Promoting natural regeneration of oak by manipulating disturbance

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Doctoral thesis
Swedish University of Agricultural Sciences
Alnarp 2019

Acta Universitatis agriculturae Sueciae
2019:66

Cover: Simulating a low-intensity fire in oak-dominated forest with naturally regenerated oaks (*Quercus robur* L. and *Q. petraea* (Matt.) Liebl.) in southern Sweden.
(photo: L. Petersson)

ISSN 1652-6880
ISBN (print version) 978-91-7760-450-1
ISBN (electronic version) 978-91-7760-451-8

Print: SLU Repro, Alnarp 2019

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Abstract

Oak regeneration is thought to be promoted by natural disturbance and past management practices that create semi-open conditions, such as periodic livestock grazing and low-intensity fire. The overall goal of this thesis was to examine whether disturbance factors can promote natural oak regeneration. The first study quantified demographic changes in the Swedish oak (*Qurecus robur* and *Q. petraea*) population and examined the role of altered land use for these changes. Despite a continuous increase in large oak trees in southern Sweden since 1953, oak saplings declined continuously after the early 1980s. This development was connected to widespread changes in land use and game management that created darker forests with more herbivores, likely reducing oak regeneration at a regional scale. Field experiments showed negative effects of present ungulate browsing pressure on oak seedlings and saplings. The combination of competing woody vegetation and browsing had greater negative effects on oak (*Q. robur*) survival than individual effects of either factor. Although woody vegetation provided some protection against ungulate browsing, the long-term effect on oak survival and growth was overall negative. Oak seedlings (*Q. robur* and *Q. alba*) displayed a high sprouting capacity following shoot-destructive disturbance (artificial clipping) in a greenhouse experiment. A field experiment including low-intensity fire and oak seedlings (*Q. robur* and *Q. petraea*) gave similar results. Greater light availability increased oak performance in both cases, suggesting that their tolerance to disturbance, such as browsing and low-intensity fire, is greater in high light environments. These results also indicate that fire could promote oak regeneration in temperate Europe, consistent with the North American fire-oak hypothesis. However, further research is needed to determine the long-term vitality of these oaks and their main competitors, and whether oaks gain competitive advantages after such disturbance. Oak-dominated forests are important for biodiversity and the effects of fire on species and communities also needs to be studied. In conclusion, the results suggest that in the absence of natural disturbance, active management that resemble previous disturbance regimes and restore habitats with semi-open canopies, and low to moderate browsing pressure, seem essential to promote natural oak regeneration.

Keywords: browsing, competition, oak, disturbance, fire, light, natural regeneration, seedling, ungulate

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Förbättra naturlig föryngring av ek genom att efterlikna ekologiska störningar

Abstract

Ekologiska störningar och historisk skötsel anses gynna naturlig föryngring av ek. Det finns dock en kunskapsbrist om hur olika störningsfaktorer samverkar och därmed påverkar ekföryngring. Syftet med detta arbete var att kvantifiera förändringar hos den svenska ekpopulationen (*Quercus robur* och *Q. petraea*), samt att undersöka hur ekplantors tillväxt och överlevnad påverkas av olika störningsfaktorer. Resultaten visade att antalet ekplantor har minskat drastiskt i södra Sverige sedan början på 1980-talet, trots att antalet stora ekträd har ökat kontinuerligt sedan 1953. Denna utveckling kunde kopplas till omfattande förändringar i markanvändning och viltvård, vilket har orsakat mörkare skogar med fler växtätande hjortdjur. Sammantaget har dessa förändringar troligtvis förhindrat naturlig föryngring av ek på landskapsnivå. Negativa effekter av ett högt betestryck på ekplantors överlevnad och tillväxt kunde även påvisas genom fältexperiment. Den kombinerade effekten av konkurrerande buskvegetation och bete hade större negativ påverkan på ekplantors överlevnad än de individuella effekterna. Trots att buskar kan ge ekplantor ett visst skydd mot bete, och även stimulera höjdtillväxt, var den långsiktiga effekten övervägande negativ. Ekplantor hade en hög skottskjutningsförmåga både i växthus (efter klippning) och under fältförhållanden (efter en lågintensiv brand). Tillväxt och överlevnad var högre hos de skottskjutande ekplantor som hade tillgång till mer ljus, vilket tyder på att ekplantors tolerans för ekologiska störningar är högre i miljöer med mer tillgängligt ljus. Naturligt föryngrade ekplantor hade en hög överlevnad och tillväxt efter en lågintensiv markbrand. Detta tyder på att brand kan användas för att gynna ekföryngring i Europa, vilket överensstämmer med den Nordamerikanska brand-ek hypotesen. Det krävs dock ytterligare forskning som undersöker den långsiktiga vitaliteten hos ek och konkurrerande trädslag för att avgöra om brand ger ek en konkurrensfördel. Den lågintensiva markbranden förändrade hjortdjurens betesfrekvens, det verkar därför även nödvändigt att utvärdera hur det lokala betestrycket kan påverkas av brand. Då ekskogar har stor betydelse för biodiversitet är det även nödvändigt att noggrant undersöka hur den biologiska mångfalden påverkas av brand. Sammanfattningsvis visar mina studier att aktiv skötsel som efterliknar ekologiska störningar och återskapar skogar med mycket tillgängligt ljus och måttligt betestryck från hjortdjur krävs för att gynna ekföryngring när ekologiska störningar saknas.

Keywords: bete, brand, ek, hjortdjur, konkurrens, ljus, naturlig föryngring, plantor, störning

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Dedication

To my family.
To Max.

The beauty of the natural world lies in the details.
Natalie Angier

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Petersson L.K.*, Milberg P., Bergstedt J., Dahlgren J., Felton A.M., Götmark F., Salk C., Löf M. (2019). Changing land use and increasing abundance of deer cause natural regeneration failure of oaks: six decades of landscape-scale evidence. *Forest Ecology and Management*, 444, 299-307. DOI: 10.1016/j.foreco.2019.04.037

II Jensen A.M.*, Petersson L.K., Felton A.M., Löf M., Persson M. What happens to oak growth and survival when there is both competition *and* browsing? (Manuscript).

III Petersson L.K.*, Löf M., Jensen A.M., Chastain D.R., Gardiner E.S. Sprouts of shoot-clipped oak (*Quercus alba* and *Q. robur*) germinants show morphological and photosynthetic acclimation to contrasting light environments. (In review).

IV Petersson L.K.*, Dey D., Felton A.M., Gardiner E.S., Löf M. Influence of canopy openness, ungulate exclosure, and low-intensity fire for improved oak regeneration in temperate Europe. (In review).

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* Corresponding author.

The contribution of Linda Petersson to the papers included in this thesis was as follows:

I Developed the research idea together with PM, JB, AMF, FG, and ML. Conducted analyses including statistics. Wrote the manuscript in collaboration with the co-authors.

II Participated in planning and performing fieldwork. Conducted analysis of fisheye photographs and participated in writing of the manuscript that was led by AMJ.

III Developed the research idea and planned the experiment together with EG and ML. Responsible for data collection together with EG. Conducted analyses including statistics. Wrote the manuscript in collaboration with the co-authors.

IV Planned the experiment together with the co-authors. Conducted data collection and analyses including statistics. Wrote the manuscript in collaboration with the co-authors.

1 Introduction

Forested ecosystems worldwide are under increasing pressure from a changing climate and anthropogenic activities, which have caused large-scale deforestation and degradation, as well as altered previously prevailing disturbance regimes. Production forests and plantations have led to loss of forest biodiversity and an urgent need for forest restoration, i.e. measures that aim to reintroduce natural forest structures, species, and processes that have been reduced or entirely removed following human influence (Halme *et al.*, 2013).

Natural regeneration can be a cost-efficient approach for forest restoration that preserve local genetic diversity, increase forest resilience, and ensure temporal continuity of forests (Chazdon, 2017; Fischer *et al.*, 2016). The natural regeneration process and the associated species-specific life histories have been described as the "regeneration niche" (Grubb, 1977). The regeneration niche consists of several stages, from seed production and dispersal, germination, to seedling growth and survival. The concept suggests that suitable and species-specific environmental conditions occur simultaneously and in sequence for regeneration to occur. This thesis will focus on the seedling developmental stage of the natural regeneration process, i.e. the growth and survival of individuals after successful germination has taken place (Fischer *et al.*, 2016).

1.1 Oaks

The oak genus (*Quercus*) includes about 600 species that provides a range of ecosystem services, such as high quality timber, recreational areas, watershed protection, and possibilities for adaptation of forest management to climate change (Mölder *et al.*, 2019; Löf *et al.*, 2016). Furthermore, oaks are foundation species in temperate forests (Lindbladh & Foster, 2010), with disproportionate importance for biodiversity and ecosystem functions (Ellison *et al.*, 2005; Dayton, 1972). Habitats created by oak can persist for centuries due to the long lifespan of individual trees and the durability of the dead wood. Oak is therefore one of the most important tree genera for endangered invertebrates (Tallamy & Shropshire, 2009; Ranius & Jansson, 2000), lichens, fungi (Thor *et al.*, 2010; Ranius *et al.*, 2008), and birds (Felton *et al.*, 2016; Rodewald & Abrams, 2002).

