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Effects of Facilitation and Competition on Oak Seedlings

Using Shrubs as Nurse-plants to Facilitate Growth and Reduce Browsing from Large Herbivores

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Cover: Oak seedling with newly developed leaves.
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Abstract

Plant–plant interactions have been indicated as a potential means to facilitate oak seedling establishment and reduce herbivory when restoring oak forests. The aim of this thesis was to investigate mechanisms and outcomes of competitive and indirectly facilitative interactions between oak (*Quercus robur* and *Q. petraea*) seedlings and neighboring plants, primarily shrubs. The associational resistance of planted oak seedlings to larger herbivores provided by naturally occurring shrubs was tested in ten temperate broadleaved forests across southern Sweden. The results showed that shrubs reduced ungulate browsing frequency and intensity by concealing the oak seedlings and by sharing enemies (*i.e.* ungulate herbivores) with surrounding and more preferred shrub species, thus providing numeric dilution and associational plant refuges. The occurrence of naturally regenerated oak seedlings, five years after a conservation-oriented thinning, was negatively influenced by the presence of tall ground vegetation and positively influenced by high soil moisture. For oak seedlings planted in an open field, shrubs indirectly facilitated biomass accumulation by reducing competition from herbaceous vegetation. However, shrubs became net competitors three years after planting. The oak seedling response, in terms of biomass accumulation, transpiration and photosynthesis, to competition from shrubs was proportional to resource availability. Aboveground competition for light had a greater effect on oak seedling growth than belowground competition. Nevertheless, oak seedlings were able to produce a second shoot flush, over-topping the shrub canopy. This periodic flushing enabled light-acclimation in a stratified light environment. In conclusion, management of shrubs has the potential to reduce browsing and herbaceous competitors during oak regeneration, particularly during the first years after planting. Although shrubs alone may not replace fences as an effective means of reducing browsing on oaks, they provide a complement to improve the growth of seedlings during the early stages of establishment.

Keywords: Pedunculate oak, Deciduous forest, Forest restoration, Neighboring effect, Vertical light gradient, Gas exchange, Sap-flow, Developmental plasticity, Phenology, Leaf morphology.

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Dedication

To Viggo, for evoking the strong mechanistic curiosity in me.
To Mia, for always believing in me.
To *Farmor*, who struggle against invasive oak seedlings in her garden.

Contents

List of Papers

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

I Jensen, A.M., Götmark, F. and Löf, M. Shrubs protect oak seedlings against ungulate browsing in temperate broadleaved forests of conservation interest: A field experiment. (Manuscript).

II Götmark, F., Schott, K. M. and Jensen, A. M. (2011). Factors influencing presence-absence of oak (*Quercus* spp.) seedlings after conservation-oriented partial cutting of high forests in Sweden. *Scandinavian Journal of Forest Research* 26, 136-145.

III Jensen, A.M., Löf, M. and Witzell, J. Competition and indirect facilitation from shrubs on *Quercus robur* seedlings during establishment. (Manuscript).

IV Jensen, A.M, Löf, M. and Gardiner, E.S. (2011). Effects of above- and below-ground competition from shrubs on photosynthesis, transpiration and growth in *Quercus robur* L. seedlings. *Environmental and Experimental Botany* 71, 367-375.

V Jensen, A.M., Gardiner, E.S. and Vaughn, K.C. High-light acclimation in *Quercus robur* L. seedlings upon over-topping a shaded environment. (Submitted manuscript).

Papers **II** and **IV** are reproduced with the permission of the publishers.

My contribution to the five papers included in this thesis was as follows:

I I planned the experiment together with Frank Götmark and Magnus Löf. I conducted most of the fieldwork and all statistical analyses. I am the first and corresponding author in the manuscript.

II Frank Götmark and Kaitlin Schott planned and carried out the main part of the work. I participated in planning parts of the design, fieldwork and made comments on the manuscript.

III I planned the experiment together with Magnus Löf. I conducted the fieldwork with the assistance of Magnus Löf and Johanna Witzell. I carried out most of the calculations and statistical analyses. I am the first and corresponding author in the manuscript.

IV I developed the research idea and planned the experimental design together with Magnus Löf and Emile Gardiner. I conducted most of the fieldwork, except for the sap-flow measurements, which were conducted by Magnus Löf. I carried out all the calculations (except for sap-flow data) and statistical analyses. I am the first and corresponding author on the paper.

V I developed the research idea, and together with Emile Gardiner developed the experimental design. Except for the microscopy preparations (undertaken by Kevin Vaughn), I was responsible for the collection of data and the analyses. I am the first and corresponding author in the manuscript.

1 Introduction

1.1 Background

Oaks (*Quercus robur* and *Q. petraea*) have decreased in abundance in southern Scandinavia over the last 4000 years, with a particularly rapid decrease due to human activities during the 18th and 19th centuries (Nilsson 1997, Lindbladh and Foster 2010). In southern Sweden, this land-use change favored Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) H. Karst), and currently southern Sweden (Götaland) has a forest cover of 63%. Out of the total standing volume (846.3 mill. m^3), 3.4% is oak timber (Loman 2010).

Large oak trees and oak-rich forests often harbor many rare cryptogams, vascular plants and invertebrates (Berg *et al.* 1994, Ranius and Jansson 2000, Götmark 2007). Many of these species-rich stands, were once small semi-open pastures or fields, have through secondary succession become closed-canopy mixed stands (Götmark and Thorell 2003). Due to crown closure and relatively high browsing pressure, recruitment of new oaks to the canopy was and is often poor (Götmark *et al.* 2005b), potentially resulting in a shift towards more shade tolerant species in these forests. Concern over loss of these semi-open species-rich oak forests has led to a realization that there is a need to evaluate the effects of past management interventions and to develop new silvicultural restoration tools (Wagner and Lundqvist 2005, Brunet *et al.* 2010, Götmark 2010).

In Sweden, oak regeneration is mostly the result of clear-cutting followed by mechanical site preparation, cleaning (*i.e.* removing woody vegetation) and planting bare-rooted seedlings. Natural regeneration and direct seeding are used less frequently (Birkedal 2010). Fencing is nearly always required because browsing damages from ungulates, *i.e.*, moose (*Alces alces*) and deer (*Capreolus capreolus* and *Cervus elaphus*), causes biomass loss and growth stagnation, thus prolonging the regeneration phase (Kullberg and Bergström 2001, Bergquist *et al.* 2009, Swedish Forest Agency 2009a). The current methods of seedling protection (*e.g.* fencing) are costly for the forest owners, especially in species-rich stands which are often small (< 3 ha; Götmark and Thorell 2003) and in which invasive methods, such as use of heavy equipment, may be inappropriate because of conservation considerations (Swedish Forest Agency 2009b). Therefore, cost-efficient and less invasive regeneration methods that reduce damage by ungulate browsers to oak seedlings are required to ensure continuous recruitment of new oak trees to the overstory.

