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Sous la direction de Sonia SAÏD et Catherine COLLET

**Interactions entre chêne et cervidés durant le
processus de renouvellement - cas des
peuplements forestiers tempérés de plaine
(*Quercus petraea* et *Q. robur*)**

Soutenu le 7 Septembre 2021

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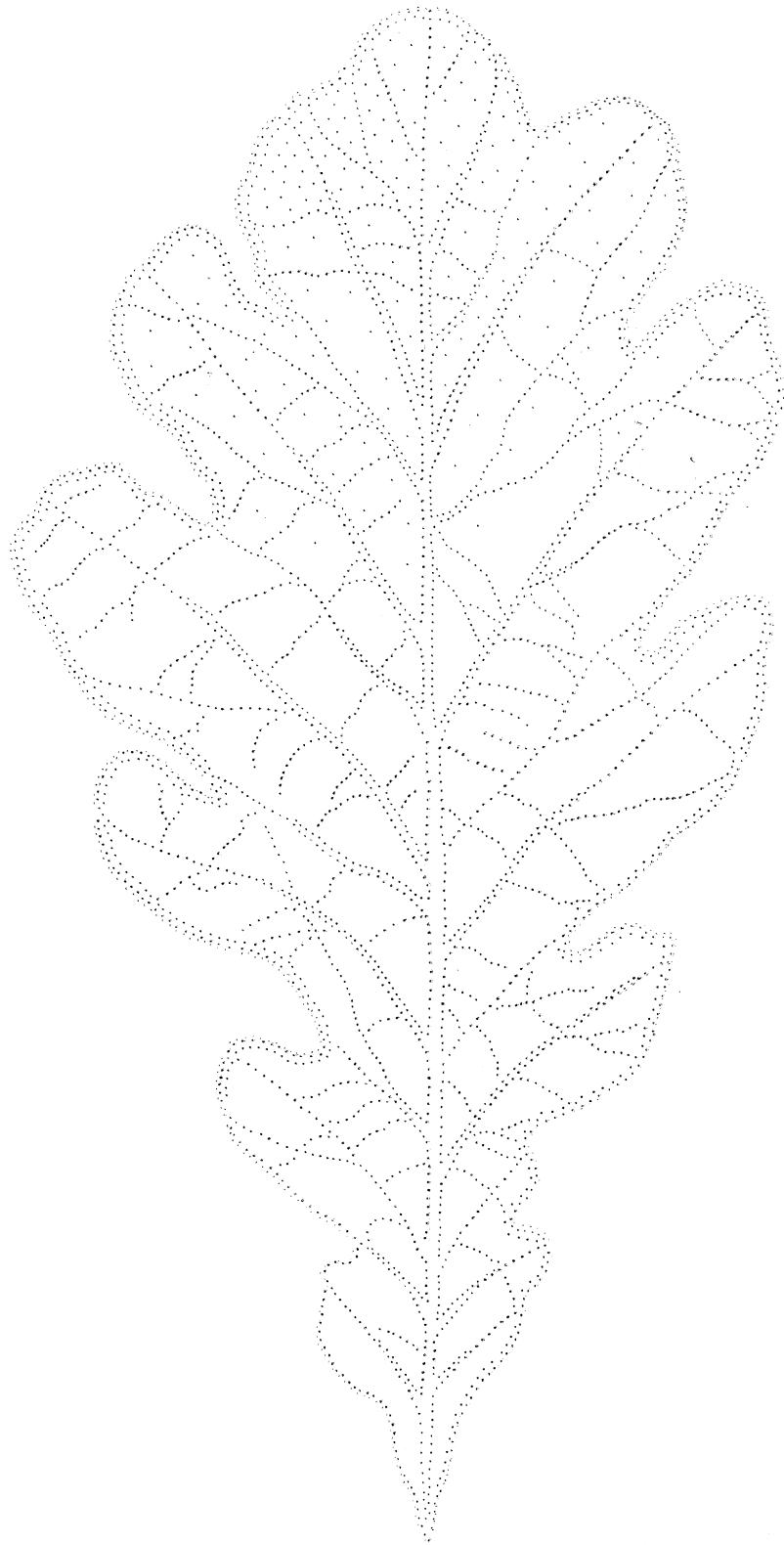
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Interactions between oak and cervids during the process of forest regeneration – the case study of plain temperate oak stands (*Quercus robur* and *Q. Petraea*).

PhD Thesis - Julien BARRERE - September 2021





From the book "The Art of the Leaf" by [illegible]

A Boker

*Il y a une patience dans le vie sauvage - obstinée,
inlassable, pendant d'interminables heures, l'araignée
dans sa toile, le serpent dans ses anneaux, la panthère
en embuscade ; cette patience est tout
particulièrement celle de la vie quand elle chasse la
nourriture qui la fait vivre.*

Jack London, L'appel de la forêt

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(English part in italics)

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Preamble

This PhD was co-funded by the French Office for Biodiversity (OFB), the National Forest Office (ONF) and by the National Research Institute for Agriculture, Food and Environment (INRAE), via a research convention between these three institutions (CNV-REC-2018-07). This work was also supported by OFB-CIRAD convention [convention CNV-REC-2019-09]. I conducted this work in two laboratories: the INRAE center of Champenoux (SILVA research unit) and in the OFB-DRAS center of Birieux. During the second year of my PhD, I was also hosted during three months in a Swedish laboratory (Southern Swedish Forest Research Center, SLU, Alnarp). This mobility was funded by the Dream mobility grant of Lorraine University. To make this manuscript accessible to the Swedish partners, and more generally to the English-speaking scientific community, it was written in English. **A summary in French of 10 pages is included at the end of the manuscript.**

INRAE



Scientific publications associated with the thesis

Barrere, J., Boulanger, V., Collet, C., Walker, E., Siat, V., Henry, L., Saïd, S., 2020. How does oak mast seeding affect the feeding behavior of sympatric red and roe deer? *Basic and Applied Ecology* 47, 1–20.

Barrere, J., Collet, C., Saïd, S., Bastianelli, D., Verheyden, H., Courtines, H., Bonnet, A., Segrestin, J., Boulanger, V., 2021. Do trait responses to simulated browsing in *Quercus robur* saplings affect their attractiveness to *Capreolus capreolus* the following year? *Environmental and Experimental Botany*. 194, 104743.

Barrere, J., Petersson, L.K., Boulanger, V., Collet, C., Felton, A.M., Löf, M., Saïd, S., 2021. Canopy openness and exclusion of wild ungulates act synergistically to improve oak natural regeneration. *Forest Ecology and Management* 487, 118976.

Barrere, J., Courbaud, B., Ligot, G., Collet, C., Boulanger, V., Saïd, S., Marell, A., Nilsson, U., De Coligny, F., Balandier, P. 2022. The influence of deer browsing on oak regeneration is conditioned by the shrub layer - insights from a modeling approach. (in prep.)

Collaboration in relation to the thesis topic

Löf, M., **Barrere, J.**, Engman, M., Petersson, L.K., Villalobos, A., 2021. The influence of fencing on seedling establishment during reforestation of oak stands : a comparison of artificial and natural regeneration techniques including costs. *European Journal of Forest Research* 1-11.

Science popularization article

Barrere, J., Boulanger, V., Collet, C., Beroud, T., Bonnal, L., Saïd, S. 2021. La simulation d'abrouissement: un outil pour mieux comprendre l'influence des cervidés sur la régénération forestière. *Biodiversité, des clés pour agir*. (in press)

Oral communications

Because of the covid-19 pandemic that started in the middle of this thesis, I did not have the opportunity to participate to any national or international symposium. Therefore, oral communications associated with this thesis are restricted to internal meetings

Annual meeting of the Wild Ungulates Unit (OFB). 12 November 2018, Arc-en-Barrois (France). *Influence des ongulés sauvages sur le renouvellement des peuplements de feuillus de plaine.*

Scientific council of the Pierre Vérots Foundation. 29 November 2018, Monthieux (France). *Impact de l'abrouissement par le chevreuil sur la croissance et l'appétence de semis de chêne pédonculé.*

Weekly seminar of the silviculture group. 13 March 2020, Alnarp (Sweden). *Influence of wild ungulates on the regeneration of plain hardwood forests.*

Scientific council of the National Action Plan for Wolf. 9 October 2020, online. *Influence des ongulés sauvages sur les forêts françaises.*

Annual seminar of the SIRENa doctoral school. 26 March 2021, online. *Réponse du chêne à l'herbivorie par le chevreuil en terme de croissance et de traits fonctionnels.*

Internship supervision

Agathe Le Goff (2nd year master - University of Nancy). 2019 (full supervision). *Influence des trois grands ongulés de plaine sur la dynamique de régénération forestière.*

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CHAPTER

1

INTRODUCTION

1.1 The anthropic origin of an imbalance between forest trees and wildlife

1.1.1 Global change as a disruptor of trophic interactions

The recent development of human activities has now been recognized as the main cause of most contemporary environmental changes (Lewis & Maslin, 2015). These global changes notably include the conversion of terrestrial ecosystems into cropland and pasture, nutrient eutrophication, changes in the atmospheric composition, increasing air temperatures accompanied by changes in precipitation regimes and by greater inter- and intra-annual fluctuations in temperature and rainfall (IPCC, 2014). By affecting plant, animal and fungal species differently, global changes have the potential to modify interactions between species at a global scale with significant consequences for ecosystem functioning (Emmerson *et al.*, 2004; Putten *et al.*, 2004).

Trophic interactions among plants and animals, defined here as feeding relationships between species, are a crucial driver of ecosystem functioning (Holt & Loreau, 2013). Numerous studies show that significant changes in the relative abundance or performance of interacting species can have cascading effects at the ecosystem level (Putten *et al.*, 2004). A well-known illustration of this phenomenon is the overexploitation of sea otters in the early twentieth century: these species controlled the structure of kelp forests by consuming sea urchins (Reisewitz *et al.*, 2006). In the absence of this predator, sea urchins proliferated and drastically altered the structure and diversity of the kelp forests (Hale & Koprowski, 2018).

Plant-herbivore interactions also provide an enlightening example of how global changes influence ecosystem functioning via trophic interactions at a larger spatial scale. Plant-herbivore interactions structure ecosystem functioning by linking primary productivity and food webs. This trophic interaction has been widely studied and is the foundation of major ecological theories such as co-evolution (Ehrlich & Raven, 1964). Recent meta-analyses have shown that changes in climatic conditions, more specifically elevated temperatures, droughts and increased atmospheric CO₂ concentrations have benefited leaf-feeding insects populations, and increased herbivory rates (Hamann *et al.*, 2021; Massad & Dyer, 2010), especially by generalist species (Filazzola *et al.*, 2020). Thus, human-induced changes in climatic conditions could indirectly decrease the net productivity of forest and grassland ecosystems by enhancing insect herbivory. Additionally, northern hemisphere forests are facing a globalized increase in large-herbivore populations, which is compromising these forests economic and ecological value (Beguin *et al.*, 2016). This phenomenon is the result of a combination of a wide range of anthropogenic factors, beyond the sole effect of climate.

1.1.2 Large herbivore population dynamics as a component of global change

Over the last few decades, significant increases in the abundance and spatial distribution of large-herbivore populations have been reported in North America (Côté *et al.*, 2004; Nuttle *et al.*, 2014), Europe (Clutton-Brock *et al.*, 2004; Linnell & Zachos, 2011) and Japan (Takatsuki, 2009). In all cases, the phenomenon was related to several anthropogenic factors whose relative importance varies depending on the geographic area. To illustrate the drivers of this population trend, the section below more specifically focuses on the well-documented case of Europe.

In Europe, the transition of human societies from hunting-gathering to an agricultural lifestyle initiated a long decline in cervid populations (Linnell & Zachos, 2011). Deer were intensively hunted for food and the expansion of agricultural areas reduced and fragmented their habitats while competition with livestock decreased resource availability. As a result, cervid populations in Europe reached their lowest levels between the end of the 19th century and the beginning of the 20th century. Throughout the 20th century, populations gradually recovered due to a combination of several factors (Valente *et al.*, 2020). First, the abandonment of traditional agricultural practices and changes in land use lead to an expansion of deer habitats (notably forests) and reduced the competition with livestock. Second, the importance of cervid populations for human society, especially for hunting, encouraged management policies to restore these populations – *i.e.* hunting restrictions, reintroductions, supplementary feeding, *etc.* The combination of these two phenomenon was likely the main driver of the increase in cervid populations observed throughout the 20th century. Other secondary factors are also frequently mentioned in the literature, but their contribution to the trend remains highly debated, contrary to changes in land use and wildlife management policies. Cervid populations are assumed to have benefited from less top-down control during the 20th century due to a decline in natural predators such as the grey wolf (*Canis lupus*) and the Eurasian Lynx (*Lynx lynx*) (Ripple *et al.*, 2014) and to the fact that hunters in Europe are aging and becoming less numerous (Massei *et al.*, 2015). Climate-induced changes, such as milder winter and forest expansion, may have also contributed to promoting cervid populations (Weiskopf *et al.*, 2019), but their effect is more uncertain since climate change also has negative effects on cervid populations (Gaillard *et al.*, 2013).

