coarse root rather than in fine roots (Maillard et al., 2001). Though, according to Vivin et al. (1997) under drought conditions and low nitrogen, especially root biomass increased and in particular the fine root biomass, which increased as much as 47% and the overall total biomass increased by 1.52 times during the 22 weeks long study. One explanation to increasing root biomass is that when the tree is subjected to elevated CO_2, the reaction is to assimilate carbon for growth, though, the rapid growth decreases nitrogen concentration and to restore the imbalance, the root system expands to locate nutrients. Asshoff et al. (2006) also observed growth in the root system with the conclusion that the carbon was not used for storage and had a rather short longevity in trees.

Temperature

According to Morin et al. (2009; 2010), there will most definitely be a change in leaf phenology in the future, though, it seems as if a more moderate climate scenario like B2, with lesser CO_2 emissions, will be more effective in early bud burst than a scenario with higher emission. The observed early bud burst may be reversed in an extreme climate scenario like A2, with very high CO_2 concentrations and a high temperature increase, bud burst might be delayed due to the need of bud break dormancy in the colder winter months to prepare for the coming warmer period of bud burst and leaf unfolding which promotes cell expansion and growth. In case of events with to high temperatures during winter, exceeding average by 5^{o}C, the bud burst will be delayed or even a scenario with abnormal leaf unfolding may occur. Even the higher spring temperatures may not be able to compensate for this lack of dormancy period. Abnormal leaf unfolding is an indicator that points towards that, even though there may exist flexibility in bud burst events, the warming may exceed trees capability to adapt to changes in climate. The inability to adapt may generate downsides in survival such as being less frost resistance (Morin et al., 2009). There may be complications with air warming but an increase in temperature may also generate positive effects such as shoot growth and higher carbon mobility within the tree (Arend et al., 2011).

According to Hlasny et al. (2011), it seems however, as if the oaks are relatively insensitive to a changing climate when it comes to both growth and mortality. Simulations show that growth will probably be the same as present and also that mortality may decrease in a future climate. Distribution would, according to the same simulation, increase and suggests that oak will even grow on higher elevations. Potential expansion of the distribution will likely be on behalf of other species and they would seem more competitive on drier and nutrient poor sites. Also, due to the expanded distribution it is projected that carbon sequestration would increase by 64% in 2070 (Hlasny et al., 2011).

May *Phytophthora* be affected by the changing climate?

As already noted, extreme weather events will be a part of the future climate and in the event of heavy precipitation or high amount of precipitation during a longer period the result will be an increase in soil moisture. This periodic increase in soil moisture will benefit both the production and dispersal of *Phytophthora* zoospores which will increase the range of root infection (Jönsson, 2006; Venette & Cohen, 2006). If a flooding period is during a longer time interval and temperatures are relatively low there is a possibility according to Jönsson, (2006) that the disease may develop into an epidemic state. The damage caused by the root infection might lead to a loss in carbohydrates. Also, the possible state of hypoxia due to long inundation periods might reduce the microbial activity in soils which enhances the pathogen activity (ibid). Also, according to Venette & Cohen (2006), it is indeed implausible that moisture will prohibit growth. Even though it seems as if oak species are rather resistant to events of flooding in general, infection can cause severe damage. Due to a defense reaction of the tree, much of the carbon will be allocated to damaged parts. This in turn will leave less carbohydrate for growth in root and shoot and repeated infections may deplete the trees' carbohydrate storage. A reduction in growth and the damage exerted by *Phytophthora* will reduce the length of healthy roots which will deteriorate water and nutrient uptake. So, if wet events are followed by dry periods oak may suffer when not reaching available water in the soil (Jönsson, 2006).

Drought on the other hand, will prohibit dispersal of *Phytophthora* and zoospores will not expand as much. Instead, a long period of drought has a direct effect on the tree, which weakens tissues making them more vulnerable to infection. After a period of weakening, if just enough precipitation occurs, *Phytophthora* has the ability to react quickly. In addition, soil microbial activity reduces during drought and this is beneficial to *Phytophthora* if moisture is added to the soil due to its extremely quick response (Jönsson, 2006).

Bergot et al. (2004) simulated the potential risk of an extended distribution of *Phytophthora* in the year 2100 due to climate warming. Using temperature data, both measured and simulated, from 503 meteorological stations in France in an epidemiological model, future high and low risk areas was identified. The results showed a definite increase in areas with disease risk, areas with high risk increased by 14% and may extend from the Atlantic coast to about 100 km eastward. Moderate risk areas increased by 19% located mostly in the north-central parts of France and those areas considered as low risk areas or areas at no risk, decreased by 33% by 2100 (ibid).