Currently, the extent of oak-dominated forests and woodlands is much lower in many regions than in previous centuries, this being a consequence of forest degradation, deforestation, and changing climate (Dey *et al.*, 2019; McEwan *et al.*, 2011; Lindbladh & Foster, 2010). About 4000 years ago, oak-dominated forests were widespread across southern Sweden, but due to a colder climate and human activities, such as selective harvesting and deforestation for agriculture, oak has declined drastically (Lindbladh & Foster, 2010). By the late 20^{th} century, oak abundance had reached historically low levels in Sweden. Today, about 65 % of the land area in southern Sweden is covered by forests (Forestry statistics, 2014). Due to active forest management favouring conifers for pulp and timber production, the two dominant tree species are Norway spruce (*Picea abies* (L.) Karst) and Scots pine (*Pinus sylvestris* L.). Out of the total standing volume in southern Sweden (1748.3 million m^3), 2.2 % is oak timber (Forestry statistics, 2014).

Two oak species are considered native to Sweden, pedunculated oak (*Q. robur*) and sessile oak (*Q. petraea*). Ecologically and morphologically the two species are similar and they are known to form hybrids (Jensen *et al.*, 2009). In Sweden, oak is usually regenerated through planting of bare-rooted seedlings following vegetation control at old agricultural fields or clear-cutting and mechanical site preparation at forest sites, while natural regeneration and direct seeding are rarely used (Löf *et al.*, 2012). Due to high population densities of wild ungulate browsers, i.e. moose (*Alces alces* L.) and deer (*Capreolus capreolus* L., *Cervus elaphus* L., and *Dama dama* L.), fencing is almost always necessary to reduce browsing damage that otherwise cause growth stagnation (Bergquist *et al.*, 2009). The current methods for artificial oak regeneration in Sweden are therefore costly, about 4,000-7,000 Euros ha^{-1} in comparison with about 2,000 Euros ha^{-1} for conifer regeneration (Löf *et al.*, 2012). Furthermore, these standard methods may not always be appropriate due to conservation considerations. Therefore, there is a need for development of cost-efficient regeneration methods for oaks, e.g. including natural regeneration.

1.2 Natural regeneration of oak and disturbance

Insufficient natural regeneration of oak for human purposes has been cause for concern for over a century (Annighöfer et al., 2015; Crow, 1988; Shaw, 1968; Watt, 1919), and poor oak regeneration in forests has been reported virtually everywhere oaks grow (Leonardsson et al., 2015; Fei et al., 2011; Pulido & Díaz, 2005; Li & Ma, 2003; Kelly, 2002). The reasons for this is still not fully understood, but successful oak regeneration at the seedling stage is dependent on multiple environmental factors that often influence each other, including light availability, site conditions, competing vegetation, browsing damage, and pathogens (Jensen & Löf, 2017; Annighöfer et al., 2015; Leonardsson et al., 2015; Rizzo & Garbelotto, 2003; Rooney & Waller, 2003; Kelly, 2002; Lorimer et al., 1994). It is, however, important to keep in mind that what constitute "sufficient" or "successful" natural regeneration is not strictly defined. From a silviculture perspective, successful oak regeneration results in high quality production stands (Drössler et al., 2012). While from a conservation perspective, survival of young oaks at a lower density that could form future habitat trees may be considered successful (Götmark & Kiffer, 2014).

Natural disturbance and management interventions, especially past land-use practices that included grazing regimes, wood cuttings of shade tolerant species, and low-intensity fire, are considered to promote oak regeneration by increasing light availability and reducing competing vegetation (Bobiec et al., 2018; Vera, 2000; Abrams, 1992). Grime (1977) defined disturbance as the partial or total destruction of plant biomass, e.g. browsing, while stress was defined as unfavourable environmental conditions that reduce plant growth, e.g. light availability. Many oak species have traits that make them tolerant to disturbance, such as abundant dormant buds and large carbohydrate reserves in their root systems that give them a high-sprouting capacity (Rebbeck *et al.*, 2011; Kabeya & Sakai, 2005; Del Tredici, 2001), and thereby a certain competitive advantage following disturbance. Furthermore, oak regeneration can indirectly benefit from periodic disturbance due to changes in environmental conditions that reduce plant stress, e.g. increased light availability following wind throw.

1.2.1 Light requirements

Inadequate light is often a limiting factor for oak regeneration and its recruitment into the overstory (Annighöfer *et al.*, 2015; Götmark, 2007) and the effects of light availability on oak seedling biology has therefore received considerable study (e.g. Jensen *et al.*, 2012b; Rebbeck *et al.*, 2011; Gardiner *et al.*, 2009; Rodríguez-Calcerrada *et al.*, 2008). Although the large acorns enable establishment in dark understory conditions, adequate light for survival and growth is needed once energy reserves of the cotyledons are exhausted (Johnson *et al.*, 2018; Rodríguez-Calcerrada *et al.*, 2008). Oak seedlings generally benefit from high light availability, but minimum light requirements and functional optima are species-specific and depend on plant developmental stage (Rebbeck *et al.*, 2012; Fleck *et al.*, 1998; Kruger & Reich, 1993b). Seedlings of *Q. robur* and *Q. petraea* require a minimum of 15-20 % of full light for sustained growth (Löf *et al.*, 2007; von Lüpke, 1998). Compared to all other Swedish temperate hardwood species and the common conifers Norway spruce and Scots pine, *Q. robur* and *Q. petraea* are more light demanding than all but Scots pine (Niinemets & Valladares, 2006 Appendix A; Diekmann, 1996).

1.2.2 Browsing by ungulates

Oaks are among the most palatable species for ungulate browsers (here: members of the family Cervidae), especially compared to conifers (Bergqvist *et al.*, 2018; Kullberg & Bergström, 2001). Through selective browsing, ungulates have the ability to reduce tree species diversity and favour browse-tolerant species (Côte *et al.*, 2004; Rooney & Waller, 2003). Browsing reduces height growth and chronic browsing may thereby keep palatable tree species, such as oak, from establishing in the overstory (Kuijper *et al.*, 2010a; Bergquist *et al.*, 2009), a phenomenon referred to as the "browse trap" (Churski *et al.*, 2016; Staver & Bond, 2014). Paradoxically, oaks can often survive extended periods of browsing and may therefore be regarded as browsing-tolerant species (Götmark *et al.*, 2005; Gill, 1992).

Neighbouring woody vegetation has been shown to reduce short-term browsing risk for palatable tree species in temperate forests (e.g. Jensen *et al.*, 2012a; Harmer *et al.*, 2010). However, it is still uncertain whether this facilitative effect provide long-term protection or whether positive effects are overshadowed by competition. In this thesis, competition was defined as direct and indirect plant-plant interactions with negative effects on growth and survival for at least one of the plants (Connell, 1990).

1.2.3 Fire

In eastern North America, failed oak regeneration has been linked in part to the suppression of fire during the last century (Dey *et al.*, 2019; Brose *et al.*, 2001; Abrams, 1992). This led to the development of the fire-oak hypothesis, which states that fire has been an integral part of temperate oak ecosystems in eastern North America and that oaks are better adapted to survive and exploit periodic fire compared to most other tree species (Arthur *et al.*, 2012; Nowacki & Abrams, 2008; Brose *et al.*, 2001; Abrams, 1992). Many North American oak species have traits that at different points throughout their life cycle give them a competitive advantage in a periodic fire regime (Fig. 1) (Johnson *et al.*, 2018). Further, the hypothesis states that the efficient fire suppression since the early

20th century has a major part in the current oak regeneration problem and that prescribed fire can be used to regenerate and restore oak ecosystems under certain conditions. Thus, prescribed burns are used extensively for oak timber production and ecological restoration of oak ecosystems in the United States (Fig. 2), often combined with stand thinning to increase the available understory light (Brose *et al.*, 2014; Brose *et al.*, 2013).