Global changes have led to a drastic, globalized population increase at the European level of nearly all the cervid species present on the continent (Beguin *et al.*, 2016). Due to the difficulty of accurately estimating the density of cervid populations (Pfeffer *et al.*, 2018), the trend is not precisely quantifiable. However, trends of several metrics that positively correlate with cervid densities such as harvest rate (Kahlert *et al.*, 2015) or the number of

deer-vehicle collisions ([Anderson et al., 2021](#); [Saint-Andrieux et al., 2020](#)) suggest a considerable increase in populations. For instance, in France over the last 40 years, the number of red and roe deer harvested annually increased by a factor of eight and nine, respectively (Fig. 1.1).

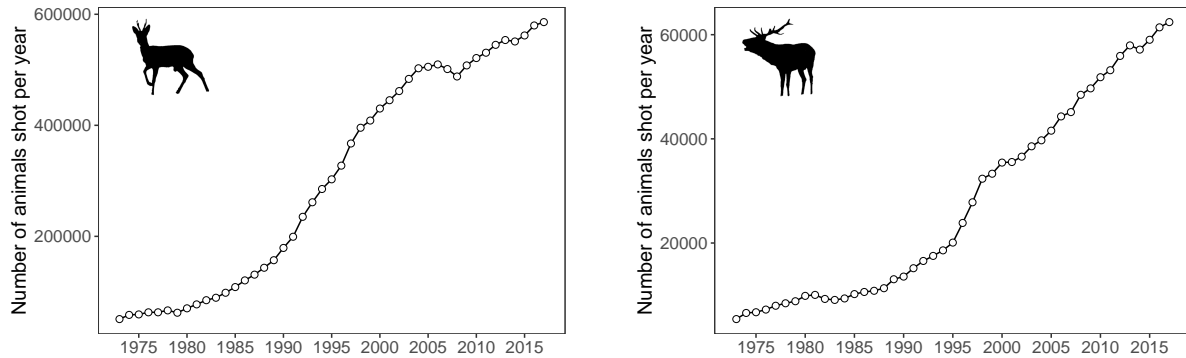


Figure 1.1: Annual number of roe deer (left) and red deer (right) harvested in France from 1973 to 2017 (Réseau Ongulés Sauvages OFB/FNC/FDC).

This population increase has numerous consequences for forest ecosystems, among which increased trophic interactions between deer and forest vegetation, which constrain forest regeneration. Furthermore, in addition to the increase in abundance and spatial distribution of large-herbivore populations, forest ecosystems are simultaneously facing other disturbances brought about by global change, most notably climatic variations, which compromise forest functioning and the ecosystem services they provide.

1.1.3 How global changes influence forest ecosystems

Forests cover a third of the world's terrestrial area ([FAO, 2020](#)), and are estimated to host around 80% of the world's terrestrial biodiversity. Through the multitude of ecosystem services they provide, forests are vital not only to humans but also to the functioning of other ecosystems. The study by [Brockerhoff et al. \(2017\)](#) grouped forests' ecosystem services into three broad categories: regulation, provisioning, and culture. Forests regulate ecosystem functioning by storing atmospheric carbon – *i.e.* around 45% of all terrestrial carbon is stored in forests ([Gamfeldt et al., 2013](#)) -, by providing habitats for various species and a physical protection against natural events - *e.g.* storms, avalanches, erosion, floods, and by contributing to soil formation and composition. Forests provide our societies with wood, and with non-wood products (*e.g.* fruits, game meat, mushrooms and honey). Finally, forests are part of our cultural life through the multiple interactions they offer us with the plants and animals inhabiting them, be they experiential (*e.g.* hiking, wildlife observation), physical

(hunting, fishing) or even spiritual (e.g. sacred trees).

In a world free of human influence, forest structure, dynamics and functioning are controlled by (i) climate, (ii) topographic and soil conditions, and (iii) natural disturbances, both biotic (e.g. herbivory, pathogens) and abiotic (e.g. wildfires, wind-storms) (Ehbrecht *et al.*, 2021). The recent explosion of human activity has drastically affected forest ecosystems by both directly and indirectly influencing these three biotic and abiotic controls. Despite forest communities' remarkable resilience and ability to adapt to variations in climatic conditions, the current changes are occurring at a rate and a magnitude that may exceed their adaptation or migration capacity (Aitken *et al.*, 2008). Certain forest communities may benefit from these changes in the short-term through increased nitrogen deposition and extended growing seasons, leading to greater primary productivity (Zhu *et al.*, 2016). However, although tree mortality is still mostly driven by tree and stand characteristics, current observations show that the combination of increased temperatures and decreased rainfall is already a significant factor of mortality, and that its impact is likely to gain importance in the years to come (Allen *et al.*, 2010; Taccoen *et al.*, 2019). A warmer and drier climate has also been shown to promote pathogen abundance (Seidl *et al.*, 2017) while simultaneously increasing tree sensitivity to pathogens (Ayres & Lombardero, 2000). This process, along with the previously mentioned climate-induced promotion of leaf-eating insects and the rise in large herbivore populations in the northern hemisphere, indicates that global changes overall strengthen the effect of biotic disturbances on forests.

The influence of climatic variations on abiotic disturbances is less straightforward. Warmer and drier conditions are known to increase the magnitude and frequency of wildfires and droughts (Abatzoglou & Williams, 2016; Seidl *et al.*, 2017), but there is currently no consensus on the magnitude or direction of climate-induced variations for storms frequency, which is likely to differ depending on the geographic area (Mölter *et al.*, 2016). Global changes also alter forest soil conditions: reduced groundwater supply in forest soils is leading to drought-induced tree mortality (Allen *et al.*, 2010; Greenwood *et al.*, 2017), while the rise in sea level is increasing flooding and soil salinity in many coastal forests (Williams *et al.*, 1999).

Lastly, anthropogenic deforestation (*i.e.* human-induced conversion of forests to other land uses) is causing the loss of millions of hectares of forest every year, especially in tropical areas in Africa and South America. Deforestation is recognized as one of the most threatening components of global change for these forests. Nevertheless, some trends are encouraging: the net change in forest area, defined as the sum of all forest losses (deforestation) and all forest gains (forest expansion) in a given period, has slowed over the last several decades: -7.8 million ha in 1990-2000, versus -4.7 million ha in 2000-2010 (FAO, 2020). This is the consequence of a reduction in deforestation in South America, combined with significant

natural and artificial forest expansion in Europe and Asia (FAO, 2020). In European forests, as only three quarters of the net annual increment is harvested per year, the volume of living wood has increased by 50% over the last thirty years, along with the quantity of carbon sequestered (ForestEurope, 2020). Tree species diversity in forest stands has been increasing since 2005, while forest bird populations have remained stable for the last 40 years (Gregory *et al.*, 2019; Ram *et al.*, 2017). Interestingly, Europe is also the continent with the highest proportion by far of forests under management plans (*i.e.* 96%, versus 24% in Africa, and only 1% in South America) (FAO, 2020); this suggests that appropriate forest management could be the key to the sustainable coexistence of forests and human activities.

In 1992, during the Helsinki Ministerial Conference on the Protection of Forests in Europe, sustainable forest management was defined as “*the stewardship and use of forests and forest lands in a way, and at a rate, than maintains their biodiversity, productivity, regeneration capacity, vitality and their potential to fulfil, now and in the future, relevant ecological, economic and social functions at local, national and global levels, and that does not cause damage to other ecosystems*”. This almost 30-year-old definition raises numerous challenges that are more relevant than ever in the current context. These challenges are ecological (*i.e.* adaptation to climate change and changing disturbance regimes) (Aitken *et al.*, 2008), economical (*i.e.* maintaining the profitability of silvicultural activities) (Clasen *et al.*, 2011) and social (*e.g.* the promotion of close-to-nature forestry) (Bauhus *et al.*, 2013). In northern-hemisphere temperate forests, the constraint exerted by large herbivore populations on forest regeneration is growing, and is already regarded as a significant threat for the sustainable management of these ecosystems (Beguin *et al.*, 2016). In this context, managing the compatibility between on the one hand the presence of a rich and diversified wildlife on the one hand and the sustainability and profitability of silvicultural activities on the other hand represents a crucial challenge from an economic, social and ecological point of view.

1.2 Managing the balance between forests and large herbivores

1.2.1 Social and economic dimensions

Large herbivores are associated with two provisioning services provided by forest ecosystems that generate high economic outcomes: wood production and hunting. In Europe alone, wood production represented 21 billion € in 2015, while income generated by hunting licenses was estimated at around 500 million € (ForestEurope, 2020). The importance of these two activities is not only economical but also social. Around 2.6 million people were employed in the forest sector (forestry, wood manufacturing and the paper industry)

at the European level in 2015 (ForestEurope, 2020). In comparison, a study by Massei *et al.* (2015) showed that, in a subset of 16 European countries, the number of hunters, though declining, was still over 7 million in 2011, which represents 1.38% of the countries total population. Studies investigating the relationships among forest ecosystem services have shown that wood production and hunting tend to be negatively correlated (Brockerhoff *et al.*, 2017; Gamfeldt *et al.*, 2013). On the one hand, forests with low cervid densities have a higher timber productivity, but are less attractive from the hunter's perspective due to the difficulty of harvesting animals. On the other hand, in forests with high cervid densities, hunting licenses generate important incomes for landowners, but cervid herbivory pressure exerted on the vegetation can cause considerable economic losses for the forest sector. These economic losses stem from delays in forest regeneration, changes in species assemblages which are unfavorable to the stand's economic value, compensatory plantations and the cost of protecting juvenile trees from browsing (*e.g.* with fences, individual protections or repellents) (Boulanger & Rakotoarison, 2013).

In addition to these economic aspects, there are important social considerations to take into account. Hunting is the primary lever of action used to regulate deer populations. However, in many countries, hunts are not only a management tool but also a central social event for millions of people (von Essen *et al.*, 2019). Consequently, many hunters wish to keep cervid populations at a sufficiently high level to maintain the attractiveness of the activity. A growing proportion of the public opinion – spurred notably by environmentalists from both urban and rural areas – is also in favor of abundant cervid populations, regardless of silvicultural considerations, and tends to disapprove of regulating these populations through hunting (Byrd *et al.*, 2017; Peterson, 2004).

The balance between silvicultural activities and cervid populations therefore perfectly illustrates the concept of ecosystem multifunctionality (Hector & Bagchi, 2007). Forests are associated with a wide range of ecosystem services, and a compromise among these ecosystem services must be found, rather than seeking to optimize any single one (such as timber production or hunting). Consequently, restoring the balance cannot simply be achieved by drastically reducing cervid populations: forests and cervid populations must be co-managed by implementing measures that will satisfy all the different actors (*i.e.* foresters, hunters, environmentalists, scientists).

1.2.2 Levers of action in forest and wildlife management

When cervid populations impede the regeneration of tree species at a magnitude that compromises the objectives set by foresters, wildlife and forest managers mainly use two types

of approach to restore a balance: management policies targeting the animals directly (hereafter referred to as an "animal-focused" approach) or an alternative that aims to protect the vegetation from herbivores (hereafter, a "vegetation-focused" approach).

Lethal control through hunting has always been the primary and most efficient wildlife-focused strategy for regulating deer populations (Brown *et al.*, 2000). Hunters may limit population growth by increasing the number of animals shot, and by targeting females in priority. Conversely, hunters can lighten the constraint exerted on population growth by targeting antlered individuals to protect females or by limiting the number of animals shot. However, due to the declining number of hunters (Massei *et al.*, 2015), and the declining social acceptance of this practice, experiments to limit population size with alternative methods have been carried out, especially in Northern America (Warren, 2011). Translocating cervids is a relatively efficient way to reduce local populations but it comes with several drawbacks: important costs, the difficulty of finding appropriate release sites, and higher mortality at the release sites. Fertility control using vaccines has proved to efficiently decrease deer populations (Boulanger *et al.*, 2012; Rutberg & Naugle, 2008), but the labor required to apply the vaccines compromises their applicability at large scales (Warren, 2011).