Physical structures such as dead wood barriers and living shrubs have been found to reduce damage by ungulate browsers and grazers to tree seedlings (de Chantal and Granström 2007, van Uytvanck *et al.* 2008, Pihlgren 2009, Harmer *et al.* 2010), suggesting that naturally occurring shrubs could be used as a tool to facilitate oak regeneration when fencing or browser population control is not an option. In Mediterranean ecosystems, shrubs are known to indirectly facilitate oak seedling establishment by reducing competition from herbaceous vegetation (Gómez-Aparicio *et al.* 2004, Cuesta *et al.* 2010). Less research about facilitation has been carried out in temperate European broadleaved forest ecosystems.

1.2 The Focal Plant: Oaks

In Sweden, two white oak species are considered native, *Quercus robur* L. (Pedunculate oak) and *Q. petraea* (Matt.) Liebl. (Sessile oak). The two species form hybrids (Siegismund and Jensen 2001). The plant material used in this thesis came from either mixed *Q. petraea* and *Q. robur* (papers **I** and **II**) or pure *Q. robur* (papers **III**, **IV** and **V**) seed source stands. Ecologically the two species are similar, although *Q. petraea* trees are thought to be more drought-tolerant than *Q. robur* (Parelle *et al.* 2007). In temperate broadleaved forests both species are considered intermediate in terms of their light requirements (Diekmann 1996).

Oaks exhibit episodic growth and are capable of developing multiple shoot flushes during a single growing season (Fig. 1) (Johnson *et al.* 2002). After the acorn has germinated and developed a radicle, the first shoot develops and elongates in a process called ‘flushing’. The seedling then enters a lag stage, during which the first flush leaves mature and a new terminal bud develops.

If environmental conditions are favorable, the plant may flush again (Collet and Frochot 1996, Collet *et al.* 1997, Welander and Ottosson 2000). For phenotypic classification, Hanson *et al.* (1986) divided the process of flushing into: the ‘stem linear stage’ of stem elongation, the ‘leaf linear stage’ of leaf maturity and the ‘lag stage’ of bud development. Development of multiple flushes within one growing season may expose the seedling to variations in light availability, especially if it is growing in a dense plant community. At the seedling level, the production of multiple flushes can be considered an adaptive trait that increases phenotypic plasticity, thus providing potential for acclimation to heterogeneous light availability (Novoplansky 2002). Alternatively, flushing could provide capacity to cope with various forms of disturbance. For example, browsing alone rarely causes mortality of oak seedlings since the seedling can produce a new shoot following damage (Löf *et al.* 2010).

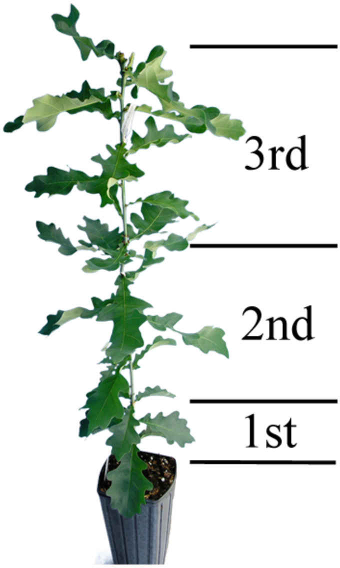

Figure 1. One-year-old *Q. robur* seedling with three subsequent flushes. The seedling is in the third lag stage.

Despite the fact that oaks contain fairly high levels of tannins with anti-herbivore effects (Feeny 1970, Schindler *et al.* 2003), they are more palatable to ungulate browsers than most conifers. However, oak palatability compared to other deciduous seedlings is less clear and appears to be site dependent (*e.g.* Gill 1992b, Kullberg and Bergström 2001). Oaks, therefore, may be regarded as browsing-tolerant species (Gill 1992b and references there in).

1.3 Neighboring Vegetation

Increasing light availability on the forest floor, for example as a result of overstory thinning, increases oak seedling growth (*e.g.* Lorimer *et al.* 1994, Collet *et al.* 2002, Abrams 2003, Götmark 2007, Harmer and Morgan 2007), but also the growth of herbaceous and other woody understory species, which may affect the growth of oak seedlings (Löf 2000, Brudvig and Asbjornsen 2007). Shrubs can directly and indirectly affect the growth

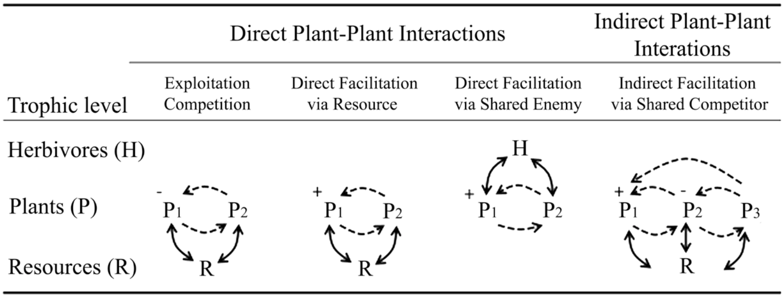

Figure 2. Conceptual model for direct and indirect plant–plant interactions across three trophic levels: herbivores (H), plants (P) and resources (R). Arrows indicate direct interactions (solid lines) and indirect interactions (dashed lines). Negative or positive responses are indicated - or +, respectively. The figure is modified from Connell 1990.

and survival of other plant species, either negatively (through competition) or positively (through facilitation) (Fig. 2). Direct plant–plant interactions occur when one plant species modifies resource availability or predation risk to such an extent that the change facilitates or reduces the growth of another plant species (Connell 1990, Brooker *et al*. 2008). Hence, direct facilitation and exploitative competition represent opposing trajectories (Fig. 2). In open and arid environments shrubs have been shown to facilitate the establishment of *Q. ilex* (Holm oak) and *Olea europaea* (Olive) seedlings directly by reducing photoinhibition and drought stress (Aerts *et al*. 2007, Cuesta e*t al*. 2010). In addition to increased light stratification, shrubs may also alter soil properties such as pH, temperature, moisture and erosion risk (Callaway 1995, Brooker *et al*. 2008, Heinrichs and Schmidt 2009). Such microhabitat alterations can indirectly facilitate establishment of tree seedlings by reducing or eliminating competitors, including herbaceous vegetation (Cuesta *et al*. 2010). Indirect facilitation between plants occurs when one of at least three species benefits from competition between the two other plant species (Fig. 2) (Levine 1999). For indirect facilitation to occur, the positive effect resulting from increased belowground resource availability because of lower water and nutrient uptake of the herbaceous vegetation has to compensate for the negative effect from the shrubs. The magnitude and duration of indirect facilitation may differ, depending on plant size and competition strategy, as well as external factors (*e.g.* herbivory, pathogens and environmental factors) (Rousset and Lepart 2000, Gómez-Aparicio *et al*. 2004, Treberg and Turkington 2010).