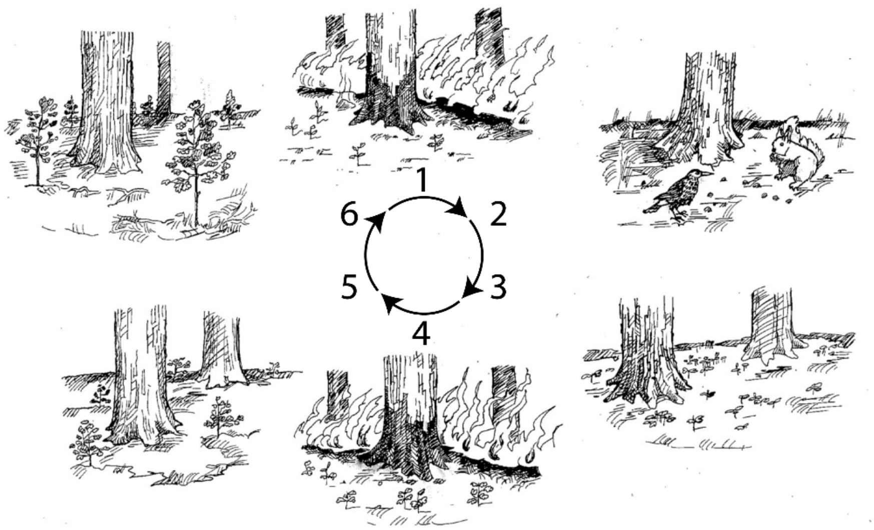

Figure 1. Conceptual model for natural regeneration of oak influenced by ground fire. 1) Ground fire reduces mid- and understory competition, while large oak trees survive fire with little damage; 2) small mammals and birds prefer to bury acorns in areas with thin litter layer; 3) ground fire favours successful germination of oak and other species; 4) reoccurring ground fire favour accumulation of oak in the advance regeneration pool and reduce competition; 5-6) temporary suspension of ground fire allows oaks in the advance regeneration pool to develop into saplings and overstory trees. Illustration after (Van Lear & Watt, 1992) by Tove Vollbrecht.

In Europe, forest fires have mainly been associated with the boreal and Mediterranean zones, and studies of fire effects on oak regeneration have almost entirely been constrained to Mediterranean species (e.g. Catry *et al.*, 2012). However, reconstructions of past forest conditions suggest that fire may have had an important part in forest dynamics for certain European temperate forest types as well (Adámek *et al.*, 2015; Niklasson *et al.*, 2010; Tinner *et al.*, 2005). High pollen percentages of oak (*Q. robur* and *Q. petraea*) have been found together with abundant charcoal particles, suggesting fire may have favoured these oak species in the past by keeping forests open (Bradshaw & Lindbladh, 2005; Lindbladh *et al.*, 2003). Furthermore, a survey in Ukraine indicates that frequent woodland fires favour *Q. robur* regeneration by preventing understory development of shade tolerant species (Ziobro *et al.*, 2016). These findings suggest that fire may have similar positive effects on oak regeneration in temperate Europe as in eastern North America; however, this has not been studied in detail.

Figure 2. Photos illustrating the role that prescribed fire can fulfil in sustaining oak forests and woodlands in eastern United States. Upper left: dormant season prescribed fire in an oak-dominated forest (photo: Daniel C. Dey). Upper right: larger oak trees, >10 cm dbh, remain essentially unharmed after the prescribed fire (photo: Daniel C. Dey). Lower left: oak woodland with abundant, vigorous oak sprouts following prescribed fire (photo: Shelley M. Griffin). Lower right: oak woodland with high biodiversity values, restored through a combination of overstory thinning and prescribed fire (photo: Shelley M. Griffin).

2 Objectives

The overall goal of this thesis was to examine whether disturbance factors can be used to promote natural oak regeneration and its recruitment into the overstory. In the first part of the thesis (Paper I), we examined demographic stages of the Swedish oak population and their long-term development. We particularly focused on oak saplings to understand how the rapid and large-scale land use changes during the 20th century altered the regeneration niche for this disturbance-dependent tree species.

In the second part of the thesis (Paper II-IV), we experimentally examined the effect of specific disturbance-related factors on oak seedling and sapling performance, i.e. survival and growth. In paper II, we studied the effects of neighbouring woody vegetation and ungulate browsing on oak performance. In paper III and IV, we explored how the light environment affects oak seedlings' ability to respond to disturbance. Further, we investigate if the North American fire-oak hypothesis could be applicable to European temperate oaks (Paper IV).

The following research questions are addressed in the papers that are included in this thesis:

- I How has different demographic stages of the Swedish oak (*Q. robur* and *Q. petraea*) population developed during the last 60 years and what was the role of altered land use for these changes?
- II What is the relative effect of competition from a woody understory, ungulate browsing, and the combination of these two factors on oak (*Q. robur*) performance?
- III Does the light environment affect sprouting capacity and photosynthetic response in oak germinants, and is the response species-specific for the European *Q. robur* and the North American *Q. alba*?
- IV Can a low-intensity fire promote naturally regenerated oaks (*Q. robur* and *Q. petraea*) and does light availability or ungulate browsing affect the oaks' response to fire?

3 Methods

Both field (Paper II and IV) and greenhouse (Paper III) experiments, as well as national forest inventory data (Paper I), were used to address the research questions outlined in this thesis. In the following section, I briefly summarize these methods, while detailed descriptions can be found in the individual papers.

3.1 Swedish National Forest Inventory study

Data from the Swedish National Forest Inventory (NFI) was used to quantify the development of different demographic stages of the Swedish oak population (Paper I). Since 1953, the Swedish NFI conducts annual inventories using a randomized cluster design where sample plots are aggregated in rectangular clusters (Fridman *et al.*, 2014). Sample plot radius vary between 6.64-10 m depending on sample year, variable, and plot type. Many variables are recorded, e.g. tree and sapling measurements, site conditions, and management history (Fridman *et al.*, 2014).

Our study area roughly comprises the natural distribution of oak in Sweden (Fig. 3a). As the Swedish NFI does not distinguish between *Q. robur* and *Q. petraea* they were combined for the purpose of this study. We used data from all NFI plots on productive forest land (i.e. land that can produce at least 1 m^3 wood ha^{-1} $year^{-1}$) collected during the period 1953-2015 to quantify oak volume and stems ha^{-1}. To determine the effect of changes in land use on oak sapling densities we combined site conditions and management history information from the NFI data with annual ungulate hunting data (1960-2015) from the Swedish Association for Hunting and Wildlife Management. To roughly quantify the combined browsing pressure from the wild browsing ungulates (moose, roe deer, red deer, and fallow deer), we calculated a ‘deer index’ as the metabolically corrected weight of animals shot.

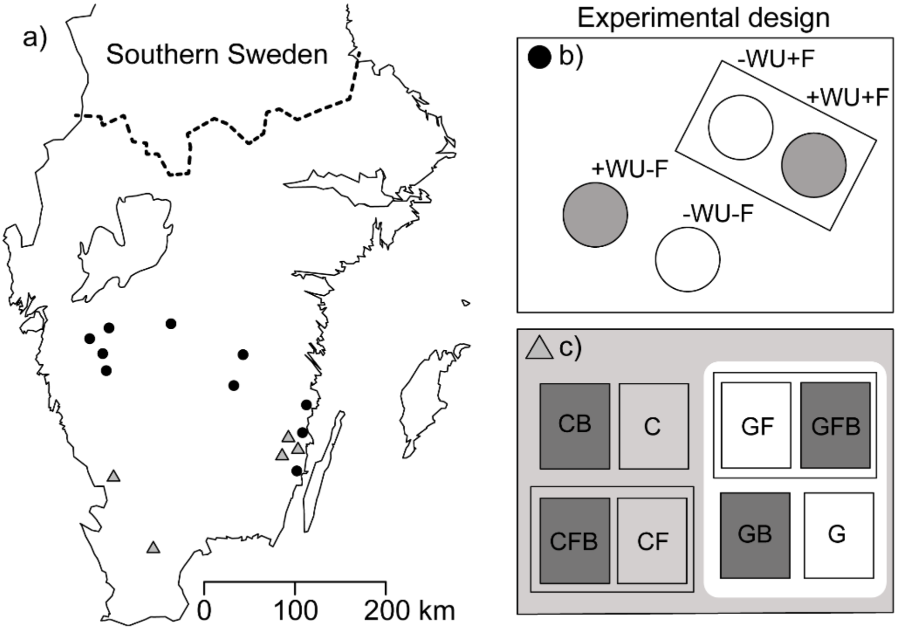

Figure 3. a) Map of southern Sweden, the dashed line denotes the northern limit of the study area in paper I, which roughly corresponds to the natural distribution of oak in Sweden. Ten mixed broadleaved forest sites (black circles, Paper II) and five oak-dominated forest sites (grey triangles, Paper IV) studied during this research. b) Illustration of the experimental design of four 30 m^2 treatment plots at one site (paper II): fenced with woody understory (+WU +F), fenced without woody understory (-WU +F), not fenced with woody understory (+WU -F), and not fenced without woody understory (-WU -F). c) Illustration of the experimental design of eight 25 m^2 treatment plots at one site (paper IV): closed canopy (C), closed canopy and fence (CF), closed canopy, fence, and burn (CFB), closed canopy and burn (CB), canopy gap (G), canopy gap and fence (GF), canopy gap, fence, and burn (GFB), and canopy gap and burn (GB).