An intuitive and extensively used vegetation-focused approach is to exclude cervids from the forest stands that need protection by erecting fences around the area (Mårell *et al.*, 2012; VerCauteren *et al.*, 2006). Though a few negative effects for forest regeneration have been reported inside fences – *e.g.* shrub proliferation (Ward *et al.*, 2018), or increased seed predation by rodents due to the absence of trampling (Muñoz & Bonal, 2007) –, a recent meta-analysis showed the efficiency of this method in promoting the height growth, abundance and diversity of saplings inside fences (Bernes *et al.*, 2018). One of the main drawbacks is the financial cost, which can often be prohibitive for forest managers (Löf *et al.*, 2021). Fencing can also have additional repercussions at larger spatial scales, by increasing landscape fragmentation, and heterogeneity in large herbivore spatial distribution, resulting in increased browsing pressure in unfenced areas (Baltzinger *et al.*, 2018). Other means of protection that target specific individual trees exist as well. Mechanic individual protection can be used (plastic or metal grids that surround the tree) to prevent browsing and fraying on specific trees in the stand and to "divert" the browsing pressure towards other, less valuable saplings. Similarly, chemical or natural repellents applied to individual trees are increasingly being used to deter browsing (Kimball *et al.*, 2009; Stutz *et al.*, 2019). However, studies investigating the efficiency of these repellents have shown highly contrasted results (Elmeros *et al.*, 2011; Lindmark *et al.*, 2020).

The influence of large herbivores on the regeneration of a given tree species is not only conditioned by herbivore density, it also depends on the tree species' palatability (Bernes *et al.*,

2018; Borowski *et al.*, 2021) and tolerance to browsing, or on the abundance of alternative forages (Jarnemo *et al.*, 2014; Spitzer *et al.*, 2021). As such, manipulating these factors can constitute an alternative approach to limiting the negative influence of deer browsing on forest regeneration. The attractant-decoy hypothesis predicts that woody plants gain protection from being surrounded by more palatable neighbors, since the herbivory pressure is diverted toward the neighbors (Bee *et al.*, 2009; Hjältén *et al.*, 1993). Planting less palatable species could thus limit the impact of high deer densities on regeneration. The genus *Picea* provides an interesting example supporting this theory. Indeed, deer are known to frequently avoid these species, and in this case, deer presence can actually benefit spruce regeneration by removing more palatable competitive species and leave the spruce relatively untouched (Bernard *et al.*, 2017; Vriendt *et al.*, 2020; Potvin *et al.*, 2003). More generally, the abundance of alternative forage negatively correlates with browsing damage on planted saplings (Jarnemo *et al.*, 2014). Maintaining palatable alternative forages of poor silvicultural interest could therefore divert the browsing pressure toward these species with positive outcomes for forest regeneration; however, studies testing this approach under field conditions are still lacking. Some components of the understory, more particularly shrubs, have also been shown to protect the seedlings and saplings growing beneath them from browsing (Jensen *et al.*, 2012; Walters *et al.*, 2020). Maintaining a protective shrub layer could therefore also reduce the impact of deer browsing but, here again, empirical support for this approach is lacking.

In this context, the present thesis aims to clarify some of the direct and indirect interactions between cervids and forest regeneration by focusing on tree - pedunculate and sessile oak (*Quercus robur* and *Q. petraea*) - and cervid - red and roe deer (*Cervus elaphus* and *Capreolus capreolus*) - species emblematic of European forests.

1.3 Presentation of the studied species and their specificity

1.3.1 Red and roe deer

Red deer and roe deer are both members of the *Cervidae* family, characterized by the antlers grown each year by the males of all species (apart from water deer *Hydropotes inermis*). Due to their large influence on forest vegetation structure and diversity (Boulanger *et al.*, 2018), and to the potential cascading effects of this influence for other animal communities (Martin *et al.*, 2011), cervids are often considered keystone species (Rooney, 2001). In addition to their ecological importance, cervids have played a crucial role for human societies since prehistory, first as a resource (*e.g.* meat for food, skins for clothing or antlers and bones for

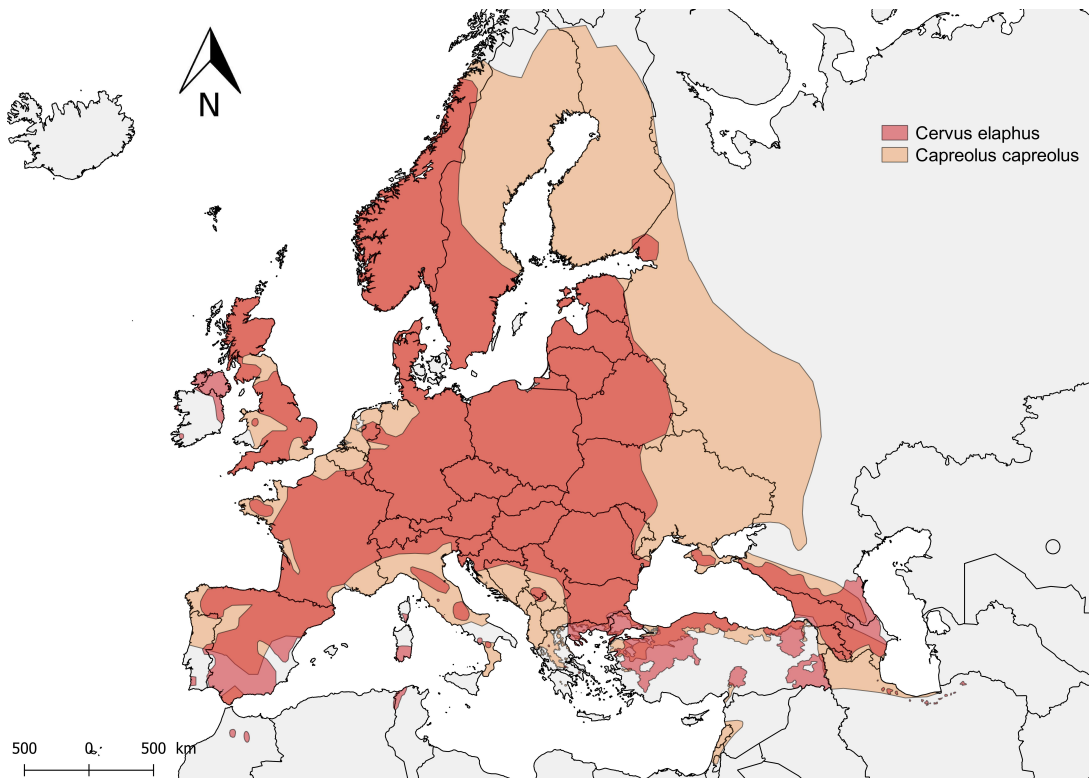


Figure 1.2: Distribution range of red and roe deer based on IUCN data.

tools) but also from a spiritual and cultural point of view (e.g. symbol in many religions and myths, representation in art and literature, hunting as a recreational activity). Red and roe deer are two of the most common cervid species in Europe, along with fallow deer (*Dama dama*) and, in Scandinavia, reindeer (*Rangifer tarandus*) and moose (*Alces alces*). Their distribution range covers the vast majority of European forests (Fig. 1.2) thanks notably to the segregation of their feeding niche (Storms *et al.*, 2008). Like all cervids, red and roe deer are ruminants: the complex organization of their digestive system enables them to pre-digest their food after ingestion (Ruckebusch & Thivend, 1980), which means that they can digest large quantities of plant material. Depending on the resources available in their habitats, and on the other herbivores that coexist with them, wild ruminants like cervids have become specialized in different types of food sources. Based on 26 African species, Hofmann & Stewart (1972) identified three categories of ruminants, differing both in the morphology of their stomach structure and in their feeding behavior.

- “Grazers” (grass/roughage eaters in Fig. 1.3) are able to digest plants particularly rich in fibers, and therefore include large amounts of herbaceous species in their diet – e.g. domestic ruminants.
- “Browsers” (concentrate selectors in Fig. 1.3) are highly selective thanks notably to their developed sense of smell, and only consume digestible items of high quality

(forest fruits, stems, buds) – e.g. moose.

- “Intermediate feeders” (intermediate types in Fig. 1.3) have a broad dietary niche; they are relatively selective and avoid fibers when possible, but are capable of consuming fiber-rich items when it is the only resource available – e.g. reindeer.

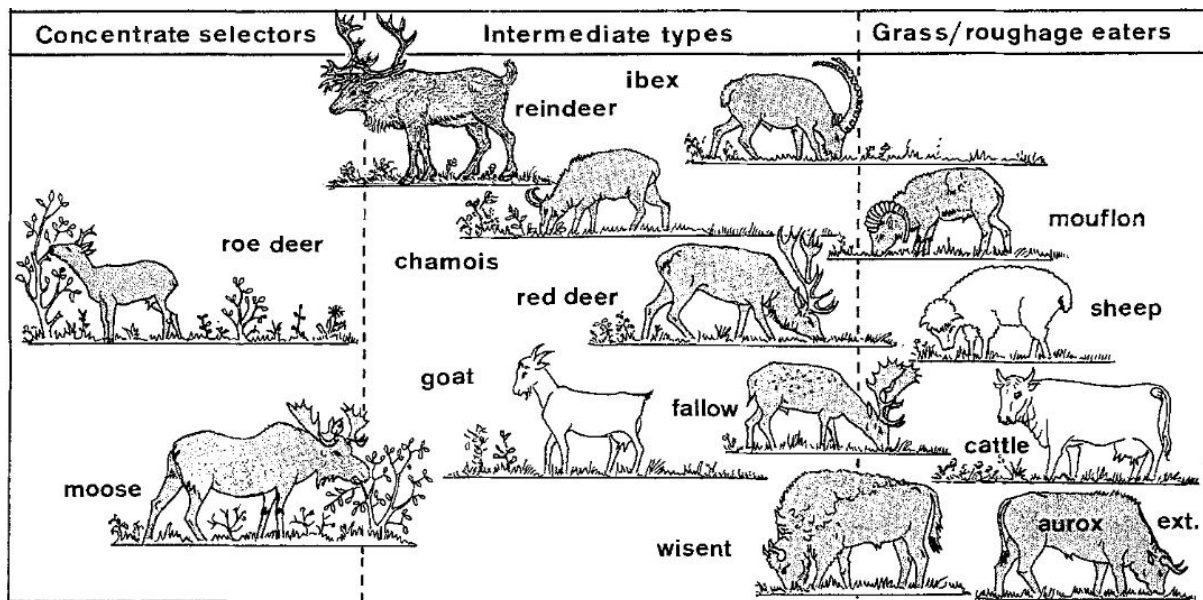


Figure 1.3: Hofmann’s classification of European domestic (white) and wild (shaded) ruminants (Hofmann & Stewart, 1972; Hofmann, 1989)

The roe deer is a typical browser: it is highly selective in its diet (Tixier & Duncan, 1996) – i.e. some highly available species with a high fiber content are never consumed while some highly digestible rare species are systematically consumed (de Jong *et al.*, 1995; Tixier *et al.*, 1997a). Forest fruits, and the leaves and shoots of saplings and shrubs generally dominate the roe deer diet, while roots or flowers are occasionally consumed but in much lower proportions (Tixier *et al.*, 1997a). The red deer, on the other hand, is a typical intermediate feeder, in that it is perfectly adapted to fluctuations in resource availability throughout the different seasons (Storms *et al.*, 2008). In winter, when resources are scarce, the red deer diet is similar to that of grazers and includes a large proportion of monocotyledonous herbaceous species (Renaud *et al.*, 2003). In spring and summer, the proportion of herbaceous species decreases in favor of more digestible species (e.g. the young leaves of deciduous saplings).

1.3.2 Pedunculate and sessile oak

The pedunculate and sessile oaks are two of the most economically and ecologically important tree species in Europe, and provide a vast array of ecosystem services (Löff *et al.*, 2016).

From an ecological point of view, oaks provide crucial habitat and food resources for a vast number of birds (Felton *et al.*, 2016a), invertebrates (Jonsell *et al.*, 1998), fungi and lichens (Ranius *et al.*, 2008), and oak-dominated forests have been shown to support a high amount of biodiversity (Mölder *et al.*, 2019b). A recent study showed that in the UK only, over 2300 species are associated with oaks, among which 326 were obligate associates (Mitchell *et al.*, 2019). Oaks are also associated with a vast array of cultural ecosystem services – *i.e.* non material benefits people obtain from ecosystems (Löf *et al.*, 2016). For instance, these trees were considered sacred in many European countries – *e.g.* Germany, Croatia and Britain – as reflected by their presence on the coins of these countries (Fig. 1.4). Lastly, oaks represent a crucial economic resource. Historically, oak timber was extensively used to build ships and acorns were a crucial food resource for livestock. Nowadays, the high quality timber produced in large volumes by oak is still highly valued for manufacturing, furniture making and construction.