1.4 Objectives

The aim of my thesis was to determine whether interactions between oak seedlings and the neighboring vegetation, mainly shrubs, could be utilized when restoring temperate broadleaved forests of conservation interest. I hypothesized that the potential of shrubs as a regeneration tool would be because of their direct and indirect facilitation of oak seedlings. In addition, I wished to broaden our understanding of the acclimation of oak seedlings at different structural and functional levels (whole plant, flush and leaf) to vertically stratified light availability in dense plant communities.

I studied these objectives by means of field and growth chamber experiments (papers **I-V**), asking the following questions:

I Can naturally occurring shrubs reduce browsing damage to planted oak seedlings caused by large herbivores?

II Which microhabitat characteristics, other than light availability, favor natural regeneration of oaks?

III Can shrubs indirectly facilitate oak seedling biomass accumulation by suppressing competing herbaceous vegetation? If so, are there circumstances under which shrubs become competitors rather than facilitators for oak seedlings after establishment?

IV How does above- and belowground competition from shrubs affect photosynthesis, transpiration and biomass accumulation in oak seedlings?

V How do vertically stratified light environments, occurring when an oak seedling grows up through and then over-tops a shaded environment, affect morphological plasticity and photosynthetic acclimation at the levels of the whole seedling, flushes and individual leaves?

2 Methods

In the following section, I briefly summarize the methods used to quantify interactions between oaks and their neighboring vegetation. Detailed descriptions of materials and methods can be found in the individual papers.

2.1 Field Studies (Papers **I**, **II**, **III** and **IV**)

Fifteen temperate broadleaved forest stands (sites) were used in the study of ungulate browsing on oak seedlings in the presence of shrubs (paper **I**), and microhabitat factors affecting the presence or absence of naturally regenerated oaks (Fig. 3, paper **II**). These stands were former oak-rich pastures or small fields that were invaded by woody vegetation through secondary succession. Five years before study **I** was initiated and study **II** was conducted, 15-37% of the basal area of the overstory was cut (initial basal area was ca. 27 m^2 ha^{-1}). After thinning, the overstory consisted of a mixture of broadleaved species such as *Quercus*, *Betula*, *Populus tremula* and *Fraxinus excelsior* (paper **II**, Götmark *et al.* 2005b, Franc and Götmark 2008). At the start of the two studies, the woody understory typically consisted of a mixture of shrub species such as *Corylus avellana*, *Rubus idaeus*, *R. fruticosus* coll., *Frangula alnus* and *Lonicera xylosteum*, as well as seedlings of overstory trees, such as *F. excelsior*, *Sorbus aucuparia*, *B. pendula*, *Q. robur* and *Q. petraea*. These mixed woody understory species are grouped together and treated as a functional group denoted ‘shrubs’ in this thesis and in papers **I, III** and **IV**. In the study described in paper **II**, this woody understory was grouped together with herbaceous species and denoted ‘ground vegetation’. To study ungulate browsing frequency and intensity on oak seedlings growing among naturally occurring shrubs (paper **I**), bare-rooted oak seedlings were

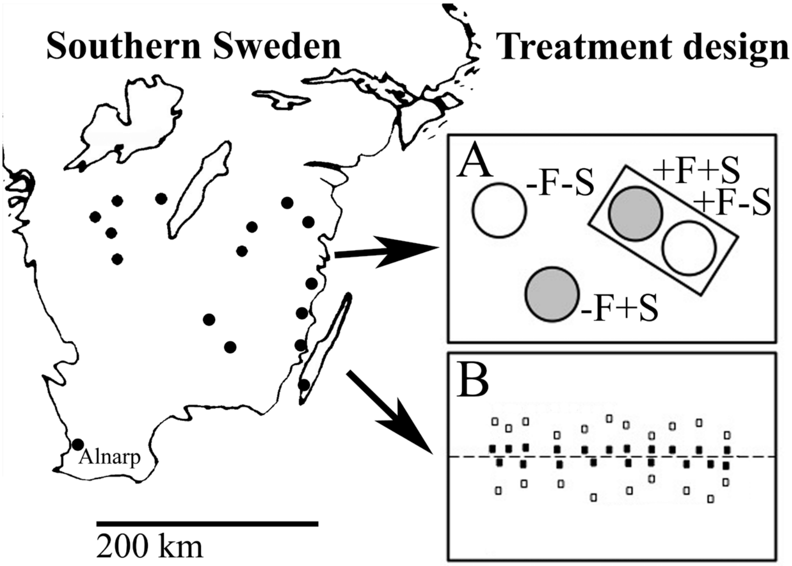

Figure 3. Fifteen forest sites (papers **I** and **II**) and the open field site in Alnarp (papers **III** and **IV**) studied during this research. Panel A illustrates a study site (1 ha) with the experimental design of four 30 m^2 treatment plots used to examine the effects of shrubs on ungulate browsing (paper **I**); two plots with shrubs (filled circles, +S), two without shrubs (open circles -S), and two of the treatment plots with fencing (+F). Panel B illustrates the design used to study microhabitat factors affecting presence–absence of naturally regenerated oaks after conservation-orientated thinning (paper **II**). Twenty oak-subplots (1 m^2) (filled squares) and 20 non-oak-subplots (1 m^2) (open squares) were located along a transect (dashed line). The two panels and the plots are not to scale.

planted in four plots replicated at ten of the fifteen sites. The four treatment combinations assigned to plots were: fenced with shrubs (+F+S), fenced without shrubs (+F-S), not fenced with shrubs (-F+S) and not fenced without shrubs (-F-S) (Fig. 3A). Oak seedling growth (height and stem diameter) and ungulate browsing (browsed or not browsed) were recorded twice a year during the period 2008-2010.

Factors influencing the presence or absence of naturally regenerated oak seedlings were studied at eleven of the fifteen sites (Fig. 3, paper **II**). At each site, we used a transect across the plot to select twenty 1 m^2 subplots, each with a naturally regenerated oak seedling in the center. Each oak subplot was matched to another 1 m^2 plot of similar canopy openness (31-32% visible sky) that did not contain an oak seedling (in total 40 subplots per site) (Fig. 3B). For each subplot we recorded a set of microhabitat variables (ground vegetation cover, soil moisture, inaccessibility to large

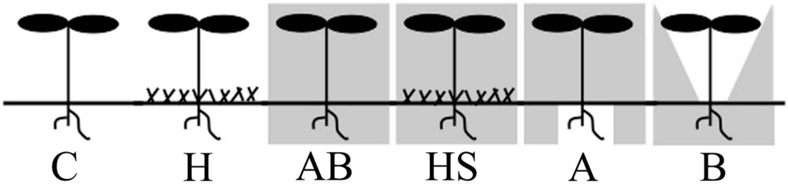

Figure 4. Treatments used to study competition and indirect facilitation by shrubs on oak seedlings, here shown with one flush (papers **III** and **IV**). The gray area indicates the general outline of the shrubs. The treatments were: no competition (C); above- and belowground competition from herbaceous vegetation (H); above- and belowground competition from shrubs (AB); above- and belowground competition from herbaceous vegetation and shrubs (HS); aboveground competition from shrubs (A) and belowground competition from shrubs (B).

herbivores *etc*.,) that have the potential to affect oak seedling survival and growth.