3.2 Field studies

Both field studies (Paper II and IV) were conducted in southern Sweden, which lies in the transition zone between the temperate forest in continental Europe and the boreal forest in central and northern Scandinavia (Sjörs, 1965). The region is lowland, not exceeding 350 m.a.s.l., with a mosaic landscape of forests, agricultural land, and lakes. Ten temperate mixed broadleaved forest stands were used in the study of ungulate browsing on young oak plants in the presence of a woody understory (Fig. 3a, Paper II). These stands were previously semi-open pastures or small fields, abandoned 50-90 years ago, and closed canopy mixed forests had subsequently developed through succession and planting. We used a long-term field experiment, established in 2000 (Götmark, 2013; Götmark, 2007), and a study from this project started in 2007 when bare-rooted *Q. robur* seedlings were planted in four plots at each site, two of which had an established woody understory (Jensen *et al.*, 2012c) (Fig. 4). At each site, four treatment combinations were created: fenced with woody understory (+WU +F), fenced without woody understory (-WU +F), not fenced with woody understory (+WU -F), and not fenced without woody understory (-WU -F) (Fig. 3b). Oak survival, growth, and ungulate browsing (browsed or not browsed), as well as characteristics and species composition of the woody understory, was recorded in April/May and August/September annually during the period 2008-2010 and in August/September in 2013, 2015 and 2016. We calculated an index of the relative effect of competition (RCI), browsing (RBI), and the combination of competition and browsing (RCBI) on oak survival and growth as follows:

$$RCI = \frac{X_{(-WU+F)} - X_{(+WU+F)}}{X_{(-WU+F)}}$$

$$RBI = \frac{X_{(-WU+F)} - X_{(-WU-F)}}{X_{(-WU+F)}}$$

$$RCBI = \frac{X_{(-WU+F)} - X_{(+WU-F)}}{X_{(-WU+F)}}$$

where X is the individual performance variable (survival, basal diameter, or height) for the respective treatment combination (Goldberg *et al.*, 1999).

Five oak-dominated forest stands were used in the study of how natural oak regeneration respond to canopy cutting, ungulate browsing, and a low-intensity fire (Fig. 3a, Paper IV). At the start of this experiment, all sites had naturally regenerated oak (*Q. robur* and *Q. petraea*) seedlings and saplings present in the understory. As the two species naturally hybridize, they were treated as one species for the purpose of this study. At each site, eight plots with the following treatment combinations were created: closed canopy (C), closed canopy and fence (CF), closed canopy, fence, and burn (CFB), closed canopy and burn (CB), canopy gap (G), canopy gap and fence (GF), canopy gap, fence, and burn (GFB), and canopy gap and burn (GB) (Fig. 3c). A minimum of 50 oaks within browsing height, i.e. ≤300 cm tall (Nichols et al., 2015), were chosen for measurements in each treatment plot. In April 2016, the canopy gap and fences (nested within the canopy treatment) were established. The burn treatment (nested within the fence treatment) was implemented using a propane fired blow torch to simulate a low-intensity fire at the end of that growing season (Fig. 4). Oak survival and growth were recorded at the start of the experiment and in August every year 2016-2018. Ungulate browsing (browsed or not browsed) was recorded in April and August of 2016-2018 and competing woody vegetation (height and species composition) was recorded in August of 2016-2018.

Figure 4. Pictures from the two field studies in southern Sweden (paper II and IV) Left: oak plant surrounded by understory vegetation and protected by a fence, nine years after planting (paper II). Top right: simulating a low-intensity ground fire in early October 2016 using a propane fired blowtorch (paper IV). Bottom right: oaks growing in a canopy gap and protected by a fence two years after burning, oaks to the left inside the fence were burned and oaks to the right were not burned (paper IV). Similar fences were used in both field studies (photos: Linda Petersson).

3.3 Greenhouse study

Sprouting capacity and photosynthetic response in oak germinants established in contrasting light environments was studied in a greenhouse experiment (Paper III). This work included two temperate oak species with similar ecological characteristics, the North American white oak (*Q. alba* L.) and the European *Q. robur*. Oak seedlings were germinated and kept in their assigned light environment (low light and high light) throughout the duration of the experiment (Fig. 5). We stem-clipped the new germinants when they were at the beginning of leaf expansion of the initial growth flush to emulate shoot loss caused by disturbance. Photosynthetic light- and CO_2 response were measured in mature leaves when sprouts reached 1-Lag stage of development (Hanson *et al.*, 1986). Sprouting capacity and morphological variables (size and number of sprouts, biomass, leaf area and number) were recorded after the photosynthetic measurements were completed.

Figure 5. Left: part of the study set up in paper III. Each replicate, i.e. box, contained 30 oak seedlings (either *Q. robur* or *Q. alba*) and was assigned low or high light environment, creating four treatment combinations that were replicated three times. Right: the low light treatments were shaded using 80 % neutral density shade cloth (photos: Shelley M. Griffin).

4 Main results and discussion

4.1 Effects of changed land use on the Swedish oak population

Results from paper I revealed that the standing oak volume on productive forestland in southern Sweden increased dramatically between 1953 and 2015, from 1.7 to 4.7 m^3 ha^{-1} (Fig. 6a). This increase was reflected by the density of large oak trees, which almost tripled during this period, from 0.4 to 1.5 stems ha^{-1} between 1953 and 2015 (Fig. 6b). The density of oak saplings initially increased, however, after 1982 they went into a rapid decline (Fig. 6c). Similar demographic changes as revealed in paper I, with successively ageing oak populations due to lack of regeneration, have previously been indicated in small-scale case studies (Brunet *et al.*, 2014; Rogers *et al.*, 2008; Takahashi *et al.*, 2003). At a stand level, natural oak regeneration could be expected to mainly occur in pulses following disturbance events, followed by a period of low regeneration as the cohort ages (Peterken & Tubbs, 1965). At a landscape scale, however, one would expect a mix of successional stages that would even out such demographic patterns. It appears that such disturbance events are very rare in today's homogenous forest landscape.

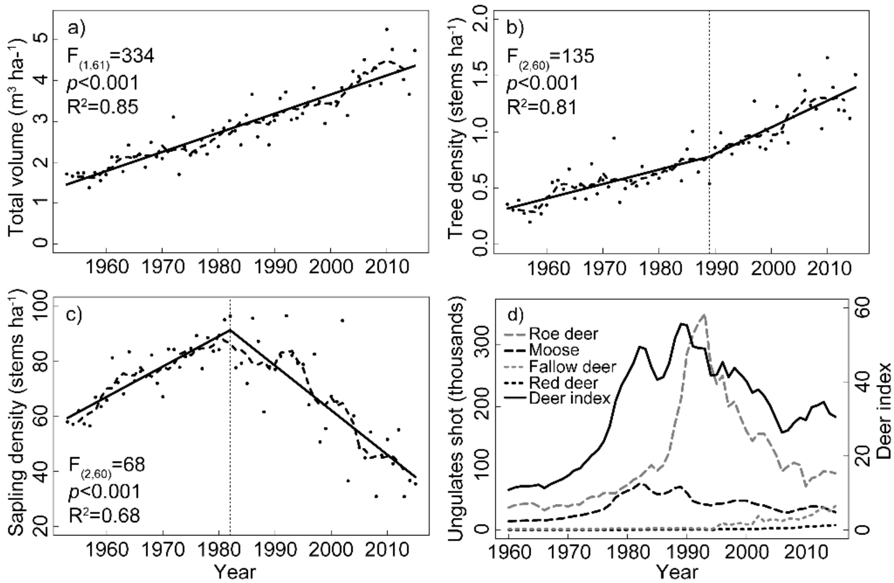

Figure 6. a-c) Oak population development 1953-2015 on productive forestland and d) number of deer shot and deer index (estimated total metabolic weight of deer shot per km^2) 1960-2015 in southern Sweden. a) Total standing oak volume (m^3ha^{-1}), b) density of large oak trees, ≥35 cm dbh, and (c) density of oak saplings, ≥1.3 m tall and ≤9.9 cm dbh. Points = annual values, dashed lines = five-year moving averages, black line = linear regression, b-c) including an AIC supported breakpoint marked with a vertical dotted line. Note the different scale on the y-axes.

It is likely that secondary succession due to lack of management or natural disturbance in broadleaved forests, in combination with introduction of retention trees on clear-cuts during the 1990s (Simonsson *et al.*, 2015; Götmark *et al.*, 2009), explain the observed increases in oak volume and large oak tree density. The Swedish oak population had reached historically low levels during the last 200 years (Lagerås *et al.*, 2016; Lindbladh & Foster, 2010) and, despite the increase in recent decades, the adult oak population remains sparse today.

The initial increase in oak sapling density may be explained by the implementation of large-scale clear-cuts from the 1950s and onward, as these create large open areas suitable for oak regeneration (Götmark & Kiffer, 2014). However, between 1985 and 2010 the proportion of middle-aged forest, the successional stage with the darkest understories (Oliver & Larson, 1996), increased from 30 to 40 % (SLU, 2015). Furthermore, throughout the study period the basal area, a commonly used proxy for understory light (e.g. Hale *et al.*, 2009; Sonohat *et al.*, 2004), increased from 17 to 22 m^2ha^{-1} on productive forestland. This created continuously denser and darker forests. Our statistical analysis suggests that greater basal area had a negative effect on oak sapling density and reduced the probability of finding oak saplings. As the regeneration requirements of *Q. robur* and *Q. petraea* are best met in semi-open forests, where moderate disturbance maintain relatively high light levels over time (Bobiec *et al.*, 2018; Vera, 2000), these results were not surprising.