Figure 1.4: European coins representing oak leaves: (a) British pound, (b) German Deutsche Mark and (c) Croatian Lipa.

From a biological point of view, oaks are long-lived species, reaching heights of around 30m and diameters of 1m at maturity (Eaton *et al.*, 2016). They grow best in fertile, moist soils, and have very demanding light requirements. Pedunculate and sessile oak overlap in the vast majority of their range, and frequently hybridize. The two species are morphologically very similar (Bacilieri *et al.*, 1995), but differ in their ecological requirements. Pedunculate oak has greater resource requirements (*i.e.* light, water, nutrients) and can withstand periodic flooding while sessile oak is more drought-tolerant (Friedrichs *et al.*, 2008). Both species have a broad ecological niche, as reflected by their large distribution range at the European scale: from the Iberian peninsula to Turkey southward, and from northern Scotland to Scandinavia and Russia northward (Fig. 1.5). This large distribution range results from a particularly dynamic expansion following the latest glaciation in Europe (*i.e.* around 13000 BP) (Brewer *et al.*, 2002; Petit *et al.*, 2002). During this glaciation, the two species were geographically restrained in glacial micro-refugia located in the Iberian peninsula, in Italy and in the Balkans (Brewer *et al.*, 2002). Post-glaciation, both oaks expanded at a speed

above expectations (Petit *et al.*, 1997), to reach their current distribution around 6000 years ago (Petit *et al.*, 2002).

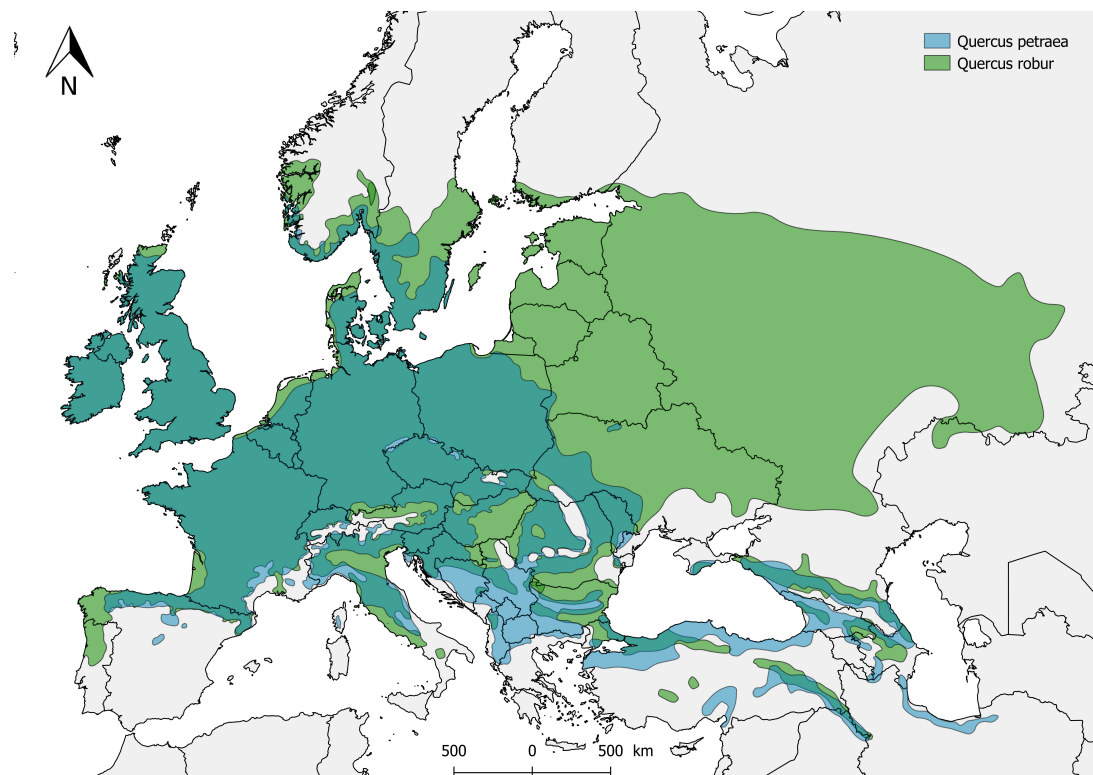


Figure 1.5: Native spatial range of sessile and pedunculate oak based on EUFORGEN data (Caudullo *et al.*, 2017)

Since the beginning of the 20th century, oak regeneration failure have been documented throughout the continent (Bobiec *et al.*, 2018; Watt, 1919). Despite the positive expansion dynamics of oaks since the last glaciation, their current regeneration speed is often insufficient to meet the objectives set by foresters for timber production. This likely results both from a particularly high demand for oak timber in our current society and from changes in the factors constraining oak regeneration (Bobiec *et al.*, 2018; Mölder *et al.*, 2019b). Consequently, significant research efforts are being made to identify the factors constraining oak regeneration (Annighöfer *et al.*, 2015; Kohler *et al.*, 2020; Petersson, 2019). Red and roe deer interact with the process of regeneration by consuming oak seeds and saplings and, as such, they represent a significant constraint for oak regeneration (Kohler *et al.*, 2020). Fossil records indicate that both red and roe deer appeared in Europe in the mid-Pleistocene (Sommer *et al.*, 2008, 2009), at a time when oaks were already widespread throughout the continent (Barron *et al.*, 2017). Thus, these two cervid species have coexisted with oak throughout their entire existence in Europe, and cervid and oak distribution ranges still largely overlap nowadays (Fig. 1.2 and 1.5). This coexistence in time and in space raises the question of how much red and roe deer contribute to the patterns of oak regeneration failure observed since the last century, relatively to other factors constraining this process.

1.4 On the drivers and constraints of oak regeneration

1.4.1 Patterns of oak regeneration failure: placing deer in a complex system

Forest regeneration is defined as the re-establishment of a forest stand by natural or artificial means following the removal of the previous stand by felling or as a result of natural causes (TBFRA, 2000). Observations of oak failing to regenerate under its own canopy, or in canopy gaps, have been reported since the beginning of the 20th century (Watt, 1919), and up to very recently (Bobic et al., 2018; Petersson et al., 2019; Woziwoda et al., 2019). Interestingly, the first observations of regeneration failure seem to coincide with the acceleration of global changes during the 20th century. Recently, two controversial hypotheses have attempted to explain this phenomenon: the ‘wood-pasture hypothesis’ (Bobic et al., 2018), and the ‘pathogen-mildew hypothesis’ (Demeter et al., 2021). The ‘wood-pasture hypothesis’ suggests that the oak regeneration niche has always been misinterpreted: oak is a pioneer species that colonizes abandoned pasture or heavily disturbed forests but does not regenerate under its own canopy (Bobic et al., 2018). This is supported by evidence of successful oak regeneration on former agricultural lands (Bobic et al., 2011; Minotta & Degioanni, 2011) and by historical records showing that oak thrived when previous land use maintained forests sufficiently open. Before the wood-pasture hypothesis, Vera (2000) established an analogous theory: the natural vegetation in Europe before human intervention consisted of a mosaic of grasslands, shrubs, solitary trees and groups of trees. This landscape, analogous to woodland pastures, was maintained open by dense populations of grazers and browsers (Fig. 1.6.b) and it is the suppression (or reduction) of these large herbivores that caused the formation of closed forests (Fig. 1.6.a), thus preventing light-demanding species such as oak from regenerating (Vera, 2000; Vera et al., 2006). Alternatively, the “pathogen mildew hypothesis” starts from the premise that the introduction of the invasive pathogen *Erysiphe alphitoides* into Europe at the beginning of the 20th century coincides with the first observations of oak regeneration failure (Demeter et al., 2021). This theory assumes that oak was perfectly able to grow and survive under its own canopy before the 20th century, but then, the newly introduced pathogen became specialized in oak, causing the oak to become more light-demanding and less competitive, and thereby impeding its ability to regenerate below its own canopy (Demeter et al., 2021).

Though these two hypotheses provide interesting arguments, most scientists currently support an alternative theory: oak is in theory perfectly able to regenerate under its own canopy, but global change has increased the importance of several constraints with a synergetic, negative effect on oak regeneration (Annighöfer et al., 2015). For instance, Petersson et al. (2019) evidenced changes in land use leading to denser and darker forests, and an increase in large herbivore populations as the main factors explaining oak regeneration failure pat-



Figure 1.6: Two contrasted landscapes taken from Vera (2000) to illustrate his theory. (a) a 300-year-old stand in the New Forest (UK): selective felling of oak for the shipbuilding industry allowed beech to become dominant in the canopy. Shrubs and saplings are absent from the understory due to insufficient light availability (photo: H. Koop). (b) A young oak tree growing in the middle of hawthorn (*Crataegus sp*) shrubs in a heavily grazed landscape in the Borkener Paradise (Germany). Herbivores (cattle, horses) maintained the landscape sufficiently open for the oak to regenerate and the shrubs protected the oak from browsing (photo: F.W.M. Vera).

terns in Scandinavia. A recent review identified five main factors driving oak regeneration in Europe: light availability, competitive vegetation, browsing by cervids, initial seedlings density and tending effort (Kohler *et al.*, 2020). The respective influence of these different factors and of their interactions varies depending on the stage of the oak regeneration process (Annighöfer *et al.*, 2015). A global overview of the oak regeneration process and of the constraints exerted at each step would contribute to a better appreciation of the relative role played by deer among these different constraints.

1.4.2 The process of forest regeneration and the specificities of oak

The process of natural regeneration is commonly divided into five distinct steps: seed production, seed dispersal, germination, seedling establishment and sapling growth (until the tree joins the overstorey) (Dey *et al.*, 2019). For each tree species, a range of environmental conditions enables each step to occur. The concept of “regeneration niche”, introduced by Grubb (1977), specifies that for the regeneration of a given tree species to occur successfully, these environmental conditions must be met in sequence throughout the regeneration process. Under this framework, each step of the regeneration process represents a filter that

removes individuals from the population. Forest trees adopt a typical *r* reproductive strategy by investing in a high number of offspring with a low survival probability (MacArthur & Wilson, 1967). At the beginning of the regeneration process, the number of individuals (fruits) is extremely high, but the probability for these individuals to pass each step is low due to multiple constraints, most of which are highly stochastic (e.g. climate, disturbance), making the probability of a successful regeneration particularly unpredictable. To improve the chances of a successful regeneration, it is therefore crucial to identify the main factors constraining each step, and to determine the appropriate forest management operations to limit these constraints (Dey *et al.*, 2019).

1.4.2.1 Seed production

A wide range of biological constraints, of varying importance depending on the species, may hinder seed production in temperate forest trees: inadequate floral initiation, asynchrony in floral development, floral or ovular abortion, embryo abortion or the failure of seeds and fruits to mature (Owens, 1995). In northern hemisphere forests, the fructification strategy of mast seeding (or masting), characterized by significant inter-annual fluctuations in seed production synchronized at the population level, is common across tree species (Herrera *et al.*, 1998; Janzen, 1976; Kelly, 1994; Waller, 1993). This is notably the case for pedunculate and sessile oak populations, which exhibit bimodal masting (Kelly, 1994): large amount of acorns are produced during infrequent mast years followed by several non-mast years where fructification is low, though rarely absent (Nussbaumer *et al.*, 2016). From an evolutionary point of view, masting is mainly interpreted as a strategy that aims to satiate seed predators (Bogdziewicz *et al.*, 2018a; Moreira *et al.*, 2017), and is the result of increased pollination efficiency during high flowering years (Lebourgeois *et al.*, 2018; Schermer *et al.*, 2018; Pearse *et al.*, 2016). Two factors have been identified as drivers of oak mast seeding: internal resource allocation to pollen production and climatic conditions – i.e. warmer and drier spring weather conditions increase the chances of a mast-seeding event (Lebourgeois *et al.*, 2010; Schermer *et al.*, 2018). As for other species practicing this strategy, oak regeneration necessarily begins in a mast years. Since mast years cannot be anticipated more than a few months in advance, masting is a major constraint for forest managers planning the stand's regeneration phase, which requires several years of preparation (Mölder *et al.*, 2019a). The difficulty of predicting oak masting patterns is therefore the main factor constraining oak regeneration during the seed production stage, and since the masting process is mostly climate driven (Lebourgeois *et al.*, 2010; Schermer *et al.*, 2018), levers of action to limit this constraint are limited. In Northern Europe, direct seeding of acorns collected in other forests is frequently practiced to compensate for low fructifications (Löf *et al.*, 2019; Villalobos *et al.*, 2020).