An experiment was established in an open field in Alnarp, Sweden to study oak seedling growth, biomass distribution, transpiration and photosynthesis in response to competition and indirect facilitation from herbaceous vegetation and shrubs (Fig. 3, papers **III** and **IV**). In December 2007, 600 two-year old, bare-rooted *Q. robur* seedlings were planted at a spacing of 1 × 1 m in six plots replicated four times in a randomized block design. Six competition treatments were randomly assigned to the plots (Fig. 4). The treatments were: control/ no competition (C), above- and belowground competition from herbaceous vegetation (H), above- and belowground competition from shrubs (AB), above- and belowground competition from herbaceous vegetation and shrubs (HS), aboveground competition from shrubs (A) and belowground competition from shrubs (B). In treatment plots assigned AB, HS, A and B a shrub community consisting of 35% *R. idaeus*, 25% *B. pendula*, 20% *C. avellana,* 10% *F. excelsior* and 10% *P. tremula* was established at a density of 12 stems m^{-2}. Shrub species composition and density were chosen to mimic the naturally occurring shrub community recorded in study **I**. A dense herbaceous community developed spontaneously during spring and summer 2008 in plots assigned to treatments H and HS. During the entire experiment, plots under treatments C, AB, A and B were manually weeded to remove herbaceous vegetation. To ensure that there was only aboveground competition between shrubs and oak seedlings in treatment A, the planting holes for the oak seedlings were lined with open-ended polyethylene bags that served as a barrier to root ingrowth. To ensure that there was only belowground competition between shrubs and oak seedlings in treatment B, the canopy of competing shrubs was kept away from the shoots of oak seedlings with metal wires. The experiment in Alnarp was fenced to exclude deer, hares and rabbits. Growth (height, stem diameter and biomass) (papers **III** and **IV**), transpiration (paper **IV**) and photosynthesis (paper **IV**) in oak seedlings were measured. In studies **III** and **IV** air temperature, precipitation, light levels, soil water content and soil temperature were measured in the treatment plots from 2008 to 2010.

2.2 Growth Chamber Study (Paper **V**)

Morphological and photosynthetic acclimation in oak seedlings (*Q. robur*) as they over-topped a low light environment was studied at the seedling-, flush- and leaf-level in a growth chamber experiment. The experiment was designed to mimic a situation where oak seedlings over-top a shrub canopy. Oak seedlings were raised under a range of artificial light environments (high light, partial high light and low light). Seedlings assigned to the high-light (HL) and low-light (LL) environments developed all three flushes under high and low light, respectively. In contrast, seedlings in the partial high-light (PHL) environment were exposed to a vertically heterogeneous light environment at the seedling level. These seedlings developed their first flush in the LL environment, and when they reached the second stem

Figure 5. Picture of first-flush leaves with the second-flush stems passing through the artificial canopy for oak seedlings assigned to the partial high-light environment. The artificial canopy consisted of neutral shade net and plastic foil that modified the red to far-red ratio (paper **V**).

elongation stage the shoot grew through an artificial canopy into a HL environment (Fig. 5). Thus, the second leaf linear stage, lag stage and the whole third flush occurred under HL (Hanson *et al*. 1986). Photosynthetic light- and CO_2 response were measured in mature leaves of three subsequent flushes during the third lag stage. Morphological and chemical variables (biomass, leaf area, -number, -thickness, pigments and nitrogen concentration) of seedlings, flushes and leaves were recorded after physiology measurements were completed.

3 Main Results and Discussion

3.1 Reduced Browsing in Shrubs (Paper **I**)

Tree seedlings can gain protection by growing in association with other plants and thereby experience reduced browsing, a phenomenon referred to as associational resistance (Gómez *et al*. 2001, Aerts *et al*. 2006, Barbosa *et al*. 2009). In study **I**, oak seedlings planted among naturally occurring shrubs gained such associational resistance from the shrubs. Ungulate browsing frequency was between 13 and 30 percentage points lower for oak seedlings grown amongst shrubs than for oak seedlings without this protection (Fig. 6A). Browsing intensity, quantified as loss in height growth per year, was also significantly lower for oak seedlings protected by shrubs (Fig. 6B). Similarly, Ripple and Beschta (2005) reported that *Salix* spp. thickets protected *P. tremuloides* seedlings from elk browsing.

Associational resistance to browsing may be affected by three distinct factors: concealment of the focal plant from the herbivores, deterrence and attracting the herbivore to enter the shrubs (Bakker *et al*. 2004, Barbosa *et al*. 2009). The lowered browsing frequency on oak seedlings among shrubs (paper **I**) suggests that shrubs may either deter browsers from entering plots, or conceal the seedling, preventing it from being detected by the browser. Our results suggest that concealment is the most likely explanation, since tall seedlings, especially if they over-topped the shrubs, experienced a higher risk of being damaged by ungulate browsers (paper **I**). Our finding that tall seedlings suffered a greater loss is in line with earlier reports (Kullberg and Bergström 2001) and may be the result of a higher risk of detection by the herbivores (Feeny 1976, Partl *et al*. 2002, Ripple and Beschta 2005).

Physical traits (*e.g.* thorns) or chemical unattractiveness of neighboring plants are known to reduce herbivory on tree seedlings (Hjältén *et al.* 1993, Harmer *et al.* 2010). Thorny shrub species (*e.g. Crataegus* spp. *Juniperus communis*, *Prunus spinosa* and *Rubus* spp.) in pastures and temperate forests have been shown to provide protection to a focal tree species (van Uytvanck *et al.* 2008, Harmer *et al.* 2010). We found, however, that the browsing frequency on oak seedlings was unaffected by the presence of *Rubus* spp., suggesting that, in our experiment, the two thorny shrub species *R. idaeus* and *R. fruticosus* coll. did not deter browsers from entering patches with shrubs. Instead, we found that a high frequency of *Rubus* decreased browsing intensity, suggesting that ungulate browsers may prefer *Rubus* over oaks (paper **I**). Support for this finding comes from the fact that many of the shrub species in temperate broadleaved forests and at the study sites evaluated in paper **I**, for example *R. fruticosus* coll. and *S. aucuparia*, are greatly preferred by ungulate browsers, (Gill 1992a, Boulanger *et al.* 2009). Ungulate browsers may therefore be attracted to patches containing these shrubs (Schreiner *et al.* 1996).