The annual total number of wild browsing ungulates shot in southern Sweden increased dramatically from 52,000 to 167,000 between 1960 and 2015 (Fig. 6d). Although hunting data should not be considered an exact estimate of ungulate population changes (Pettorelli *et al.*, 2007), the increase does reveal extreme population growth for all four species during the study period. This population growth can partly be explained by a combination of game management focused towards high animal densities and the large-scale creation of clear-cuts that increased food availability (Lavsund *et al.*, 2003). The deer index, used as a proxy for browsing pressure, increased with almost 200 % during the same period (Fig. 6d), and our statistical analysis indicates that increased deer index reduced the probability of finding oak saplings. Even though oaks are tolerant to moderate browsing (Gill, 1992), the high browsing pressure since the 1980s has likely had a disproportionate negative impact on oak regeneration. Oaks are among the most palatable tree species for browsing ungulates in this region (Bergqvist *et al.*, 2018; Månsson *et al.*, 2007; Shipley *et al.*, 1998) and high deer densities that limit natural regeneration of palatable tree species has been observed in many north-temperate ecosystems (Bradshaw & Waller, 2016; Kuijper *et al.*, 2010b; Takatsuki, 2009; Rooney & Waller, 2003). However, paper I is limited by the exclusion of oak saplings under 1.3 m from the NFI data. As all ungulate species included here mainly browse below this height (Nichols & Spong, 2014), it is likely that the high browsing pressure has prevented oaks from reaching the height necessary to be recorded in the NFI. These small oaks might be caught in the "browse trap", where chronic browsing does not necessarily kill the trees but rather keep them in small size classes (Churski *et al.*, 2016; Staver & Bond, 2014).

In conclusion, paper I revealed clear ongoing decreases in oak saplings in the Swedish forest landscapes, despite a substantial increase in mature oak trees during the same period. We could connect this development to extensive land use and game management changes that have created continuously denser and darker forests with more herbivores. These conditions have likely hindered the palatable and light demanding oaks from successfully regenerating at regional scale. However, it is important to keep in mind that other, unidentified factors that have changed over time, e.g. climate, might play additional roles.

4.2 Effects of disturbance-related factors on oak regeneration

The objective was to examine effects of multiple disturbance-related factors on the survival and growth of oak seedlings and saplings. We found that the combination of competition and ungulate browsing was especially harmful for oak survival and diameter growth, while the negative effects of browsing on height growth was somewhat mitigated by the competing understory providing protection from browsers (Paper II). Furthermore, we demonstrated a high sprouting capacity of oak seedlings following shoot-destructive disturbance in a greenhouse (stem-clipping, Paper III) and under field conditions (low-intensity fire, Paper IV). Positive effects of increased light availability on oak growth and survival following disturbance was also evident (Paper III and IV). Although survival rates were high following a low-intensity fire, further research is needed to determine whether oaks gain a competitive advantage (Paper IV).

4.2.1 The relative effects of competition and ungulate browsing on oak performance

Results from paper II showed that the presence of a fence resulted in better protection against ungulate browsing than the presence of a neighbouring woody understory. However, for oaks growing outside fences, the presence of a woody understory significantly reduced the probability of an oak being browsed and the browsing frequency in plots with a woody understory was 5 to 30 percentage points lower than in plots without a woody understory. While similar results have been found in previous short-term studies in open woodlands and broadleaved forests (Perea & Gil, 2014; Harmer *et al.*, 2010; Smit *et al.*, 2007), paper II demonstrated for the first time that this protective effect may persist over time.

Furthermore, the character and structure of the woody understory affected the probability of browsing. A high proportion of palatable species (*Populus tremula* L., *Salix caprea* L., *Sorbus aucuparia* L. and naturally regenerated *Q. robur* and *Q. petraea*) and greater herbaceous groundcover increased the risk of a planted oak being browsed, while the browsing risk was reduced when the woody understory was tall. It seems likely that taller understory vegetation was more efficient at visually blocking the oak plants and thereby reduced the likelihood of them being detected by browsers (cf. Pietrzykowski *et al.*, 2003; Bergquist & Örlander, 1998). While shrub communities with a high proportion of palatable species are more attractive to browsers, the risk of an individual plant being browsed might depend on the plant's relative palatability within the community. These different scales of forage selection could explain the contradictory reports as to whether palatable neighbours increase (Bee *et al.*, 2009; Baraza *et al.*, 2006) or decrease (Ward *et al.*, 2008) the browsing probability of a focal plant species. It would seem that the highly palatable oak (Kullberg & Bergström, 2001) was at a disadvantage at both these forage selection levels.

Browsing, competition from a woody understory, and the combined effect of these two factors all had significant negative effects on oak survival. Competition was more harmful than browsing, but the combination of the two factors had an even greater negative effect on oak survival (Fig. 7a). Furthermore, competition, browsing, and the combination of the two factors all had significant negative effects on oak basal diameter and height growth. For diameter growth, browsing was more harmful than competition, but the combination of the two factors had an even greater negative effect (Fig. 7b). For height growth, however, the relative effects were more complicated. Browsing was more harmful than competition; however, the combination of the two factors had a smaller negative effect on height growth than browsing alone (Fig. 7c). In other words, oaks that faced browsing gained some protection from the surrounding woody understory that allowed them to grow taller than if they only faced browsing.

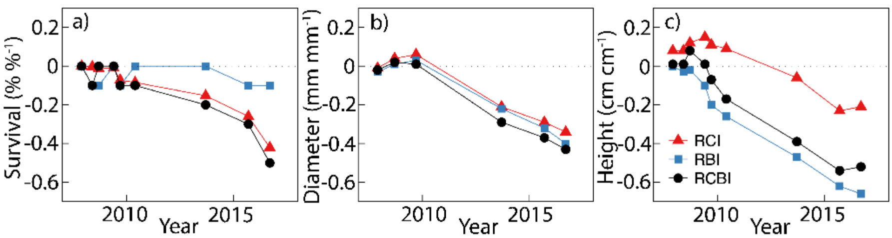

Figure 7. The relative effect of competition from a woody understory (RCI, red triangles), ungulate browsing (RBI, blue squares), and the combination of competition and browsing (RCBI, black circles) over time on oak a) survival, b) basal diameter growth, and c) height growth (paper II). Positive values indicates a facilitation effect. Values are means (n = 10).

The results in paper II are consistent with previous research that have reported negative effects on oak performance from woody understory competition (Jensen & Löf, 2017; Harmer & Morgan, 2007; Lorimer *et al.*, 1994) and ungulate browsing (Kuijper *et al.*, 2010a; Bergquist *et al.*, 2009; Rooney & Waller, 2003). However, paper II is the first study to have quantified the individual and combined effects of these two factors, which enabled a direct comparison of the magnitude of the effects over time. The results suggest that oaks outside fences might be caught in the “browse trap” (Churski *et al.*, 2016; Staver & Bond, 2014), where chronic browsing have not killed the oaks but rather severely restricted their growth. Although the high mortality rate of young oaks that experienced only competition suggests that competition is a more serious threat to oak recruitment than browsing, the combination of understory competition and ungulate browsing was even worse for oak survival.

4.2.2 Sprouting capacity and photosynthesis of seedling sprouts in contrasting light environments

Results from paper III showed that germinants of both the North American *Q. alba* and the European *Q. robur* sprout vigorously following top-kill. Furthermore, high light environment enhanced the sprouting capacity of both species, as indicated by the number of sprouts per plant (29 % greater) and the accumulated plant biomass (40 % greater). To our knowledge, this response has not previously been demonstrated for oak germinants. Enhanced sprouting capacity of deciduous tree seedlings as promoted by high light availability has been attributed to root system development (Longbrake & McCarthy, 2001) and accumulation of carbohydrate stores (Kabeya & Sakai, 2005; Kabeya *et al.*, 2003). This suggests that sprouting capacity is largely determined by the light environment prior to stem loss. However, this does not explain the results in paper III, as root mass of both species were greater in the low light environment at time of clipping (65 % greater). By the end of the experiment, however, root mass was greater in the high light environment (48 % greater). This observation demonstrates plasticity in sprout development that is attributable to the light environment of the developing sprout, rather than the light environment prior to shoot destruction.