1.4.2.2 Seed dispersal

The seed dispersal phase designates the transport by biotic (*i.e.* animals) or abiotic (*i.e.* wind, gravity) agents of the seeds or fruits from the branches of the seeding tree to the ground. Acorns are primarily dispersed by barochory (gravity dispersal) over short distances (a few meters away from the seeding trees), and secondarily, by zoochory (rodents carry the seeds over short distances and jays over much longer distances - up to 16 km) (den Ouden *et al.*, 2005; Jones, 1959). Petit *et al.* (1997) analyzed the speed of oak post-glacial colonization (*i.e.* 500m per year) and concluded that punctual events of long-distance dispersal by jays were likely the mechanism that made such fast recolonization possible. Oak seed dispersal is mainly constrained by seed predators – *i.e.* insects, birds, rodents and mammals (Crawley & Long, 1995; den Ouden *et al.*, 2005). Seed predation may occur either directly on the branch or on the ground, and in both cases, germination rates decrease after ingestion; this supports the idea that zoochory comes with an important survival cost for large-seeded species (Malo & Suarez, 1998; Mouissie *et al.*, 2005; Picard *et al.*, 2015). Mechanic protection devices (Löf *et al.*, 2021) or chemical repellents may reduce predation rates (Villalobos *et al.*, 2019). Rodents' consumption of acorns has also been shown to interact with soil conditions, and can therefore be reduced by site preparation operations such as mounding (Birkedal *et al.*, 2010).

1.4.2.3 Germination

Germination is the transition from the seed lying on the ground to a germinated seedling (*i.e.* the plant still relies on its seed reserves). Unlike some small-seeded species whose seeds germinate better after being ingested by predators, a process that removes the seed coat (Malo & Suarez, 1998; Picard *et al.*, 2015), acorns do not survive ingestion. The predation of acorns lying on the ground is therefore a significant factor constraining oak regeneration (Crawley & Long, 1995; den Ouden *et al.*, 2005). The germination stage is also highly dependent on micro-climatic and soil conditions: studies in the field of the ideal micro-climatic conditions for acorn germination are scarce, but some significant factors have been identified. In particular, acorns tend to germinate better in humid conditions (Kühne & Bartsch, 2007), or when buried at a depth of 5cm (Nilsson *et al.*, 1996). In the case of direct seeding, some treatments on acorns have been shown to efficiently improve germination, especially the partial removal of the seed coat (*i.e.* scarification) (Aniszewska *et al.*, 2020; Kaliniewicz & Tylek, 2018). Obtaining high germination rates is particularly important for the success of the regeneration since acorns only have a lifespan of one year, which prevents the constitution of a seed bank: only the acorns of the current year have the capacity to germinate.

1.4.2.4 Sapling establishment

Sapling establishment includes the survival and growth of a seedling until it becomes independent of its seed reserves (*i.e.* the sapling stage). This stage is therefore highly conditioned by the amount of reserves contained in the seed: the first year after germination, the seedlings of small-seeded species have lower growth and survival rates than the seedlings of large-seeded species (Reich *et al.*, 1995). Acorns are known to contain a particularly high amount of carbohydrate reserves (Kirkpatrick & Pekins, 2003), which enables oak seedlings to grow vigorously during their first year and to survive in large numbers even in unfavourable light conditions (Eaton *et al.*, 2016). Oak seedlings growth and survival can be constrained by climate (*i.e.* insufficient water availability), soil conditions and competition for nutrients (Čater & Batič, 2006). Site preparation to improve soil conditions and herbicide application to reduce competition can significantly improve oak seedling growth and survival (Löf *et al.*, 2006; Löf & Birkedal, 2009). At this growth stage, browsing by large herbivores is infrequent (Götmark *et al.*, 2014), but herbivory by small rodents has been identified as a potential source of mortality (Löf *et al.*, 2021).

1.4.2.5 Sapling growth

This stage in the regeneration process designates the growth of saplings from seed independence until their recruitment into the overstorey. Oak saplings have an intermediate shade tolerance: 30% of the above-canopy incident light is considered a minimum critical threshold for oak regeneration (Modrow *et al.*, 2020). Furthermore, oak saplings tend to have slower growth rates than the shade-tolerant species such as beech (*Fagus sylvatica*) that frequently co-occur with oak, and this difference in height growth tends to increase as light availability decreases (Ligot *et al.*, 2013; Couwenberghe *et al.*, 2013). Consequently, the synergetic effect of light availability and among-sapling competition has been identified as one of the main constraints on oak regeneration at this stage (Annighöfer *et al.*, 2015; Kohler *et al.*, 2020). To overcome the insufficient light availability for oak saplings under a closed canopy, shelterwood cutting – where adult trees are progressively harvested throughout the regeneration process to gradually increase light availability – is extensively used in western and central Europe (Lüpke, 1998). Competition with other species can be controlled by clearing operations, while reducing sapling density limits the competition among oak saplings (Box 1.1) (Kohler *et al.*, 2020; Lüpke, 1998).

Box 1.1. Definition of the silvicultural operations referred to in this thesis

Clearing: Removing saplings, shrubs and herbs that compete with the target species, usually with a brush cutter or clearing saw (*i.e.* "dégagement" in French)

Sapling density reduction: Removing saplings of the target species when intraspecific competition compromises regeneration (*i.e.* "dépressage" in French)

Felling: Harvesting adult trees to create a canopy gap and increase light availability for the understory (*i.e.* "coupe" in French)

Shelterwood cutting: Progressively harvesting adult trees throughout the regeneration process to gradually increase light availability (*i.e.* "coupe progressive" in French)

Mounding: Treatment of a site to create heaps of soils for seeding or planting (*i.e.* "bombement" in French)

Oak saplings withstand relatively well disturbances that remove above-ground biomass such as deer browsing (Götmark *et al.*, 2014) or low-intensity fire (Pettersson *et al.*, 2020) thanks to their high sprouting ability (Drexhage & Colin, 2003), and deep taproots which enable them to store carbohydrates (Eaton *et al.*, 2016). However, oak saplings tend to be more frequently browsed than other temperate tree species such as beech, ash (*Fraxinus excelsior*) or spruce (*Picea abies*) (Boulanger *et al.*, 2009; Kullberg & Bergström, 2001), and browsing significantly reduces their height growth (Leonardsson *et al.*, 2015; Pettersson *et al.*, 2020). Consequently, despite the oak sapling's ability to withstand browsing, deer browsing is a significant constraint for oak regeneration (Leonardsson *et al.*, 2015; Pettersson *et al.*, 2020; Kohler *et al.*, 2020). Possible measures to take against deer browsing are exhaustively presented in section 1.2.2.

This section provides a non-exhaustive review of the factors influencing oak regeneration during each step of the process, and shows that cervids mainly interfere via two mechanisms: acorn predation, which hinders seed dispersal and germination, and browsing, which interferes with sapling establishment and growth. Studies have shown that, beyond these direct effects, several factors such as canopy openness (Kuijper *et al.*, 2009), resource availability (Wise & Abrahamson, 2005), and the characteristics of the accompanying understory vegetation (Jensen *et al.*, 2012) accompanying oak could also interact with deer browsing to influence oak regeneration. A recent study by Annighöfer *et al.* (2015) highlighted the importance of taking into account the interactions between the different factors

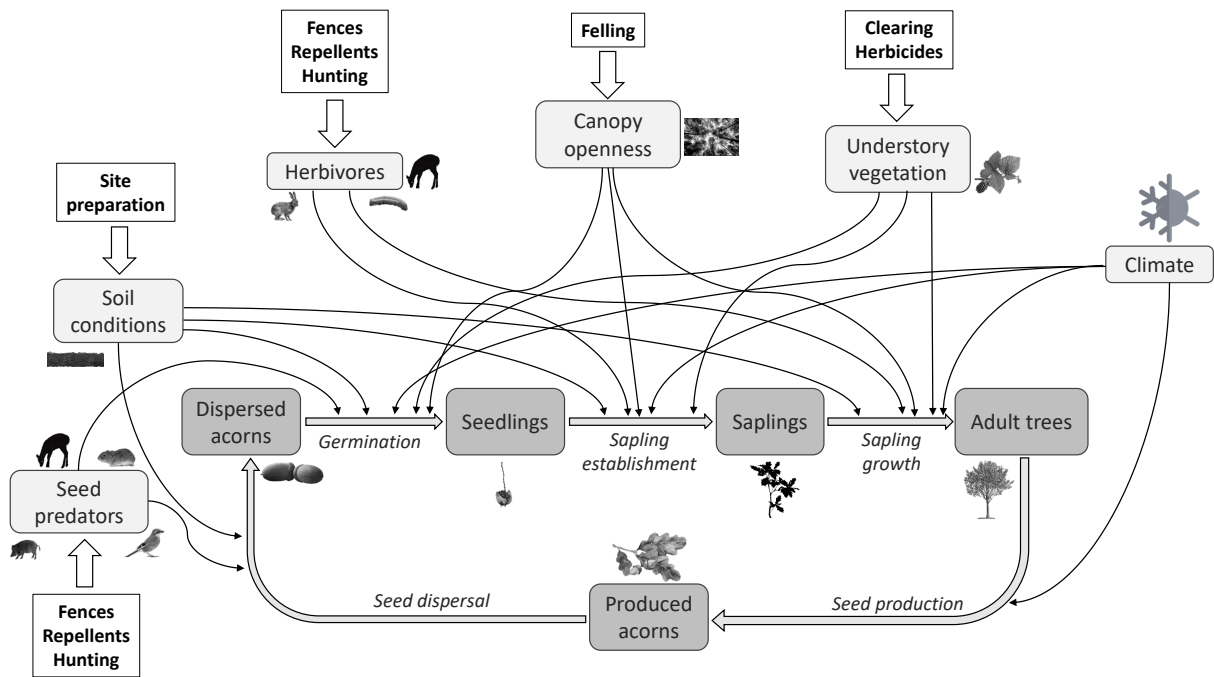


Figure 1.7: Main factors (light grey) constraining the different phases of oak regeneration (dark grey), and levers of action (white) to limit each of these constraints. The list of factors constraining oak regeneration is non-exhaustive and the interactions among these constraints are not presented.

constraining oak regeneration. Gaining insights into the factors interacting with the effects of cervids could significantly improve the efficiency of the forest management operations conducted to ensure oak-stand regeneration in areas exposed to high cervid densities.

1.5 Interactions between oak and cervids throughout the regeneration process, and remaining knowledge gaps

1.5.1 The influence of oak mast seeding on the constraint exerted by deer on oak regeneration

The previous section highlights that red and roe deer can interfere with oak seed dispersal and germination through the consumption of acorns, and with the establishment and growth of saplings through browsing. Inter-annual fluctuations in oak fructification have the potential to modify both of these constraints via the proportion of available acorns for consumption and of the browsing pressure exerted on the admixed vegetation.

1.5.1.1 Influence on the proportion of acorns consumed

The resource depletion hypothesis is one of the main hypotheses put forward to explain the evolutionary causes of mast seeding (Ims, 1990). It predicts that consecutive years of low fructification induce a decrease in the population dynamic of seed predators, so that the subsequent mast years saturate the diet of the remaining seed predators, thereby enabling a sufficient amount of seeds to survive (Ims, 1990; Janzen, 1971; Waller, 1993). This strategy notably relies on the assumption that punctual high seed availability will saturate the predators' ability to consume the seeds – *i.e.* the proportion of predated seeds will decrease with increasing seed availability (Bogdziewicz *et al.*, 2018a; Moreira *et al.*, 2017). Based on Holling's classification of predator functional responses to prey density (Holling, 1965), this relationship between seed consumption and seed availability corresponds to a type II or type III functional response (Moreira *et al.*, 2017) (Fig. 1.8). A few studies have reported that red deer (Picard *et al.*, 1991) and roe deer (Abbas *et al.*, 2011) include large proportions of acorns in their diet during mast years, but the nature of the relation between oak fructification and acorn predation by these two species has never been investigated. If this relation is indeed analogous to a type II or III functional response (Fig. 1.8), the proportion of seeds predated by deer should significantly decrease during mast years, along with the constraint exerted by these two cervids on oak seed dispersal and germination.