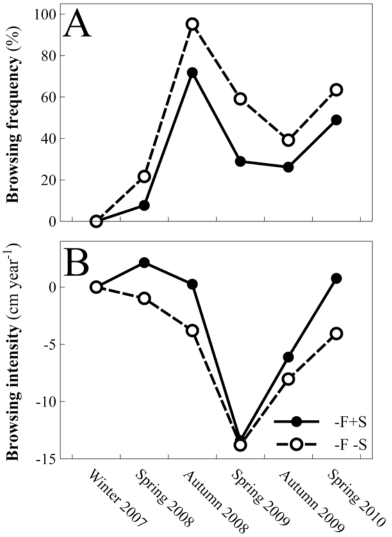

Figure 6. Browsing frequency (A) and intensity (B) by ungulates on oak seedlings grown without fences, in the presence (-F+S) and absence (-F-S) of shrubs. Browsing frequency is the proportion of damaged seedlings relative to all living unfenced seedlings, and browsing intensity is the loss of growth of the terminal leader in relation to seedlings protected by a fence. Values are treatment means (n = 10). The season labeled on the x-axis denotes the time of the measurements, and reflects damage experienced during the preceding period (paper **I**).

At least two browser driven mechanisms may explain the lower browsing intensity observed for oaks among shrubs: a numeric dilution effect, *i.e.* that browsing risk decreases if an individual oak is surrounded by many other plants; or an associational plant refuge effect, *i.e.* when oaks are growing in association with neighbors that are preferentially browsed by ungulates (Fig. 2) (Wahl and Hay 1995, Ripple and Beschta 2005). The latter explanation assumes that the herbivores detect the oak seedling, but select higher-quality plants in preference (*c.f.* Hjälten *et al.* 1993, Ball *et al.* 2000).

In conclusion, results presented in paper **I** show that shrubs, at least temporarily, can provide protection for oak seedlings against browsing ungulates, since both browsing frequency and intensity decreased on seedlings grown amongst naturally occurring shrubs. The spatial extent of this protection at the stand level is unknown, but is probably dependent on browser density and surrounding habitat quality for the browsers (*e.g.* Huntly 1991, Cassing *et al.* 2006). In addition, species composition of the shrub community and its height relative to the focal tree seedling needs more detailed study to understand better the protective potential of shrubs in temperate oak forests.

3.2 Microhabitat Factors Influencing the Presence of Naturally Regenerated Oak Seedlings (Paper **II**)

Overstory thinning for conservation purposes increases the light availability at the forest floor, stimulating natural regeneration of oaks and the growth of other ground vegetation (*e.g.* Ashton and Larsen 1996, Götmark *et al.* 2005a). In paper **II** we showed, by comparing paired subplots with similar light availabilities (canopy openness) across eleven sites (Fig. 3), that the height of naturally regenerated oak seedlings was positively correlated with the percentage cover of ground vegetation, but this variable did not affect whether oak seedlings were present or not (Table 1, paper **II**). The observation that seedling height was positively correlated with the percentage cover of herbaceous vegetation was similar to findings presented by Götmark (2007). Ground vegetation height, however, had a negative effect on the presence of naturally regenerated oak seedlings, but seedlings that did establish tended to be tall. Subplots where no oak seedlings were found had 22-34% taller neighboring ground vegetation than subplots containing oaks (paper **II**), suggesting that competition from tall ground vegetation adversely affects the establishment of oaks, but when they do establish oak seedlings exhibit increased stem elongation (Lorimer *et al.* 1994, Kelly 2002, Franklin 2008). Our results indicated that ground vegetation type had no or little effect on the presence of oak (paper **II**). Generally, the most frequent ground vegetation species (*F. excelsior*, *Convallaria majalis*, *R. idaeus* and *Oxalis acetosella*) were common both in oak and non-oak subplots.

*Table 1. Some of the microhabitat variables measured during the study of presence or absence of naturally regenerated oak seedlings. Values are means with one SD in brackets for all subplots (n = 11). See paper **II** for variable descriptions.*

Variables	Oak-subplot	Non-oak-subplot	P^*
Canopy openness (% sky)	32.3 (7.5)	31.2 (8.8)	0.07
Stone/rock (% cover)	2.2 (2.3)	2.1 (2.5)	0.95
Bryophytes (% cover)	3.5 (2.2)	4.8 (2.7)	0.04
Vascular plants (% cover)	61.3 (14.9)	57.6 (16.0)	0.18
Woody stems (no.)	0.2 (0.3)	0.5 (0.6)	0.03
Litter depth (cm)	0.8 (0.4)	0.9 (0.5)	0.19
Min. soil depth (cm)	7.6 (4.9)	7.7 (5.7)	0.82
Max. soil depth (cm)	20.9 (2.8)	21.3 (2.7)	0.34
Max. vegetation height (cm)	64.2 (14.0)	64.6 (15.7)	0.85
Mean vegetation height (cm)	15.7 (7.4)	19.1 (10.8)	0.04
Proportion of inaccessible subplots (%)	13.2 (9.8)	27.3 (17.5)	0.01
Distance to oak seed source, stem (m)	6.2 (4.9)	6.8 (4.7)	0.08
Distance to oak seed source, canopy (m)	2.6 (4.2)	3.2 (4.0)	0.04

*Results from two tailed paired t-test using SPSS.

High soil moisture increased the probability of an oak seedling occurring in a subplot (paper **II**). As acorn germination is sensitive to drought (Gosling 2002), microhabitats with high soil moisture may favor acorn germination and promote seedling survival and growth (Collet and Frochot 1996, Brudvig and Asbjornsen 2009).

Physical protection (*e.g.* small trees, shrubs, thorny *Rubus* spp. and deadwood) reduced the probability of oak seedlings being present in a subplot (Table 1). However, oak seedlings in these subplots were 37% taller than those in unprotected microhabitats (mean 27.6 cm, SE 3.2, paper **II**). The observation that seedlings in these microhabitats were tall may be a result of both shade-induced stem elongation and reduced browsing from ungulates, as found in paper **I**.

In summary, low soil moisture and tall competing vegetation disfavored presence of naturally regenerated oak seedlings. Although light availability (canopy openness) in paired subplots was kept similar in this experiment, small temporal and spatial variations in light quantity and quality at the microhabitat level may have influenced oak seedling growth.