A later study also done in France by Desprez-Loustau et al. (2007) showed an increase in suitable areas for *Phytophthora*. The pathogen can affect the tree both by stem and root disease, although, this study found that the root disease is more likely to spread. But even if the higher temperature will benefit the pathogen, there is a downside with a decrease in soil moisture. These two factors working together might lower the potential development of the pathogen according to Desprez-Loustau et al. (2007).

Discussion

The observed oak decline in north and central Europe is most probably not only due to one factor, instead there are several abiotic and biotic factors contributing (Thomas et al., 2002). Climatic elements may not have the effect of killing trees, though it can severely stress the tree making it more vulnerable to other biotic factors. Climate predictions however, need to be taken with consideration. There are still many different scenarios that may take place in the future and the effects will have different strengths. Also, regional differences will occur (IPCC, 2007) and these may be determinant for species survival. The events of extreme weather such as drought (Briffa et al., 2009) and flooding (Kundzewics et al., 2006; Christensen & Christensen, 2004) have though already been observed in Europe and will most probably remain or increase in intensity.

Drought and flooding

These extremes will affect trees to different extent, depending on the strength and duration of the event. Oaks seem rather resistant to both flooding and drought, though, the latter causes somewhat more stress and damage. There seems to be a lack of common response to drought by oaks, there would be an increase in fine root biomass to reach the lacking water. Though, oaks already long fine roots may be an explanation to the absence of carbon allocation to roots for growth, this was observed and discussed by Arend et al. (2011). However, Gieger & Thomas (2001) observed the more common response of root growth i.e. expansion in root system. It is apparent that this question of response to drought is in matter of debate due to more saplings based studies than studies on mature oaks that may react in a different way. Epron & Dreyer (1993) did study mature oaks and they concluded that oaks can sustain a high stomatal conductance and transpiration rate during drought, which they thought was due to the deep penetrating root system.

Temperature

In an addition to drought, higher air temperatures should also increase the drought condition. A warmer and drier growing season with less water abilities may play a large role in the vigor of oak and Arend et al. (2011) found that higher air temperatures, in addition to drought, inhibit growth further than when only subjected to drought. Oaks seem however, as rather tolerant to both drought and flooding in comparison to other deciduous species (Scharnweber et al., 2011). The warmer and extended growing season that will put bud burst earlier in time may still suffer from spring frost due to fluctuations in atmospheric circulations. However, the risk of such an event would decrease due to generally warmer springs. The warmer air temperature may though cause a different growth pattern, with more growth in shoots than roots, this would increase the vulnerability to mechanical stress e.g. storms. According to IPCC, (2007), there is a possibility, though not well studied, that due to warming and moisture there will be more turbulence in the atmosphere.

However, most of the studies that are reviewed are concerning saplings and there are probably difference in adaption and tolerance to stress factors. As described earlier, saplings seem to be more sensitive to flooding than mature trees. Although, this sensitivity may alter the distribution of oaks when sites that will experience flooding that inhibits mature oaks is subjected to other stress factors that actually may harm the trees.

CO_2

As CO_2 may have a direct consequence for oaks it seems as if growth that is enhanced by a CO_2 enrichment may be dependent on the amount of nitrogen that is available. On the contrary Wamelink et al. (2009) found that a decrease in nitrogen supply would not inhibit carbon assimilation to a greater extent and also that a possible increase would generate a higher rate of increase than the rate of decrease with lower nitrogen availability. Though probably, not only an increase in atmospheric CO_2 and available nitrogen alone but also climatic factors such as temperature and moisture would have to be included. Water and temperature are both essential for allocation of carbon within trees and a lack of water may reduce stomatal activity making the assimilation process less effective.

Oak trees don't seem completely unaffected by the change in climate. However, the loss in vigor or mortality is not solely dependent on events as drought and flooding. The decline is probably in combination with pathogens such as *Phytophthora* or other opportunistic pathogens and insects.

Phytophthora

Phytophthora is also, to different extents, dependent on these earlier mentioned environmental factors, such as precipitation and drought. However, drought only has the indirect effect by weakening the tree making them more susceptible to an infection. The pathogen is also rather opportunistic in that way of staying inactive in the soil during drought and as soon little moisture reaches the soil it can reactivate which could generate a possibility of greater infection rate in the already weakened tree. *Phytophthora* seems to be very much dependent on soil moisture which will be prevalent in future climate according to the prediction of increased precipitation (Jönsson, 2006). The warmer and wetter climate is likely to increase the populations and also making the season for infection more suitable, the more mild winters may also enhance their survival capacity. When roots have been infected they are even more susceptible to other pathogens and insects (Jönsson-Belyazio & Ronsengren, 2006). The more recurrent flooding in north and central Europe may not induce any direct harm on oak due to the trees high tolerance. However, *Phytophthoras* are more easily dispersed by moisture which also could imply on a greater infected area.