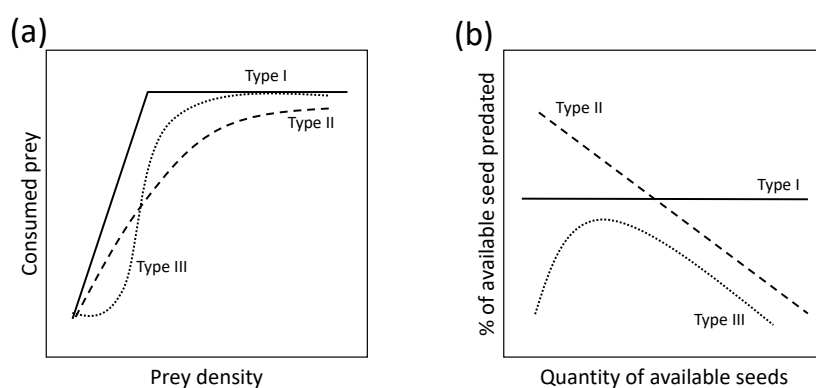


Figure 1.8: (a) Functional response of predators to prey density (Holling, 1965), and (b) re-interpretation of these theoretical relations under the framework of seed predation by Moreira *et al.* (2017).

1.5.1.2 Influence of the browsing pressure exerted on the understory

Oak mast seeding is a typical example of a pulsed resource – *i.e.* an event of increased resource availability characterized by low frequency, large magnitude and short duration relative to the lifespan of their consumers (Yang *et al.*, 2010). Events of pulsed resource have been shown to have various consequences on the population dynamics (Bieber & Ruf, 2005), conditions (Harlow *et al.*, 1975), movements (McShea & Schwede, 1993) and diet (den Ouden *et al.*, 2005; Picard *et al.*, 1991) of seed consumers. Oak masting has notably been shown to modify the population dynamics of ungulate species like wild boar (*Sus scrofa*) (Bieber & Ruf, 2005; Touzot *et al.*, 2020). If similar effects were evidenced on red and roe deer populations, an increase in the browsing pressure exerted on understory vegetation could be expected following mast years. Furthermore, because cervids balance their diet to meet their nutrient requirements (Simpson & Raubenheimer, 2011), consuming large quantities of acorns could potentially modify deer's consumption of other plant resources, and influence the browsing pressure they exert on the understory vegetation.

1.5.2 Morphological and functional consequences of browsing

The direct consumption of seedlings and saplings reduces their height growth and survival and is generally considered to be the most influential effect of cervids on forest regeneration (Ramirez *et al.*, 2018). Over the past decades, numerous studies have investigated the consequences of deer browsing on oak seedling and sapling growth and survival (Drexhage & Colin, 2003; Harmer, 2001; Götmark *et al.*, 2014; Petersson *et al.*, 2020). These studies shows that oak seedlings and saplings are more frequently browsed at the end of winter (Petersson *et al.*, 2020); this reduces height growth, but has only a limited effect on survival due to oak's sprouting ability (Drexhage & Colin, 2003; Harmer, 2001). Red and roe deer browsing pressure is concentrated on oak saplings ranging from 20 to 130cm, and is negligible on oak seedlings below 20cm in height (Götmark *et al.*, 2014; Löf *et al.*, 2021). Though the morphological consequences of deer browsing on oak saplings is covered relatively well in the literature, the functional consequences of this impact remain largely unknown.

Indeed, many studies have documented a trade-off between fast resource acquisition and the defense against herbivores (Wright *et al.*, 2004; Díaz *et al.*, 2016; Züst & Agrawal, 2017). Consequently, tree seedlings and saplings may respond to deer browsing with a gradient of strategies ranging from increased resource acquisition and promoting compensatory growth to strengthening defences to avoid further herbivory. Due to the oak's ability to survive high levels of browsing, it is more often associated with a tolerance strategy (Harmer, 2001; Drexhage & Colin, 2003); to the tree promotes fast resource acquisition rather than anti-herbivore defences in response to browsing. However, studies investigating browsing-induced changes in oak functional traits are scarce (Drexhage & Colin, 2003; Moreira *et al.*, 2018),

and more research is necessary to confirm the above-mentioned hypothesis. For instance, recent studies have hypothesized that a higher investment in fast resource acquisition following browsing to promote compensatory growth could actually increase the chances of further herbivory; this is based on the observation that, for several temperate tree species, cervids preferentially consume previously browsed individuals (Moore *et al.*, 2000; Cromsigt & Kuijper, 2011; Mathisen *et al.*, 2017). This phenomenon, observed at the individual sapling level, increases heterogeneity in sapling growth at the population level, with subsequent consequences for the stand's silvicultural value (Bergqvist *et al.*, 2003).

1.5.3 Deer browsing as a mediator of plant-plant interactions during sapling growth and establishment

The effect of deer browsing on oak sapling growth is the sum of the direct effect of deer browsing on oak saplings (*i.e.* negative for most temperate woody species), and of the indirect effects resulting from the consumption of other components of the understory (Rooney & Waller, 2003). Plant competition is considered a major factor driving oak sapling growth during regeneration (Annighöfer *et al.*, 2015; Kohler *et al.*, 2020): these indirect effects are therefore likely to have a strong influence on this process. The consumption of understory species co-occurring with oak influence its regeneration via two mechanisms: (i) by diverting part of the browsing pressure from oak and (ii) by modifying the competitive or facilitative effect exerted by these species on oak. In theory, these two mechanisms should be driven by three main characteristics of the understory: admixed understory species abundance relative to oak, their effect on oak sapling growth (competitive or facilitative), and their palatability relative to oak. Holling's functional response (Fig. 1.8.b) describes different positive relations between an animal intake rate and the abundance of its food (Holling, 1965), and this theory has been shown to apply well to the relation between a plant abundance and its consumption by herbivores (Farnsworth & Illius, 1998; Spalinger & Hobbs, 1992). For an equivalent abundance of oak and admixed understory species, whether the understory is competitive or facilitative for oak should determine the direction of the indirect effect of deer browsing on oak sapling growth – *i.e.* positive if the browsed understory is competitive, negative if it is facilitative. The palatability of the understory relative to oak determines the balance between the direct and indirect effect of deer browsing: if the browsed understory is much more palatable than oak, indirect effects should dominate over the direct effect of oak browsing since most of the browsing pressure should be focused on the understory, and vice versa (Fig. 1.9). From these assumptions, it is possible to establish a theoretical framework (valid for an equivalent abundance of oak and admixed understory species) predicting the overall effect of deer browsing on oak sapling growth depending on the effect of the understory on oak (axis 1) and of the understory relative palatability com-

pared to oak (axis 2) (Fig. 1.9).

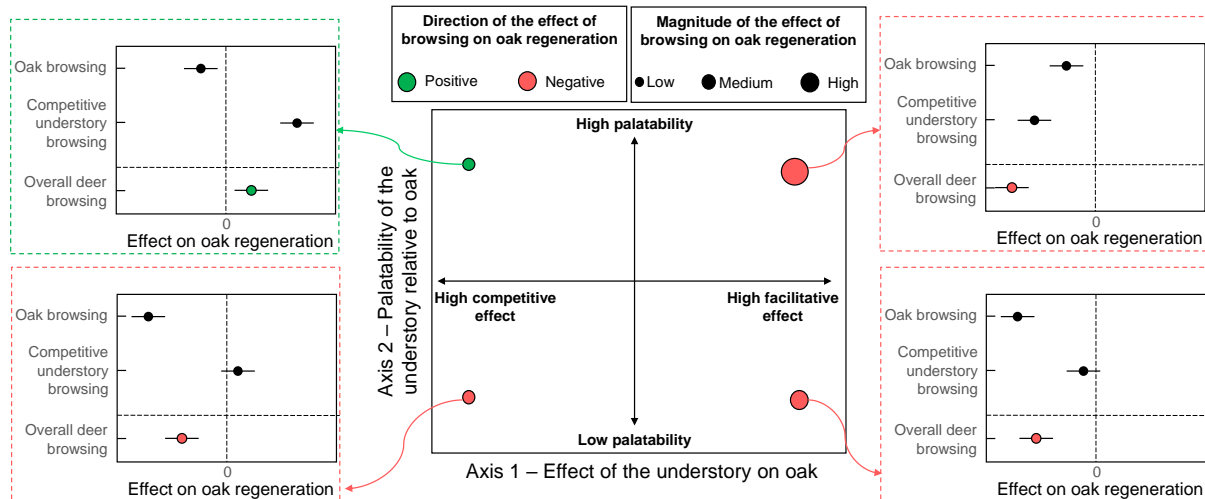


Figure 1.9: Theoretical framework predicting the direction and magnitude of the effect of deer browsing on oak regeneration as a function of the effect of the understory on oak (competitive or facilitative) and of its palatability relative to oak. This framework is valid for an equivalent abundance of oak and admixed understory species.

Studies investigating the indirect influence of deer browsing on oak sapling growth under field conditions suggest a two-step process: (i) the release of the saplings from the shrub layer, and (ii) the mediation of among-sapling competition once the saplings have outgrown the shrub layer (Jensen *et al.*, 2012; Walters *et al.*, 2020). Indeed, the shrub species that commonly accompany oak – *e.g.* bramble (*Rubus fruticosus* and *R. Idaeus*) – typically form a dense layer in high light conditions (Gaudio *et al.*, 2008), and are particularly competitive for light, water and nutrients (Balandier *et al.*, 2013). In the temperate forests of northern America, a *Rubus*-dominated shrub layer has been shown to trap sapling growing in a recruitment bottleneck (Walters *et al.*, 2020). On the other hand, saplings overtopped by the shrub layer are also more protected from browsing pressure, which is primarily exerted on the shrubs (Jensen *et al.*, 2012). By including a large proportion of shrubs in their diet, especially in winter (Storms *et al.*, 2008), deer can release the saplings from this bottleneck (Walters *et al.*, 2020). This situation corresponds to the top-left scenario in Fig. 1.9 – *i.e.* the understory is highly competitive but more intensively browsed than oak, resulting in an overall facilitative effect of browsing. Once the oak saplings have outgrown the shrub layer, they become more subject to browsing and the constraint exerted on oak sapling growth switches from shrub competition to direct browsing and among-saplings competition (Jensen *et al.*, 2012; Jensen & Löf, 2017; Walters *et al.*, 2020).

Studies investigating the patterns of oak sapling growth in species mixtures show that admixed species like beech or hornbeam, which are more shade tolerant and have faster growth rates, exert a strong competitive effect on oak (Ligot *et al.*, 2013; Couwenberghe *et al.*, 2013). Under the framework presented in Fig. 1.9, the influence of deer browsing on oak sapling growth when saplings of other tree species are present in similar proportions can be either positive (top-left scenario in Fig. 1.9) or negative (bottom-left scenario) depending on the palatability of the admixed species. Studies comparing red and roe deer browsing preference for different temperate tree species showed that oak is more palatable than beech, ash or spruce but less palatable than hornbeam or maple (Boulanger *et al.*, 2009; Kullberg & Bergström, 2001). Since oak has a rather intermediate palatability, the degree to which deer browsing constrains oak sapling growth should therefore be highly dependent on the initial species composition of the stand. However, studies relating the effect of deer browsing and sapling species composition are currently lacking to verify this assumption.

1.5.4 Interactions with forest management operations

Since oak natural regeneration is not sufficient to meet the current objectives set by foresters for timber production, silvicultural operations to accelerate the process of oak regeneration such as cutting adult trees to enhance light availability and the regulating competitive vegetation via clearing operations, are commonly conducted (Lüpke, 1998; Kohler *et al.*, 2020). However, the different oak-deer interactions listed in the previous sections highlight the risk of red and roe deer reducing the efficiency of these two silvicultural operations via several mechanisms.

Cutting adult trees is crucial to enhancing understory light availability for seedlings and saplings. In oak regeneration, shelterwood cutting (box 1.1) is probably the best and most extensively used silvicultural approach in Western and Central Europe (Lüpke, 1998). This practice may modify oak-deer interactions in two ways: by changing the attractiveness of the regeneration patch, and by changing individual plant responses to browsing. Increasing light availability tends to increase both the abundance (Willms *et al.*, 2017) and quality of the understory vegetation for deer – *i.e.* light-demanding species tend to be more palatable due to their higher nutrient content and lower chemical defenses (Kitajima *et al.*, 2012; Giertych *et al.*, 2015). One study conducted in temperate forests showed that ungulates spent more time foraging in canopy gaps than under a closed canopy (Kuijper *et al.*, 2009), thereby supporting the theory that light availability could increase the browsing pressure at the regeneration patch level. Canopy openness can also influence the degree to which individual saplings are affected by browsing but no common response across tree species has been found: light availability may improve or worsen seedling growth response to deer browsing depending on the tree species (Baraza *et al.*, 2010; Kupferschmid *et al.*, 2014). Since neither

of these two mechanisms has been investigated for oak, the overall influence of gap creation on the constraint exerted by deer browsing on oak regeneration remains largely unknown.