Seedling sprouts of both species showed morphological and physiological plasticity to the light environment, despite the young age and ontogeny at time of clipping. At the plant level, low light availability increased the proportional distribution of leaf area (51 % greater leaf area ratio), consistent with plant morphology to support light capture (Jensen *et al.*, 2012b; Rebbeck *et al.*, 2011; Gardiner *et al.*, 2009). However, the light environment had no effect on the proportional biomass distribution. This was likely an effect of the clipping treatment, which necessitated germinants to prioritize photosynthate allocation to shoot development rather than root development (Kruger & Reich, 1993a). At the leaf-level, low light availability decreased leaf mass per area (36 % lower) and increased total chlorophyll concentration (64 % greater), morphological acclimations that improve efficiency of light capture (Zhang *et al.*, 2018; Jensen *et al.*, 2012b; Abrams & Kubiske, 1990). Furthermore, high light environment increased the leaf-level photosynthetic capacity of the oak seedling sprouts. These findings in paper III are in contrast to previous studies, which found limited growth and photosynthetic response of oak seedlings, including *Q. alba*, during their first growing season (Rebbeck *et al.*, 2012; Rebbeck *et al.*, 2011). We therefore suggest that cotyledonary reserves may not be enough to simultaneously compensate for shoot loss and light limitation, and that oak seedling sprouts in this respect might be less shade tolerant than seedlings during their first growing season. However, further studies that directly compare young oak seedling sprouts and intact seedlings are needed to verify this suggestion.

While the two oak species appear similarly adapted to shoot loss, *Q. robur* displayed a greater sprouting capacity (29 % more sprouts per plant), a greater plant-level net photosynthesis (73 % greater), and lower leaf mass per area (8 % lower) than *Q. alba*, regardless of light environment. This may indicate that *Q. robur* seedling sprouts may tolerate shaded environments more readily than *Q. alba*. Nevertheless, the findings in paper III show that *Q. alba* and *Q. robur* have similar ecological characteristics and that they would likely respond in a similar way to disturbance.

4.2.3 Potential of using a low-intensity fire to promote oak regeneration in temperate Europe

Results from paper IV showed that although a low-intensity ground fire significantly reduced survival of naturally regenerated oak (*Q. robur* and *Q. petraea*), survival rates were still high across treatments two years after burning (Fig. 8a). These high survival rates were largely dependent on the oaks' ability to produce new sprouts following top-kill. At the end of the experiment, 88-96 % of surviving oaks in the burn treatment had produced new sprouts. Although these new small sprouts initially caused a strongly negative relative height growth rate (RGR_H), after two years the RGR_H was significantly greater for oaks that had been subjected to fire than those that had not (Fig. 8b). Considering that the high sprouting capacity of many North American oak species is one reason they are considered fire tolerant (Brose et al., 2013), the results in paper IV suggests that natural regeneration of European temperate oaks could be promoted by fire. However, long-term observations are needed to determine if these initial positive effects persist over time.

Two years after burning, canopy openness had a significant positive effect on RGR_H, but no significant effect on survival (Fig. 8a, b). Seedlings of *Q. robur* and *Q. petraea* require a minimum of 15-20 % of full light for sustained growth (Löf *et al.*, 2007; von Lüpke, 1998), which corresponds to the available light beneath closed canopies in this study. This relatively high light availability in the closed canopy treatment can probably explain the high survival rates of the oaks growing there. However, when only analysing oaks affected by burning, survival was significantly greater for oaks growing in the canopy gap (Fig. 8a), which suggests that oak resilience to disturbance increased with greater light availability. The increased light availability in the canopy gaps prior to burning likely favoured the development of greater belowground carbohydrate reserves in the oaks, which are needed for rapid growth following disturbance (Kabeya & Sakai, 2005; Welander & Ottosson, 1998).

There was a trend, although non-significant, that protection against ungulate browsers had positive effects on oak survival and RGR_H (Fig. 8a, b). The lack of significance could possibly be explained by the oaks' relatively high tolerance to moderate browsing pressure (Harmer, 2001), the short duration of the experiment, or large variations in browsing animal density between study sites. Interestingly, fire influenced the pattern of ungulate browsing frequency. While the peak in browsing frequency was during the winter in all the non-burned plots throughout the experiment, in plots that had been recently burnt, summer browsing was highly prominent (Fig. 8c). Similar increases of browsing in recently burned areas have been observed in the United States (Andruk *et al.*, 2014; Collins & Carson, 2003). Considering the dramatic increase of ungulate populations in Sweden and most other north-temperate ecosystems during the last decades (Takatsuki, 2009; Lavsund *et al.*, 2003; Rooney & Waller, 2003), this interaction between fire and browsing frequency becomes particularly notable. It suggests that positive effects of prescribed fire on oak regeneration could be diminished in areas subject to high browsing pressure.

To answer if the fire-oak hypothesis could be applicable to European temperate oaks it is essential not only to assess fire effects on oak, but also on competing vegetation (Arthur *et al.*, 2012; Abrams, 1996). In paper IV, however, it was necessary to combine woody vegetation into three species groups (conifers, broadleaves excluding oaks, and oaks) as oaks dominated the understory on most sites. Nevertheless, we observed clear fire effects where burning significantly reduced the number of individuals, but to different extent for the species groups. The number of conifers had been reduced by 83 %, the number of broadleaves by 44 %, and the number of oaks by 26 %. The greater reduction of conifers were expected, as unlike most broadleaves, none of the Swedish conifer species have the ability to sprout (Leonardsson & Götmark, 2015). However, burning did not have a significant effect on the relative density of oaks. Further investigations on the species-specific response of competing woody vegetation following fire are therefore needed to determine whether oaks gain a competitive advantage.

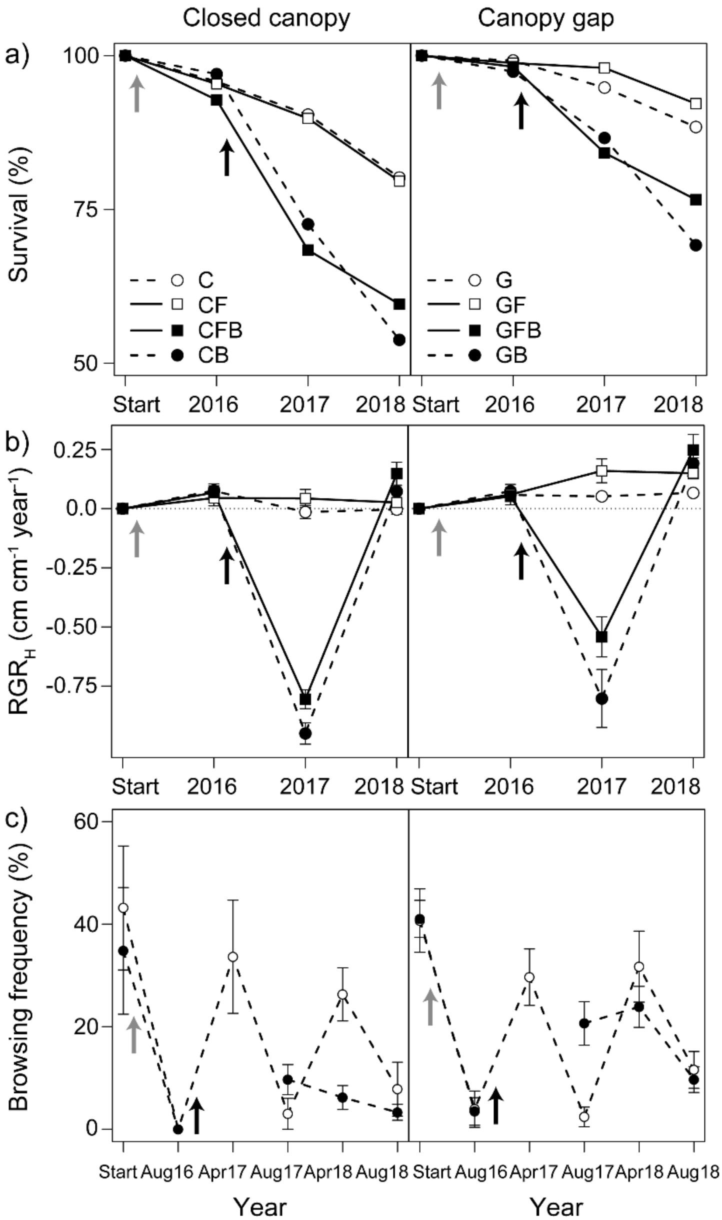

Figure 8. a) Survival and b) relative height growth rate (RGR$_H$) of naturally regenerated oaks and c) ungulate browsing frequency (proportion of browsed oaks per treatment plot; measurements in August corresponds to preceding summer browsing, measurements in April corresponds to preceding winter browsing) in paper IV. Treatment combinations: closed canopy (C), closed canopy and fence (CF), closed canopy, fence, and burn (CFB), closed canopy and burn (CB), canopy gap (G), canopy gap and fence (GF), canopy gap, fence, and burn (GFB), and canopy gap and burn (GB). Time of canopy gap creation and fencing is noted with a grey arrow. Time of burn is noted with a black arrow.

5 Conclusion and management implications

The overall goal of this thesis was to examine how multiple disturbance-related factors affect survival and growth of oak seedlings and saplings, and thereby evaluate whether natural regeneration of oak could be promoted by manipulating disturbance. To meet this goal, we also analysed the regional historical development of oak trees and saplings.