Phytophthora species have been found in most of Europe, even as far north as Sweden (Jönsson et al., 2005; Balci & Halmschlager, 2003; Jung et al., 2000). This could imply on an already wide distribution range, though, maybe it is still too cold for the pathogen to cause any severe damage. However, if, or rather when, these higher temperature caused by global warming will be present the activity may be enhanced. As earlier mentioned, *Phytophthora* has the ability to reactivate rather quickly when exposed to more favorable conditions.

OAK VERSUS BEECH

In the future climate there will most probably be a competition between tree species due to different reactions to stress and a usual combination in European deciduous forests is beech and oak. Hlasny et al. (2011) simulated a scenario between oak and beech in terms of climate change in Europe. The results show a decrease of beech in lower elevations but an increase in higher (above 400 m a.s.l.). The prediction of oak distribution on the other hand, indicates on a larger distribution area in northern and central Europe and also an increase of oaks in higher elevations. The prediction of beech at higher elevation but also oak at the same height may result in outrival of beech due to oaks higher stress tolerance. According to Scharnweber et al. (2011), oak trees seem to be more insensitive to variable climate parameters such as precipitation and temperature, thus, a warmer and drier growing period seem to affect both oak and beech negatively to some extent. However, beech is slightly more sensible to both parameters but significantly more sensible to drought. As well as drought, flooding seem to affect beech more negatively, this may be one reason why beech is predicted to grow at more elevated sites. In the year of 1999 the Rhine floodplain was flooded. Species were affected differently by this episode, adult oaks seeming to be the most resistant one. An explanation to higher tolerance to flooding by oaks may be that when inundated and subjected to hypoxia, oaks have the quality of maintaining enough carbohydrates in the roots to supply the energy demanding processes that proceed during flooding. Beech, on the other hand, does not have the ability to regulate the energy supply for these processes and may suffer from carbohydrate depletion (Ferner et al., 2012). Also, beech is more sensitive to spring frost according to Thomas & Sporns (2009), which may reduce the crown size and overall growth.

Maybe due the co-existence of these two species, beech is also subjected to *Phytophthora* infestation. However, *P. quercina* is host specific but Jung, (2009), observed other *Pytophthoras* in the soil that are likely to cause the same disease symptoms on beech as on oak, such as root rot and thinner crowns. Though, in difference to *P. quercina*, it seems as if some of those species infecting beech are able to be active in soils with lower pH which could imply a greater disease area. On the contrary to oak, beech is also more susceptible to *Phytophthora* infections and the decline seems to be less dependent on other abiotic factors.

Scharnweber et al. (2011) predicts a future with a decreasing trend in both beech and pedunculate oak, however not that significant for the oak. The loss in vigor among trees may mostly be observed in sites with more sandy than clayey soils due to less capacity of soils to contain water. However, those soils that inhibit more moisture are on the other hand more preferable to *Phytophthora* species which in turn can cause a decline in vigor and, under the right conditions, even mortality for both species.

These predictions of future forest distribution are, though, somewhat unclear on species level, most studies have been done concerning only temperate versus coniferous forest. On species levels there are mostly speculations with seemingly large regional differences. For sure, there is a probability of deciduous forests mitigating northward, though, the species composition may not be that obvious. The effect of adaption to a different climate will maybe render species susceptibility and defense against other threats as pathogens and insect.

Conclusion

This review has been focused on the effects that a climate change may have on the pedunculate oak in central and southern parts of north Europe. The risks of an increased area of infection by *Phytophthora* have been described and the injuries and effects that an infection might have on trees. The conclusion of the earlier mentioned aims with this report are the following:

1. Among those climatic factors that are discussed in this report, summer drought seems to be affecting the oaks more than flooding does in present day. Temperature is not causing any significant damage unless spring frost occurs after bud burst. Though, *Phytophthora* seems to already been spread through Europe and is causing root rot in oaks.

2. The pedunculate oak may most probably be affected by a change in climate with more intense drought and flooding episodes. Although, oaks seem to be rather resistant to stress, it's a matter of time and intensity. Drought may be prolonged and can cause significant lower carbon reserves, which may affect coming growing seasons and flooding will most probably affect saplings more than mature trees which can adapt to the environmental condition. This may generate a shift in distribution when saplings don't have the ability to grow in recurrent flooded areas. CO_2 may on the other hand enhance growth, mostly under conditions with good supply of water and temperatures that are warm enough.

3. The pathogen *Phytophthora* will most probably be positively affected by an increase in temperature as the winter survival rates increases. Even though drought will slow the activity as soon as moisture is added it may reactivate. This would generate a beneficial scenario with an already weakened tree. As well as a more enhanced infection rate the dispersal is positively affected by flooding.

Also, the potential spread of *Phytophthora* have been discussed with a conclusion that it may infect trees in a larger area of Europe due to climate change and the more easier spreading by flood events. But still, the magnitude of climate change and the effects is still uncertain and there may also be regional differences that may be of consequence of the projection of future pedunculate oak distribution and health.

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