Similarly, clearing operations assist oak regeneration by removing competing species, but as such, they may also modify the browsing pressure exerted on oak both at the inter- and intra-regeneration patch level. Indeed, a dense shrub cover can prevent deer from accessing the saplings, thus decreasing the browsing pressure exerted on the regeneration patch (Jensen *et al.*, 2012; Walters *et al.*, 2020). Therefore, removing the shrub cover via clearing could in theory increase the browsing pressure exerted on the patch, but this assumption has only rarely been tested under field conditions. Furthermore, within a regeneration patch, removing competing saplings that are more palatable than the focal species could also divert the browsing pressure toward the focal species. But here again, studies testing this theory under field conditions are rare, and do not include the species concerned in the present thesis (Miller *et al.*, 2009).

These two examples illustrate how interactions between oak and red or roe deer could result in unintended outcomes for forest management. They also highlight the need to increase our understanding of these interactions in order to be able to take these interactions into account when planning silvicultural operations in oak stands with high cervid densities.

1.6 Objective of the thesis and structure of the manuscript.

This introductory chapter highlighted some knowledge gaps concerning the direct and indirect interactions between oak and red and roe deer throughout the process of natural regeneration.

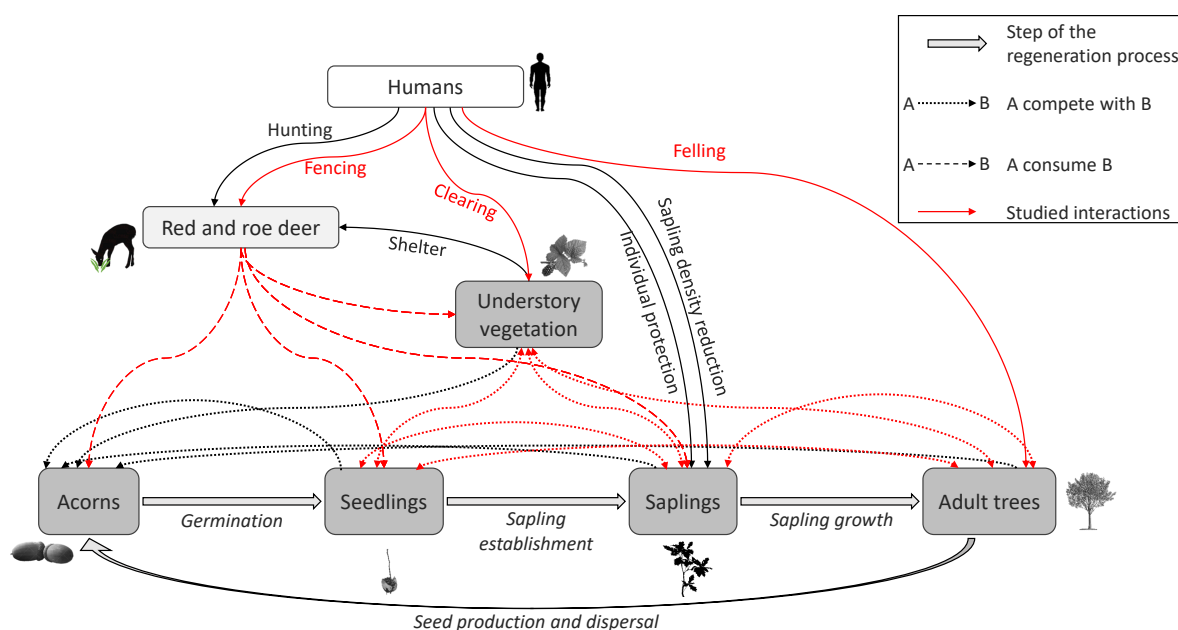


Figure 1.10: Summary of the main direct and indirect interactions between oak and deer throughout the process of oak natural regeneration, with a focus on the interactions studied in this thesis.

The objectives of this thesis are: (i) to quantify and unravel the mechanisms underlying the constraint exerted by cervids on oak regeneration through the consumption of acorns, oak saplings and admixed understory species, and (ii) to identify how specific forest management operations (*i.e.* fencing, felling and clearing) can limit or enhance this constraint (Fig. 1.10). To that end, I conducted four main studies at different stages in the regeneration process with different focuses (plant or animal, individual or population level) to investigate the following questions (Fig. 1.10):

- *Chapter 3* – What is the relation between oak fructification and acorn consumption by deer? Does acorn predation modify the consumption of other plant resources by deer?
- *Chapter 4* - Does deer browsing influence oak sapling functional traits related to de-

fense or fast carbon acquisition? How do oak sapling trait responses to browsing modify the saplings' subsequent attractiveness to deer?

- *Chapter 6* – Does canopy openness influence the constraint exerted by cervids on oak sapling growth and survival?
- *Chapter 7* – How do initial stand species composition and cervid browsing preferences influence the overall consequences of deer browsing on oak regeneration? Should the intensity of clearing operations be adapted to the browsing pressure exerted on the vegetation?

In addition to these four studies, which represent the core of this thesis, I also conducted a field experiment related to Chapter 4, which I briefly summarize in Chapter 5. Lastly, I also contributed to the publication (2nd author status) of a field experiment during my three-month assignment in Sweden (Löf *et al.*, 2021). However, since this collaboration was not originally a part of my PhD project and did not contribute to the construction of the questions raised in this manuscript, I only include a short summary in the Discussion (Box 8.1; the full manuscript appears in Appendix A). In Chapter 2, I discuss how the different methodological approaches chosen to investigate the above-mentioned questions complement each other. Chapters 3 to 7 each concern one of the five studies listed above. In the last chapter (Chapter 8), I synthesize the results obtained in all the included studies, and discuss of the perspectives opened up by these results.

CHAPTER

2

SCIENTIFIC APPROACHES

Interactions between forest trees and large herbivores have been investigated at various organizational (plant or animal, individual or population) and spatio-temporal scales ([Bergström & Edenius, 2003](#)). Because scale often dictates methodology, the diversity of my research questions led to a wide range of methodological approaches. The methods I used for each study, and the justification of their use, are presented in each related chapters, and I will not repeat these elements here. Nevertheless, I believe that the complementarity among the different approaches selected should be highlighted in a dedicated chapter. To that end, I will briefly present the most common approaches found in the literature to study the influence of large herbivores on forest regeneration, while distinguishing three categories of methodology: observational, experimental and in silico. Below, I present how I combined the exploitation of existing data and the creation of new protocols to create a complementary set of methodological approaches that cover all three categories, in order to investigate the research questions listed at the end of the first chapter.

2.1 Observational data for the study of spatial and temporal patterns

Observational data reflects the reality of ecological processes and encompasses all their complexity. As a result, these data are particularly informative when attempting to describe how ecosystem processes work; they often constitute the basis for formulating hypotheses. In the case of the influence of cervids on forest dynamics, observational data have mainly been used to understand the drivers of deer feeding behavior (animal-focused studies) and of their subsequent influence on forest vegetation (plant-focused studies) (Bergström & Edenius, 2003). By analyzing spatial and temporal variations in the browsing pressure exerted on the vegetation, plant-focused observational studies help enlighten the role played by many environmental factors such as plant species assemblage (Bee *et al.*, 2009; Boulanger *et al.*, 2009), forage availability (Champagne *et al.*, 2018), or deer density (Vourc'h *et al.*, 2002) in driving browsing pressure. Animal-focused studies mainly include diet analyses via direct observation (Agreil *et al.*, 2006; Bonnet *et al.*, 2015) or feces and rumen content analyses (Garnick *et al.*, 2018). These data have historically been used to compare herbivore species' feeding niches, and laid the foundation for Hofmann's classification of ruminant feeding types (Hofmann & Stewart, 1972; Hofmann, 1989). More recently, dietary studies have been used in the context of long-term monitoring to assess how temporal events (*e.g.* fluctuations in resource availability, storms) influence the plant species consumed by deer (den Ouden *et al.*, 2005; Picard *et al.*, 1991; Storms *et al.*, 2006).

The latter issue is the main concern of a long-term monitoring program in the State Reserve of La Petite Pierre (LPP hereafter) in northeastern France (Fig. 2.4) conducted by the French Office for Biodiversity (OFB), in charge of the State's wildlife management policy, with the support of the National Forest Office (ONF), responsible for the management of state-owned forests. The program is investigating how temporal variations in environmental factors (*i.e.* climate, red and roe deer abundance, oak fructification, windstorms) modify the feeding behavior of red and roe deer. To that end, OFB and ONF agents have collected the rumen contents of the red and roe deer shot during the hunting season on a yearly basis since 1986. The OFB analyzes these samples according to a micro-histological procedure (Chamrad & Box, 1964) to identify the items consumed to the plant species level. In parallel, deer red and roe deer abundance is measured annually through spotlight counts (Garel *et al.*, 2010) and kilometeric indices (Vincent *et al.*, 1991), and oak fructification has been monitored since 2010 following the ground-plot counting method (Touzot *et al.*, 2018). The few existing studies that investigated acorn consumption in relation to oak mast seeding were conducted with a similar approach but over shorter time-periods (*i.e.* 2 or 3 years) (McShea & Schwede, 1993; Picard *et al.*, 1991). The LPP monitoring program offered me the opportunity to evaluate the relation between oak fructification and acorn consumption

by red and roe deer over a much longer period. Furthermore, since diet composition was determined at the plant species level, I could also evaluate the consequences of acorn predation on the consumption of other plant resources, which had never been tested in the literature. To investigate these two questions, I analyzed this long-term data set in the first study for my thesis, presented in chapter 3, and published in *Basic and Applied Ecology* in 2020 (Barrere *et al.*, 2020).

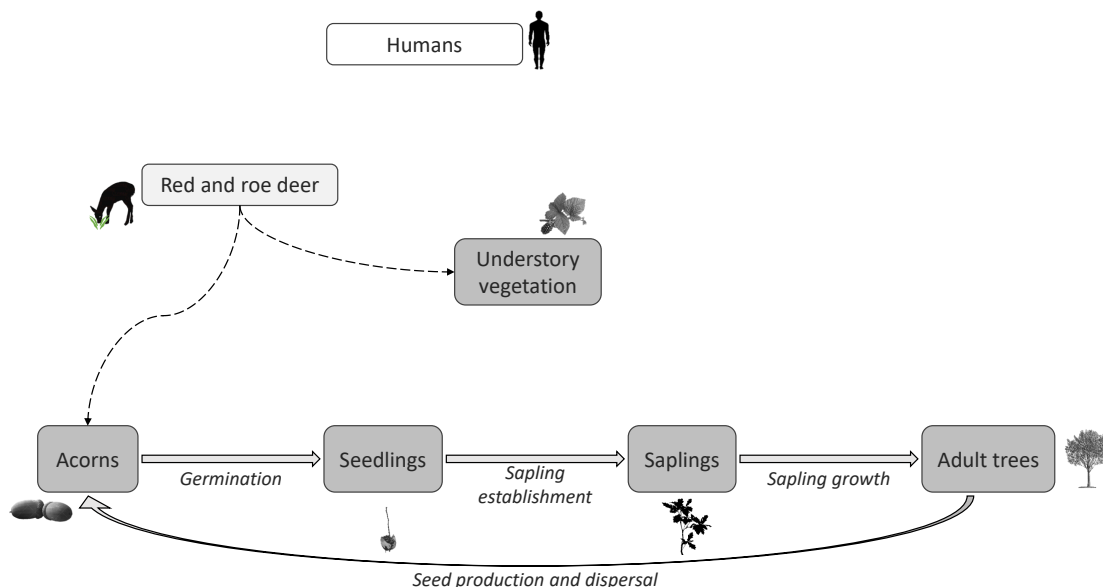


Figure 2.1: Schematic representation of the direct and indirect interaction between deer and oak regeneration investigated in chapter 3

2.2 Experimental approaches to studying forest-deer interactions

The objective of an experimental approach is to create and control the variability of one (or several) factor(s) through a specific methodology to study its (or their) influence on a variable of interest. By targeting specific factors, experiments are often used to test hypotheses that are formulated based on field observations (Spiegelberger *et al.*, 2012). In their review of the existing methodological approaches to study deer-forest interactions, Bergström & Edenius (2003) classified experimental approaches into two main categories: simulation studies and fencing experiments.