3.3 Competition and Indirect Facilitation (Papers **III** and **IV**)

3.3.1 Oak Seedling Response to Herbaceous Vegetation

Interference from herbaceous vegetation reduced total oak seedling biomass, stem diameter and height (Fig. 7A, B and C). These results are in line with several other studies (Kolb *et al.* 1990, Collet and Frochot 1996, Löf 2000). Compared to the total biomass of seedlings assigned to treatment C, seedlings assigned to treatment H had 37, 63 and 79% less biomass at the end of the 2008, 2009 and 2010 growing seasons, respectively. Furthermore, oak seedlings responded morphologically during the first two years of establishment (2008 and 2009) by accumulating a smaller proportion of biomass to their foliage (33 and 50% compared to seedlings in treatment C) (Fig. 7D). Together with reduced stem diameter and height growth, this indicates that biomass was distributed towards the development of the root system rather than production of stems and leaves (Fig. 7B and C). Assuming that oak seedlings responded morphologically to exploitative competition (Goomes and Grubb 2000), our results may indicate that they are strongly affected by belowground competition from

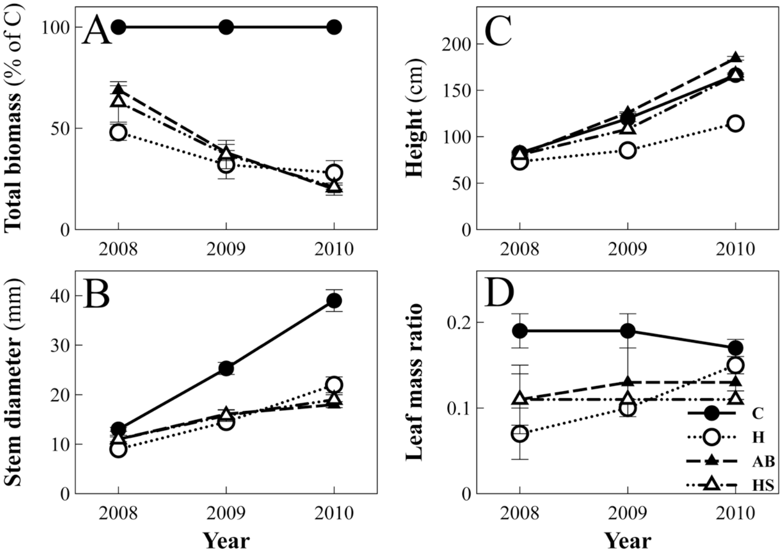

Figure 7. Growth response in oak seedlings in four treatments during three years in an open field experiment in Alnarp, Sweden (paper **III**). Total seedling biomass (A), stem diameter at ground level (B), seedling height (C) and leaf mass ratio (D). Values are means with one SE ($n = 4$). For description of the treatments see figure 4 and the text.

herbaceous vegetation during the first years of establishment (paper **III**). A reduction in the amount of biomass of herbaceous vegetation and thereby in its competitive strength may enhance the establishment success of oak under open conditions; this has been demonstrated in other studies (Löf *et al.* 1998, Davis *et al.* 1999, Bolte and Löf 2010).

3.3.2 Oak Seedling Response to Shrubs

Interference from shrubs significantly reduced total oak seedling biomass and stem diameter (Fig. 7A and B, paper **III**). However, compared to seedlings grown in the absence of competing vegetation, the seedling height was similar or even greater when there was competition from shrubs (Fig. 7C). While the seedlings assigned to treatment H distributed more biomass to the leaf component over time, seedlings in treatments AB and HS exhibited a fairly constant leaf mass ratio (Fig. 7D, paper **III**). Together these findings suggest that oak seedlings responded to competition from shrubs by favoring carbon allocation to stem elongation rather than to leaves or stem diameter growth. These morphological responses were likely driven by the shade created by the shrub canopy (Ammer 2003, Franklin 2008).

According to Grime's C-S-R[1] theory, competition intensity will increase with increased resource abundance, and therefore also with the biomass of the neighboring vegetation (Grime 1977). Davis *et al.* (1998) suggested that the biomass of neighboring vegetation had little influence on competition intensity, but that it was mainly driven by resource availability to the focal plant. In study **III**, we found that competition intensity increased with increasing amounts of neighboring biomass. Increased amounts of neighboring vegetation negatively affected light availability and soil water content (paper **III**).

Responses of oak seedlings, with respect to morphology, transpiration and photosynthesis, were greatest under treatment AB where the combined resource availability for oaks was lowest (paper **IV**). Oak seedlings exposed to both above- and belowground competition from shrubs had a 43% lower cumulative transpiration rate than seedlings not surrounded by shrubs. This impaired physiological response in oak seedlings exposed to competition was accompanied by a 60-74% lower leaf area, 29-36% smaller stem diameter, and a 38-78% lower total biomass compared to seedlings in treatment C (paper **IV**). In combination, these findings corroborate earlier reports on several oak species, showing that reduced

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[1] Competition (C), stress (S) and ruderal (R).

light availability reduces biomass accumulation and affects biomass distribution (Ziegenhagen and Kausch 1995, Gardiner and Hodges 1998, Welander and Ottosson 1998, Gardiner *et al.* 2009). Shade imposed by shrubs was also associated with a reduction in area-based maximum CO_2 assimilation rate (paper **IV**); a typical response to shade that has been reported for many tree species (*e.g.* Naidu and DeLucia 1998, Oguchi *et al.* 2006). Despite the presence of shrubs, oak seedlings were able to develop a subsequent second flush, over-topping the shrub canopy with leaves acclimated to utilize the increased light levels (paper **IV**). Together, results from papers **III** and **IV** suggest that shrubs act as competitors both above- and belowground. Although, grown under open conditions competition for light appeared to have the greatest effect on photosynthesis, transpiration and biomass accumulation. However, *Q. robur* seedlings had the capacity to acclimate vertically to this competition as long as seedlings overtopped the shrub canopy and the competition was moderate.

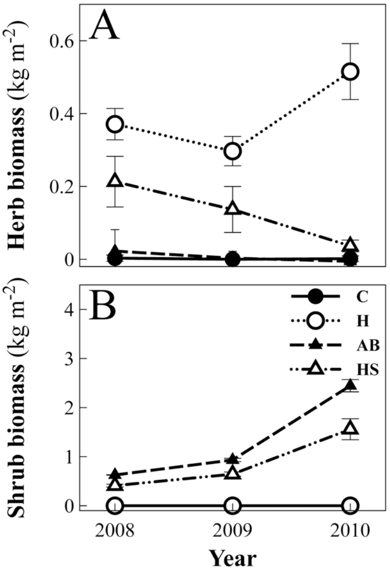

Figure 8. Aboveground biomass of herbaceous (A) and shrub (B) neighboring vegetation at the end of growing seasons 2008, 2009 and 2010 and in four treatments in an open field in Alnarp, Sweden (paper **III**). Values are means with one SE (n = 4). For a description of the treatments see figure 4 and the text.

3.3.3 Shrubs Indirectly Facilitate Oak Seedling Growth

For shrubs to indirectly facilitate oak seedling growth, the interaction between shrubs and herbaceous vegetation must be negative, thus creating enhanced belowground resource availability for the oaks. Moreover, the net effect of this enhanced resource availability has to compensate for the negative effect (shade) of the shrub canopy (Fig. 2) (Callaway and Walker 1997, Levine 1999). In study **III**, competition between shrubs and herbaceous vegetation was found to reduce aboveground biomass in both groups. This competition reduced and almost eliminated the herbaceous community, probably limiting the competitive capacity of the herbaceous vegetation (Fig. 8). Competitive effects of shrubs on herbaceous vegetation have been reported as being positive, negative or neutral (Pihlgren and

Lennartsson 2008, Cuesta *et al.* 2010, Koorem and Moora 2010). However, shade from the overstory or shrub canopy is generally the main factor responsible for reducing competition between herbaceous vegetation and tree seedlings (Li and Wilson 1998, Pagés *et al.* 2003). Similarly, shade imposed by the shrub canopy was probably responsible for the reduced herbaceous biomass observed in study **III** (Fig. 8).