We found that the Swedish oak population experienced a demographic shift during the last 60 years (Paper I). Despite a continuous increase in large oak trees, the initially increasing oak sapling population went into a steep and continuous decline after the early 1980s. We could connect this development to extensive land use and game management changes that created denser and darker forests with more herbivores. This development has likely hindered the palatable and light demanding oak from regenerating at regional scale.

Positive effects of increased light availability on oak survival and growth were demonstrated in paper III and IV, consistent with previous research (e.g. Annighöfer *et al.*, 2015; Rebbeck *et al.*, 2011; Rodríguez-Calcerrada *et al.*, 2008; Götmark, 2007; Löf *et al.*, 2007). Therefore, in the absence of natural disturbance, active management that create and maintain open canopies seem essential to promote oak regeneration. In mixed broadleaved stands, conservation oriented thinning, i.e. partial cutting as a conservation measure with the objective to increase light and stand complexity, have shown positive results (Leonardsson *et al.*, 2015; Götmark, 2013). However, greater light availability in forest understories also increase the growth of competing woody vegetation (Leonardsson *et al.*, 2015; Brudvig & Asbjornsen, 2007). As demonstrated in paper II, competition from a woody understory drastically decreases oak survival and adversely affects growth. Some form of understory vegetation control therefore seem necessary.

Prescribed burning, following the North American fire-oak hypothesis (Arthur *et al.*, 2012; Abrams, 1992), could possibly be used for such understory vegetation control. Results from paper III and IV indicate that management practices developed to regenerate North American oak species based on this hypothesis could be successfully applied to the European oaks as well. Our results suggest that oak seedling tolerance to disturbance is greater in high light environments. As low-intensity prescribed burns are not efficient in reducing the density of large trees, we suggest that some form of stand thinning or gap creation is needed to increase light availability, preferably prior to prescribed fire (Brose *et al.*, 2013; Hutchinson *et al.*, 2012).

Abundant regeneration of spruce in broadleaved forests of conservation interest is a common problem in southern Sweden and considered to threaten biodiversity (Nitare, 2014). We found that conifer regeneration was strongly reduced by burning, indicating that prescribed burns could be an efficient management tool in such situations. However, further research is needed in several areas before we can recommend prescribed burns in European oak-dominated forests, including assessment of long-term vitality of oak, species-specific response of competitors, and implications for biodiversity. Furthermore, considering that browsing frequency initially increased in recently burned plots, it seems necessary to consider local ungulate density and the potential browsing impact following fire.

Consistent with previous research (e.g. Churski *et al.*, 2016; Kuijper *et al.*, 2010a; Bergquist *et al.*, 2009; Rooney & Waller, 2003; Gill, 1992), negative effects of ungulate browsing on oak were demonstrated in paper I, II, and IV. Considering the dramatic increases in wild ungulate populations in Sweden and most other north-temperate ecosystems during the last decades (Takatsuki, 2009; Milner et al., 2006; Rooney & Waller, 2003), reducing ungulate browsing pressure therefore seem to be a major factor to promote regeneration of oak and other palatable tree species. At a stand-scale, protective structures may facilitate recruitment of palatable tree species by creating sheltered refugia (Smit et al., 2012; de Chantal & Grandström, 2007). Results from paper II showed that woody vegetation could provide protection against browsing, however, due to the high mortality of oaks surrounded by a woody understory, the practical implications are likely limited. In areas where fencing is not feasible, increasing the amount of coarse woody debris, e.g. by leaving crowns of felled trees, could be a more efficient alternative. At a landscape-scale, strategies that manage both deer populations and their available food are needed (Apollonio et al., 2017; Beguin et al., 2016). As forest management often directly influence the landscape's carrying capacity for deer populations, management strategies that integrate the two are necessary.

To summarize, results from my studies indicate that in the absence of natural disturbance, active management that resemble previous disturbance regimes and thereby restore habitats with open or semi-open canopies and low to moderate browsing pressure seem essential to promote natural oak regeneration. Furthermore, diversified forest management, including reinstatement of past land-use practices such as forest grazing regimes and cutting of shade tolerant trees, would likely be beneficial for oak regeneration and recruitment by creating a more heterogeneous forest landscape (Mölder *et al.*, 2019; Rooney *et al.*, 2016; Kirby & Watkins, 2015).

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Populärvetenskaplig sammanfattning

Skogen har genom historien bidragit till mänsklig utveckling och kultur, samtidigt som människan radikalt har påverkat skogens utbredning, artsammansättning och struktur. Under det senaste århundradet har människans allt högre efterfrågan på virke och bränsle skapat ett intensivare skogsbruk. Vi har gått ifrån historiska skötselmetoder, såsom skogsbete för tamdjur, plockhyggesbruk och hamling av träd, samtidigt som vi i stor utsträckning har begränsat naturliga ekologiska störningar som kan minska produktionen, t.ex. skogsbränder. Detta intensiva skogsbruk och brist på naturliga störningar har skapat ett mer homogent skogslandskap och en förlust av många naturtyper, vilket har stor negativ påverkan på den biologiska mångfalden.

Det finns ungefär 600 olika arter av ek runtom i världen och de har ofta en mycket stor betydelse för biologisk mångfald. I Sverige finns två närbesläktade ekarter, bergek och skogsek, och uppskattningsvis är 1500 andra arter mer eller mindre beroende av de svenska ekarna. Speciellt gamla grova ekar som ofta har skrovlig bark, döda grenar och håligheter skapar viktiga livsmiljöer för bland annat vedlevande svampar, insekter, lavar och fåglar. Ekvirke är dessutom mycket värdefullt på grund av sin hållbarhet och motståndskraft. För ungefär 4000 år sedan var ekskogar utbredda över södra Sverige, men på grund av ett kallare klimat, avskogning för att skapa mer jordbruksmark och ersättning av andra skogstyper har ekskogarna minskat kraftigt. I slutet på 1800-talet hade eken nått historiskt låga nivåer i södra Sverige.

Trots att eken är viktig både för biologisk mångfald och virkesproduktion anses den naturliga föryngringen av ek inte räcka till för mänskliga syften på flera platser runt om i världen. Med andra ord, antalet ekplantor anses inte vara tillräckligt många för att ersätta de vuxna ekträden över tid. Flera miljöfaktorer samverkar och påverkar ekplantornas överlevnad och tillväxt, bland annat mängden ljus, jordmånen, omgivande växtlighet och bete från vilda djur. Ekplantor är ganska ljuskrävande och de kan därför vara känsliga för konkurrens från mer snabbväxande och skuggtåliga träd, t.ex. bok och gran. Dessutom föredrar många vilda hjortdjur att äta ek framför andra trädslag, vilket gör att ek ofta utsätts för ett högt betestryck som hindrar tillväxten och kan minska överlevnaden. Ekologiska störningar och historiska skötselmetoder anses gynna naturlig föryngring av ek, de skapar ofta glesa skogar där mycket ljus når marken och de kan även begränsa konkurrerande växtlighet. I östra Nordamerika anses även lågintensiva bränder kunna gynna naturlig föryngring av ek, och på flera platser i USA används idag naturvårdsbränder i kombination med gallring för att återställa ekdominerade ekosystem och för att gynna ekföryngring inom virkesproduktion.

I det här arbetet undersöktes hur ekplantors överlevnad och tillväxt påverkas av olika störningsfaktorer, d.v.s. ljushuggning, bete och brand, och hur de omfattande förändringarna av skogsbruket under 1900-talet har påverkat den svenska ekpopulationen. Den svenska riksskogstaxeringen har sedan 1953 utfört årliga inventeringar för att kartlägga utvecklingen i de svenska skogarna. I studie I använde jag data från riksskogstaxeringen och kunde därmed se att den totala volymen ekvirke och antalet stora ekar per hektar har ökat kontinuerligt mellan 1953 och 2015. Troligtvis beror denna ökning delvis på att traditionell skötsel upphörde på många betesmarker och glesa lövskogar under tidigt 1900-tal, vilket orsakade en igenväxning med bland annat ek på dessa marker. Dessutom har skogsbruket sedan början av 1990-talet lämnat levande hänsynsträd på kalhyggen, vilket troligtvis också har bidragit till det ökade antalet stora ekar. Men trots att antalet stora ekar har ökat de senaste decennierna kunde jag visa att antalet små ekar har minskat kraftigt sedan början av 1980-talet. Genom att kombinera information från riksskogstaxeringen och avskjutningsstatistik från Svenska Jägareförbundet kunde jag koppla denna minskning till att skogarna har blivit allt tätare, därmed mörkare, och att antalet betande hjortdjur har ökat kraftigt. Tillsammans har detta troligtvis skapat förutsättningar som missgynnar naturlig föryngring av ek på landskapsnivå.