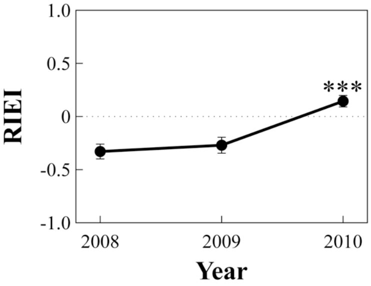

Figure 9. The relative indirect effect intensity (RIEI) imposed by shrubs on oak seedling biomass in an open field in Alnarp, Sweden during three growing seasons (paper **III**). Values are means with one SE for 68-100 seedlings. Asterisks indicate significant differences between years at α = 0.001 (***) detected by chi-square test in SAS.

During the first two years of the study (2008 and 2009), total biomass was higher in oak seedlings grown with both shrubs and herbaceous vegetation, compared to the treatments from which shrubs were absent (paper **III**). By 2010 however, seedling biomass was lower under treatment HS than treatment H (Fig. 7A). These results reflect the temporal dynamics of plant–plant interactions and suggest that shrubs may indirectly facilitate oak seedling biomass accumulation during the first years after planting and that this indirect facilitation is mediated by a suppression of the herbaceous community (Fig. 7A and 8).

By calculating the relative indirect effect of shrubs (RIEI) on oak seedling biomass (Pagés *et al.* 2003), we showed that shrub presence functioned as a facilitator during the first two growing seasons (RIEI < 0), then as a competitor (RIEI > 0) (Fig. 9). However, as the herbaceous community was strongly reduced by shrubs during the third year (2010), assumptions for indirect facilitation to occur were no longer valid (Levine 1999). With time, however, herbaceous competition may again increase as more shade-tolerant herbaceous species become established (Brunet 2007, Koorem and Moora 2010).

The underlying mechanism of indirect facilitation during the first two years was probably reduced competition for belowground resources between herbaceous vegetation and oak seedlings, since seedlings under treatment H seemed to distribute biomass to their roots instead of leaves (Fig. 7). Results presented in paper **III** indicated that shrubs indirectly facilitated oak seedling growth. Since this study was conducted in an open field with a herbaceous community consisting mainly of various grass species known to strongly reduce growth in *Q. robur* seedlings (Löf 2000), field trials are needed to test whether shrubs indirectly facilitate oak seedling growth in temperate forest systems.

3.4 Acclimation to a Stratified Light Environment (Papers **IV** and **V**)

Light quantity and quality near the forest floor is highly stratified, and present a particularly complex situation for oak seedlings growing among shrubs (Pearcy and Valladares 1998). In order to cope with heterogeneous light conditions, oak seedlings may adjust their physiology (mainly photosynthesis and respiration) and morphology, *i.e.* seedlings may show phenotypic plasticity. The different physiological and morphological changes can be detected at different structural/spatial levels in seedlings; at the whole-seedling level, within a flush and in individual leaves. In order to function in a changing environment, such adjustments can be expected to exhibit clear temporal dynamics and be activated or released at different phenological or ontogenic stages (Novoplansky 2002, Niinemets *et al.* 2004, Walters 2005, Oguchi *et al.* 2003, Rodríguez-Calcerrada *et al.* 2008).

Our findings indicate that oak seedlings showed great phenotypic capacity to acclimate to vertically stratified light availability (papers **IV** and **V**). Results from paper **V** suggest that seedling level acclimation is mainly driven by plasticity in traits at the flush level. In contrast, plasticity in traits determining flush morphology, such as leaf number and area, were largely controlled during bud formation rather than during shoot development. These findings suggest that leaf number and area are morphological traits that are probably predetermined in the primordium (Girault *et al.* 2008), whereas leaf mass appears to be more plastic within certain limits (Fig. 10, paper **V**). Consequently, the prevailing light environment during the lag stage and early bud formation may determine the limits for flush level acclimation when shoots elongate from a shaded environment into a high light environment. This is consistent with findings presented by Welander and Ottosson (1998), who showed that first flush leaf number in *Q. robur* seedlings was determined by the light environment the previous growing season. Predicting the flush level restriction of oaks grown amongst shrubs is complicated because light environment during bud development varies as a result of foliar movements (paper **IV**). Although, results presented in paper **V** indicate that prevailing light environment during bud formation affects leaf number and area, the underlying developmental processes, stimuli (light quality and quantity) and their interactions are unknown.

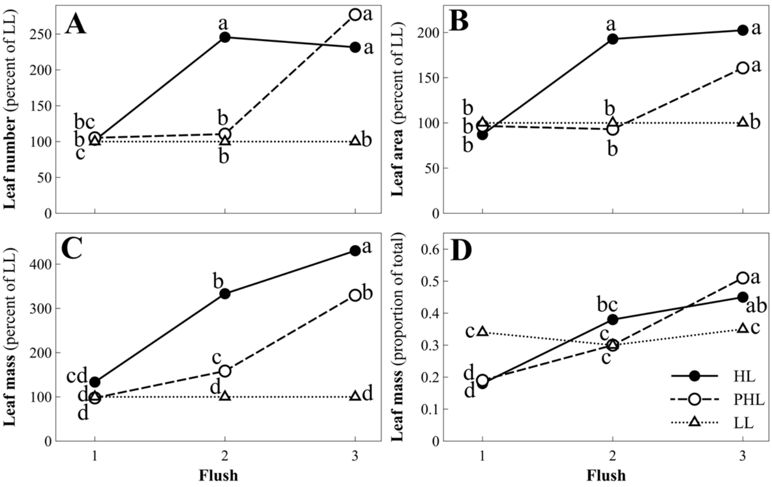

Figure 10. Flush level response to high-light (HL), partial high-light (PHL) and low-light (LL) environments in oak seedlings with three subsequent flushes (paper **V**). Leaf number (A), leaf area (B) and leaf mass (C) as a percentage of mean values for LL seedlings and proportion of total leaf mass by flush (D). Different letters indicate a significant difference between means ($\alpha = 0.05$) using a mixed model in SAS.

In contrast, traits influencing leaf level acclimation, such as leaf thickness, specific leaf area, and pigment concentrations, appeared to be driven primarily by the prevailing light environment during leaf development. The plastic response of leaf traits to light availability during leaf development enabled rapid acclimation of photosynthetic capacity to the prevailing light environment (papers **IV** and **V**). Rapid acclimation with respect to photosynthesis and respiration of mature leaves transferred from low-light to high-light environments has been reported in several tree species (Naidu and DeLucia 1997, Rosati *et al.* 1999, Fownes and Harrington 2004, Rodríguez-Calcerrada *et al.* 2008). Studies **IV** and **V** demonstrated that this is also the case in subsequent flush leaves, and that development of first flush leaves in a low-light environment did not appear to restrict photosynthetic acclimation in second and third flush leaves that developed under high-light conditions.

3.5 Management Implications

Results from my studies suggest that naturally occurring shrubs may be one regeneration tool that can be used in the restoration of oak forests of conservation interest, especially where browsing restricts oak seedling development, and permanent exclusion of ungulate browsers is either too costly or invasive. Shrubs reduced the frequency of browsing on oak seedlings by 13-30 percentage points, however as much as 70% of all oak seedlings associated with shrubs were damaged to some extent by ungulate browsers (paper **I**). In addition, we observed that tall seedlings over-topping shrubs ran a higher risk of being damaged by ungulate browsers. Therefore, before using shrubs as a regeneration tool, their protective effectiveness needs to be further tested in long term experiments, lasting until the oaks have grown tall enough to exceed the reach of ungulate browsers (>150-200 cm, Bergquist *et al.* 2009).

Utilizing vegetative structures, such as shrubs and ground vegetation, to improve the seedling microenvironment is complex, as it involves abiotic factors, biotic factors and their interactions (Byers *et al.* 2006, Brook *et al.* 2008). For example, herbivory will reduce biomass, and may decrease growth, fecundity and survival of both the focal plant and also its nearest neighbors (Begon *et al.* 1996, Ishii and Crawley 2011). Hence, herbivory will probably influence exploitative competition between the focal tree seedling and neighboring plants. The dual effect of shrubs on oak seedling growth, *i.e.* as a competitor and also as an indirect facilitator, suggests that regeneration of oaks using shrubs as a management tool requires careful monitoring of oak seedling survival and growth. Results presented in papers **III** and **IV** show that the light environment experienced by a seedling strongly affects its growth and establishment. Although, oak seedlings exhibited great developmental plasticity in stratified light environments, aboveground competition from shrubs (**IV** and **V**) may result in a net negative outcome for the oak seedling and removing shrubs may therefore be necessary.

To summarize, my results suggest that the potential of shrubs as a management tool for decreasing ungulate browsing should be considered as being complementary to other protective methods. It is possible that shrubs could be utilized as a sole method of ungulate browsing control in small-scale forestry for conservation purposes, in particular during the early phase of seedling establishment (first and second year) and where ungulate densities are low. However, fencing should still be regarded as the most effective method for protecting regeneration. More research on the competitive strength and strategies of shrubby species in isolation and also in mixtures is needed to understand better the magnitude and temporal patterns of the facilitating and competitive plant–plant interactions in different temperate forest environments.

Figure 11. A typical oak-rich forest with a well-developed shrub community.

4 Conclusion

The results presented in this thesis emphasize the temporal and spatial complexity of the mechanisms and outcomes of plant–plant interactions. Below I highlight the main findings from the five papers, addressing the five questions posed in the introduction.

I. Naturally occurring shrubs provided protection by association for oak seedlings by reducing ungulate browsing frequency and intensity. The associational resistance provided to the oak seedlings appeared to be driven by concealment and herbivore-mediated facilitation.

II. After a conservation-oriented thinning, microhabitat factors that favored the occurrence of natural regeneration of oak seedlings were high soil moisture and short ground vegetation; competition was probably the negative driving factor.

III. Shrubs indirectly facilitated biomass accumulation in oak seedlings by reducing herbaceous competitors. This effect appeared, however, to be transient for the oak seedling, since association with shrubs reduced their growth especially after three growing seasons.

IV. Competition from shrubs affected oak seedling photosynthesis, transpiration and biomass accumulation. This negative response was proportional to the level of resource availability. Integrated over one growing season, aboveground competition from shrubs affected oak seedling growth more than belowground competition.

V. Periodic flushing enabled oak seedlings to acclimate to vertically stratified light availability. The acclimation occurred at the seedling-, flush-, and leaf levels.

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Glossary

Associational plant refuge

Protection gained by a plant species susceptible to herbivores by association with other plant species or functional groups that are more or less susceptible to the same herbivore.

Associational resistance

Synonym for associational plant refuge.

Browser

Ungulate herbivore that selectively feeds on trees and shrubs (deer are also included in this group, although they also feed on herbaceous vegetation).

Competition

Plant–plant interaction that depresses growth in at least one of the participants.

Direct facilitation

Facilitation in which any positive effects on a plant are brought about by increased resource availability or reduced consumption risk caused by another plant.

Episodic tree species

Tree species that can develop several cohorts of leaves during a single growing season.

Exploitative competition

Competition in which any negative effects on a plant are brought about by reduced resource availability caused by other, competing plants.

Facilitation

Plant–plant interaction that improves survival or growth in at least one of the participants.

Flushing

Shoot development, in oaks divided into three stages: stem linear, leaf linear and lag stage.

Ground vegetation

Woody understory and herbaceous vegetation, pooled together as a functional group (used in paper **II**).

Herbaceous vegetation

Grasses and forbs, pooled together as a functional group.

Herbivory

Consumption of living plant material.

Indirect facilitation

Competition between two plants (or functional groups) that results in improved survival or growth in a third species.

Microhabitat

One square meter plot surrounding a naturally regenerated oak seedling (used in paper **II**).

Numeric dilution effect

A reduced consumption risk for an individual plant because it is surrounded by a high density of other plants.

Phenotypical plasticity

Variability in morphological and physiological responses of plants to environmental conditions or stimuli.

Primordium

An organ (leaf) in its earliest stages of differentiation.

Radicle

Initial immature root that develops from an embryo.

Restoration

The process of restoring degraded forest structure or function. In this thesis restoration is used in the context of rehabilitation of semi-open oak forests that have become encroached as a result of secondary succession, in order to conserve the former species composition.

RIEI

The Relative Indirect Effect Intensity imposed by competing plants (or functional groups) on a focal plant.

Shrubs

Various woody understory species, pooled together as a functional group.

Ungulates

Mammal browsers, in this thesis moose (*Alces alces*) and deer (*Capreolus capreolus, Cervus elaphus* and *Dama dama*).

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Plant–plant interactions have been indicated as a potential means to facilitate oak seedling establishment and reduce herbivory when restoring oak forests. In this thesis I investigate mechanisms and outcomes of competitive and facilitative interactions between oak *(Quercus robur* and *Q. petraea)* seedlings and neighboring plants, primarily shrubs. The protective capacity of naturally occurring shrubs against ungulate browsers was investigated. Further, seedling-, flush- and leaf-level developmental plasticity to vertical stratified light availability was studied.

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