Tidigare forskning tyder på att omgivande vegetation kan skydda ekar och andra välsmakande trädplantor från bete. Detta skydd kan uppstå genom att den omgivande vegetationen döljer plantorna så att betesdjuren helt enkelt inte upptäcker dem, eller genom att den omgivande vegetationen har taggar och andra fysiska och/eller kemiska egenskaper som gör området oattraktivt. Därmed har artsammansättningen och strukturen på den omgivande vegetationen troligtvis en stor påverkan på hur effektivt den kan skydda trädplantor mot bete. Eftersom ekplantor kan vara känsliga för konkurrens från andra mer snabbväxande trädslag och buskar, finns det en risk att den omgivande vegetationen har större negativ påverkan genom ökad konkurrens än positiv påverkan genom skydd från bete. I studie II undersöktes om omgivande vegetation hade större positiv eller negativ påverka på ekplantors långsiktiga (9 år) överlevnad och tillväxt. Jag fann att stängsel som utesluter betande hjortdjur gav ett bättre skydd mot bete än omgivande vegetation, men att omgivande vegetation ändå minskade sannolikheten för att en ekplanta skulle bli betad när den inte skyddades av stängsel. Dessutom observerade jag att sannolikheten att en ekplanta skulle bli betad ökade när den omgivande vegetationen hade en större andel andra välsmakande arter. Detta beror troligtvis på att dessa välsmakande arter lockar betesdjuren till området. Sammantaget observerades dock att konkurrens från omgivande vegetation hade en stark negativ effekt på ekplantornas överlevnad, men endast en svag påverkan på tillväxten. Bete hade en omvänd effekt, det vill säga en svag påverkan på överlevnad men en stark negativ effekt på tillväxt. Kombinationen av konkurrens och bete hade större negativ effekt på ekplantornas överlevnad än enbart konkurrens eller bete. Våra resultat tyder därför på att trots att omgivande vegetation ger ett visst skydd mot bete är den långsiktiga effekten på ekplantorna mer negativ än positiv.

En viktig egenskap som ökar ekplantors tolerans mot ekologiska störningar är deras förmåga att skjuta nya skott ifall plantan skadas. En anledning till att många Nordamerikanska ekar anses gynnas av lågintensiva bränder är just att de har en högre skottskjutningsförmåga än deras konkurrenter. I studie III användes ett växthusexperiment för att jämföra skottskjutningsförmågan och den fotosyntetiska kapaciteten under olika ljusnivåer hos en svensk och en amerikansk ekart. För att efterlikna en ekologisk störning, och därmed framkalla skottskjutning, klippte jag av stammen på nyetablerade ekplantor. Jag fann att båda ekarterna hade en hög skottskjutningsförmåga, och att denna förmåga var högre hos plantor som hade tillgång till mer ljus. De plantor som hade tillgång till mer ljus uppvisade dessutom en högre fotosyntetisk kapacitet. Tidigare studier har inte funnit denna typ av anpassningar till olika ljusnivåer hos så unga ekplantor. Denna studie indikerar därför att näringsreserverna som finns i ekollonen inte räcker till för att kompensera en förlust av stammen samtidigt som ljustillgången är begränsad, och att plantor som skjutit nya skott är mer ljuskrävande under det första levnadsåret än plantor som inte gjort det. Dessutom tyder våra resultat, där de två ekarterna uppvisade mycket likartade anpassningar, på att skötselmetoder som utvecklats för den ena arten troligtvis skulle kunna tillämpas framgångsrikt även på den andra.

Som tidigare nämnts används naturvårdsbränder i nordöstra USA för att återställa ekdominerade ekosystem och gynna naturlig föryngring av ek. I Europa förknippas skogsbränder framförallt med boreala barrskogar, där regelbundna bränder anses vara en naturligt förekommande ekologisk störning som är av stor vikt för att bibehålla höga biodiversitetsvärden. Nya studier har dock föreslagit att bränder även kan ha spelat en viktig roll i tempererade lövskogar, och att bränder kan ha liknande positiva effekter på ekföryngring som i Nordamerika. I studie IV användes ett fältexperiment för att undersöka hur en lågintensiv brand påverkar överlevnad och tillväxt hos de svenska ekarterna, och ifall effekten av brand beror på ekplantornas tillgång till ljus och/eller skydd mot bete. En gasbrännare användes för att efterlikna en lågintensiv markbrand. Jag fann att bränningen minskade ekplantornas överlevnad, men tack vare ekplantornas höga skottskjutningsförmåga var överlevnaden trots detta relativt hög. Dessutom var höjdtillväxten högre hos de ekplantor som utsatts för brand än hos de ekplantor som inte utsatts för brand två år efter bränningen. För de brända ekplantorna ökade överlevnaden när de hade tillgång till mer ljus. Under experimentet noterades även att bränningen påverkade hur många ekplantor som blev utsatta för bete från hjortdjur. Ett år efter bränningen blev fler ekplantor betade i de brända ytorna än i de ytor som inte bränts. Tidigare forskning från USA har funnit liknande mönster, vilket sammantaget tyder på att de positiva effekterna av brand kan minska i områden med stora populationer av hjortdjur. Antalet plantor av konkurrerande trädslag minskade även efter branden, framförallt antalet barrträdsplantor minskade kraftigt.

Sammantaget tyder min forskning på att i brist på ekologiska störningar krävs aktiv skötsel för att gynna naturlig föryngring av ek. Det är nödvändigt att återställa naturtyper med en stor mängd tillgängligt ljus vid marknivå och ett måttligt betestryck från hjortdjur. Tidigare forskning har visat att naturvårdsgallringar, det vill säga gallring som naturvårdsåtgärd med syftet att öka mängden ljus och strukturer, har haft positiva effekter på ekplantors överlevnad, tillväxt samt motståndskraft mot betesskador. En ökad mängd ljus gynnar dock även konkurrerande vegetation, därmed kan ytterligare åtgärder för att minska konkurrensen vara nödvändiga. I dessa fall skulle möjligtvis en lågintensiv markbrand kunna användas, särskilt när igenväxning med granplantor är ett problem då dessa vanligtvis inte överlever en brand. Det krävs dock forskning inom flera områden, bland annat hur brand påverkar långsiktig överlevnad hos ek och konkurrerande trädslag samt den biologiska mångfald som är beroende av ekskog, innan jag kan rekommendera naturvårdsbränder som skötselåtgärd i svensk ekskog. Att minska betestrycket från hjortdjur kan vara svårt på beståndsnivå, då djuren rör sig över stora områden och deras betesmönster påverkas av fodermängden och –kvalitén i det omgivande landskapet. Strategier som integrerar viltvård och skogsskötsel på en landskapsnivå är därför önskvärda. På platser där stängsling inte är möjligt kan dock andra skyddande strukturer, t.ex. kvarlämnade kronor från fällda träd, ge ett visst skydd mot betesskador.

Acknowledgements

This PhD thesis would not have been completed without the support and contributions from many people. Here I wish to thank all of you, both those mentioned by name but also all the rest that have made these four years a truly great experience.

First, I wish to thank my somewhat large, but well composed supervisor group. Working with all of you have been educational and a lot of fun! **Magnus Löf**, my main supervisor, thank you for giving me this opportunity and for being such an active and involved supervisor. You have always been ready to answer my questions and give advice, while still giving me the freedom to develop the project. I am very grateful to have had you as a supervisor. **Annika Felton**, thank you for all our stimulating conversations, both about my project and ecology in general. Your knowledge and enthusiasm are very inspirational! **Anna Jensen**, thank you for all the time we have spent talking about plant physiology, despite my poor Danish you have taught me a lot. **Frank Götmark**, thank you for all the good advice throughout the years and for the great idea to use NFI data while we were waiting for the oaks to grow in the forest. **Emile Gardiner**, thank you for helping me concretize my ideas into an experiment and all the detailed manuscript edits, you have improved both my scientific thinking and my writing. I also greatly appreciate the hospitality you and your family showed me during my visit to the US. **Daniel Dey**, thank you for sharing your knowledge and experience. I am also grateful for the field trip you arranged during my visit to the US; it was one of the highlights during my PhD!

Thanks to **all current and former co-workers** at Southern Swedish Forest Research Centre and the other departments in Alnarp, for creating an inspirational working environment and friendly atmosphere. Especially all the PhD students, **Adrian**, **Isak**, **Gui**, **Lisa**, **Mattias**, **Karin**, **Oscar**, **Martin**,

Mikolaj, **Delphine**, **Emma**, **Mostarin**, **Khaled**, and all the rest, you have made my time in Alnarp so much more fun!

Thanks to all **landowners** for allowing me to conduct my experiments on your land, without all of you much of this work would not have been possible!

Last but not least, my family. **Mamma** and **pappa**, there is so much to thank you for. You have always been there ready to support and help me, while still allowing me find my own way. A special thanks to you mamma, your great love for nature and genuine curiosity about my studies have inspired me more than you know. **Linus**, thank you for you endless enthusiasm and optimism. **Max**, thank you for always being there, ready to listen and discuss, for defying the ticks to help me with the oaks, and for all the tasty dinners and lunchboxes you have made throughout the years. Without you, my life and my diet would be much more tedious.