2.2.1 Evaluating oak response to browsing at the individual level through simulation studies

Plant physiological and morphological responses to deer herbivory have mainly been studied through observational studies where plants actually browsed by cervids were monitored (Drexhage & Colin, 2003), or through experiments where herbivory was simulated (Baldwin, 1990). Under field conditions, the intensity, timing and frequency of browsing tend to be highly variable and the populations of browsed and unbrowsed individual plants may have different characteristics due to herbivore selectivity, resulting in additional noise (Bergström & Edenius, 2003). Deer herbivory simulations through mechanical clipping offer the opportunity to control the intensity, timing and frequency of the browsing event(s), and to control the characteristics of the plant individuals that undergo browsing. Studies that involve simulated browsing have either applied clipping in the field on saplings that are protected from natural browsing with fences (Campa *et al.*, 1992; Canham *et al.*, 1994; Wallgren *et al.*, 2014), or on saplings growing under controlled conditions (e.g. nurseries) (Braithwaite & Mayhead, 1996). The field studies better illustrate the plant's response in its environment, but are more subject to field-related hazards, while controlled conditions minimize variations in environmental conditions and plant characteristics (e.g. ontogenic stage, genetic origin, morphology). The main drawback of simulated browsing is that it may misrepresent browsing since deer saliva and the way herbivores tear apart the plant may influence the plant's response to browsing (Bergström & Edenius, 2003). To partly overcome these drawbacks, mechanical clipping can be performed with special clamps designed to imitate the herbivore jaw (Gleizes, 2007), and deer saliva may even be applied (Ohse *et al.*, 2017) to represent the process of herbivory more accurately.

In Section 1.5.2, I highlighted the need for a better understanding of the functional consequences of deer browsing on oak saplings at the individual plant level and the influence of potential browsing-induced trait variations on subsequent attractiveness to deer. To gain better insights into these interactions, I initiated an *ex situ* experiment in a private reserve – the Pierre Vérots Foundation – to evaluate the consequences of simulated browsing on oak sapling traits related to carbon acquisition and anti-herbivore defenses, and on the subsequent attractiveness of the saplings to deer. The experiment was planned over two years and was set up at the beginning of 2019: in three fenced plots, cohorts of oak seedlings were marked individually and half of them underwent a simulated browsing treatment at the end of winter. Significant time was spent on this experiment during the first year of the thesis. The second year of the experiment, half of the seedlings were to be sampled for trait analysis, while the other half was to be exposed to wild roe deer to test the influence of the simulated browsing treatment on attractiveness to deer. This protocol represented a significant time investment in the first year of the thesis. It was set up in the beginning of 2019 but unfortunately, due to an unexpected drought in summer 2019, more than half of the

2.2. Experimental approaches to studying forest-deer interactions

seedlings did not survive the year. Because of this high mortality rate, not enough seedlings remained to conduct the rest of the study (trait analysis and behavioral tests under field conditions).

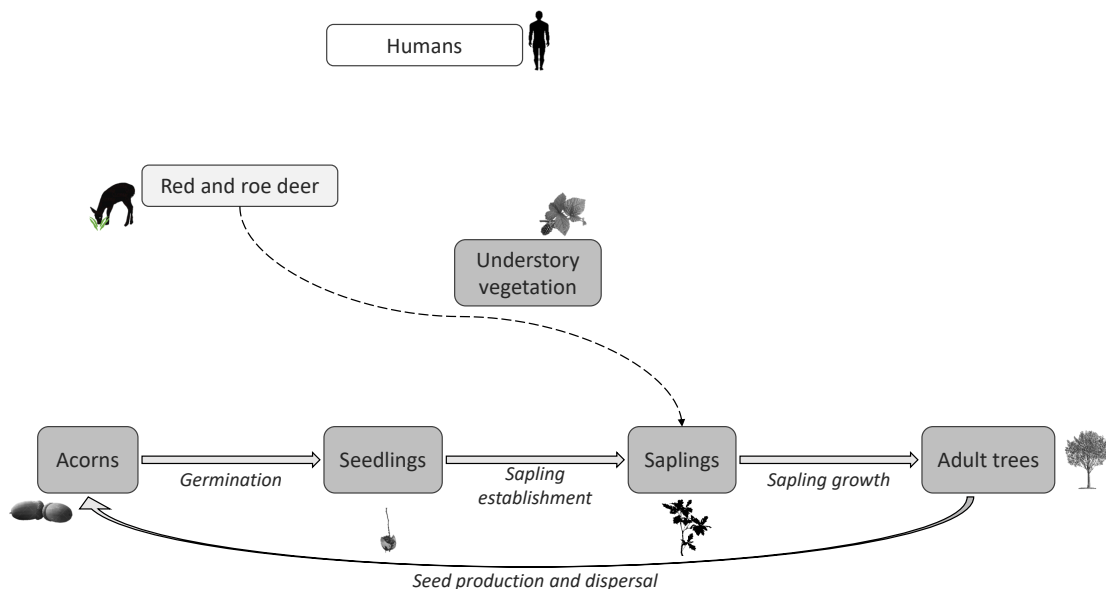


Figure 2.2: Schematic representation of the direct and indirect interaction between deer and oak regeneration investigated in chapters 4 and 5

In parallel, I designed a similar protocol *ex situ* to avoid unexpected field-related events. This protocol was applied in two steps, again over two years. At the end of winter 2019, in the ONF experimental nursery of Cadarache (Fig. 2.4), I applied different levels of simulated browsing to one-year-old oak saplings and monitored their morphology throughout the year. In summer 2019, I also sampled some of these saplings to measure leaf traits related to carbon acquisition and anti-herbivore defenses. At the end of the year, I transferred most of the remaining saplings to the INRAE experimental station in Gardouch to test the influence of the simulated browsing treatment on the preference of tame roe deer via *ex situ* feeding trials. In the literature, *ex situ* feeding trials (Duncan *et al.*, 2001; Hartley *et al.*, 1997) tend to be more frequent than *in situ* feeding trials conducted with wild animals (Loyttyneimi, 1985), notably since it gives the observer more control on the animal frequentation. However, this approach raises the questions of the potential differences in foraging behavior between tame and wild animals (Spalinger *et al.*, 1997), and, more generally, of the influence of the observer on the animals' behavior. In summer 2020, the last saplings remaining in the nursery were sampled for leaf trait analysis. This experiment was designed to investigate the same research questions as the field experiment, but under controlled conditions (Fig. 2.2). Due to the failure of the field experiment, this *ex situ* approach became the main study. It was published in the journal *Experimental and Environmental*

Botany and is presented in detail in Chapter 4. However, considering the considerable time invested in the field experiment, I chose to include it in the thesis as well, under the form of a small, independent chapter (Chapter 5).

2.2.2 Evaluating deer influence on oak sapling populations through fencing experiments

The most common experimental method used to manipulate cervid density is to erect fences around several forest plots to exclude the deer, and then to compare the vegetation growing inside these fenced plots to the vegetation growing in adjacent unfenced plots, still exposed to cervids. This method results in two modalities: fenced plots with no cervids and unfenced plots with a generally unknown cervid population density (see Waller *et al.* (2009) or Mårell *et al.* (2012) for thorough reviews of this experimental approach). Historically, fencing has been the reference methodology for testing the influence of cervids on forest structure, dynamics and functions (Bernes *et al.*, 2018), and it has now been extended to research questions beyond plant-herbivore interactions (Foster *et al.*, 2014) – e.g. the influence of deer exclusion on bird (Cocquelet *et al.*, 2019), mammal (Seki *et al.*, 2021) or arthropod (Vandegehuchte *et al.*, 2017) communities.

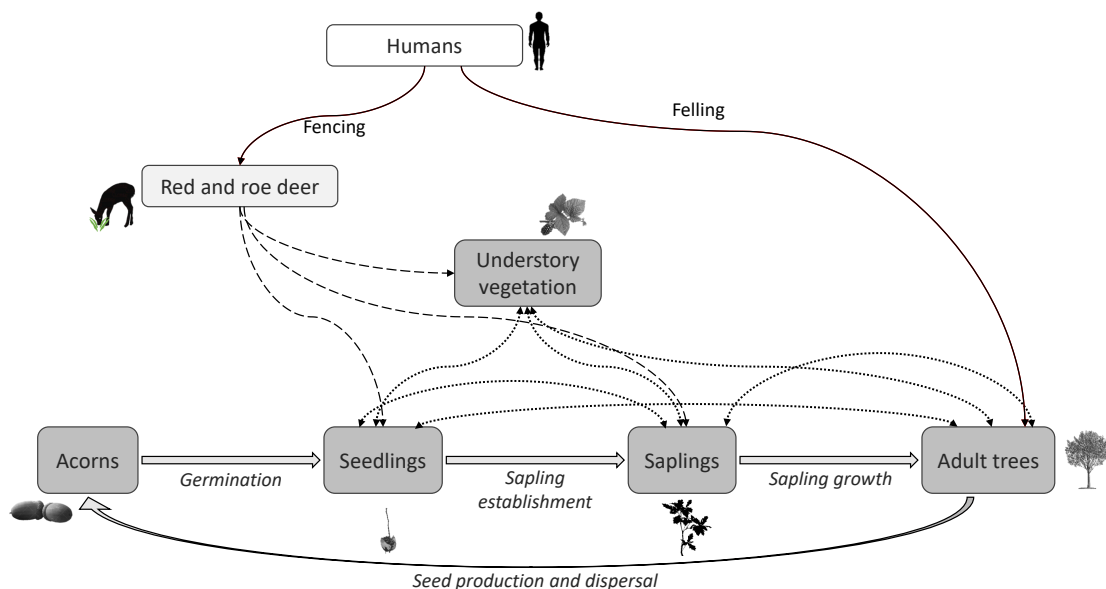


Figure 2.3: Schematic representation of the direct and indirect interactions between deer and oak regeneration investigated in chapter 6

To evaluate deer influence on oak regeneration and on the dynamics and diversity of the

understory vegetation, in 2012 the OFB initiated the EFFORT protocol, which consists of a network of fenced-unfenced plots at three study sites in Northeastern French forests: Arc-en-Barrois, Trois-Fontaines and LPP, respectively set up in 2014, 2015 and 2012 (Saïd *et al.*, 2019). In these fenced-unfenced plots, two main types of survey are being conducted on an annual basis (at the beginning of spring): (i) height, survival and browsing damage of individual oak seedlings and saplings are monitored, and (ii) exhaustive vegetation surveys are carried out on small quadrats. In section 1.5.4, I highlight the need to evaluate whether canopy openness influences the cervid effect on oak regeneration. This question arises from observational studies showing that canopy openness modifies deer frequentation (Kuijper *et al.*, 2009; Moser *et al.*, 2008), and from experiments showing that light availability can influence plant tolerance to browsing (Baraza *et al.*, 2010). To investigate this interaction, I chose to exploit the variability of the natural light conditions between the different pairs of fenced-unfenced plots by measuring canopy openness in the summer of 2019. With these additional measurements, I was able to test the interactive effects of deer exclusion and canopy openness on oak growth and survival at the population level (Fig. 2.3). The limitation of this approach was the absence of an experimental control plot for the variability in canopy openness, which may have diminished the statistical power of my calculations. Because only three years of data were available for the most recent site (Arc-en-Barrois) when I started my PhD in 2018, I also extended this dataset by monitoring individual oak seedling height, survival and browsing damage in 2019. Lastly, in early 2020, I carried out a three-month mission at the Southern Swedish Forest Research Center to initiate a collaboration on this study with Magnus Löf and Annika Felton. After I arrived in Sweden, these two researchers offered me the opportunity to merge this dataset with a fencing experiment led by their former PhD student, Linda Petersson. Her protocol crosses the effect of fencing, canopy openness and low-intensity fire on oak growth and survival (Petersson *et al.*, 2020) and is highly comparable with the EFFORT protocol. Combining the two datasets provided the opportunity to compare the studied processes in two different forest types. In the fourth study of this thesis, presented in detail in chapter 6, I adapted the Swedish dataset (notably by removing the fire factor) and analyzed the two protocols jointly for a common publication, which appeared in 2021 in *Forest Ecology and Management* (Barrere *et al.*, 2021).

2.3 An in silico approach to synthesize multiple data sources

Some specific questions remain beyond the scope of observational and experimental studies. This is notably the case when the time-scale or the number of explanatory variables to cross is too large to be reasonably investigated. To that end, computer processing enables the development of mechanistic or empirical models that synthesize data collected in observational and/or experimental studies and that can address complex ecological patterns and interactions (Spiegelberger *et al.*, 2012). Because trees are long-lived organisms, the need

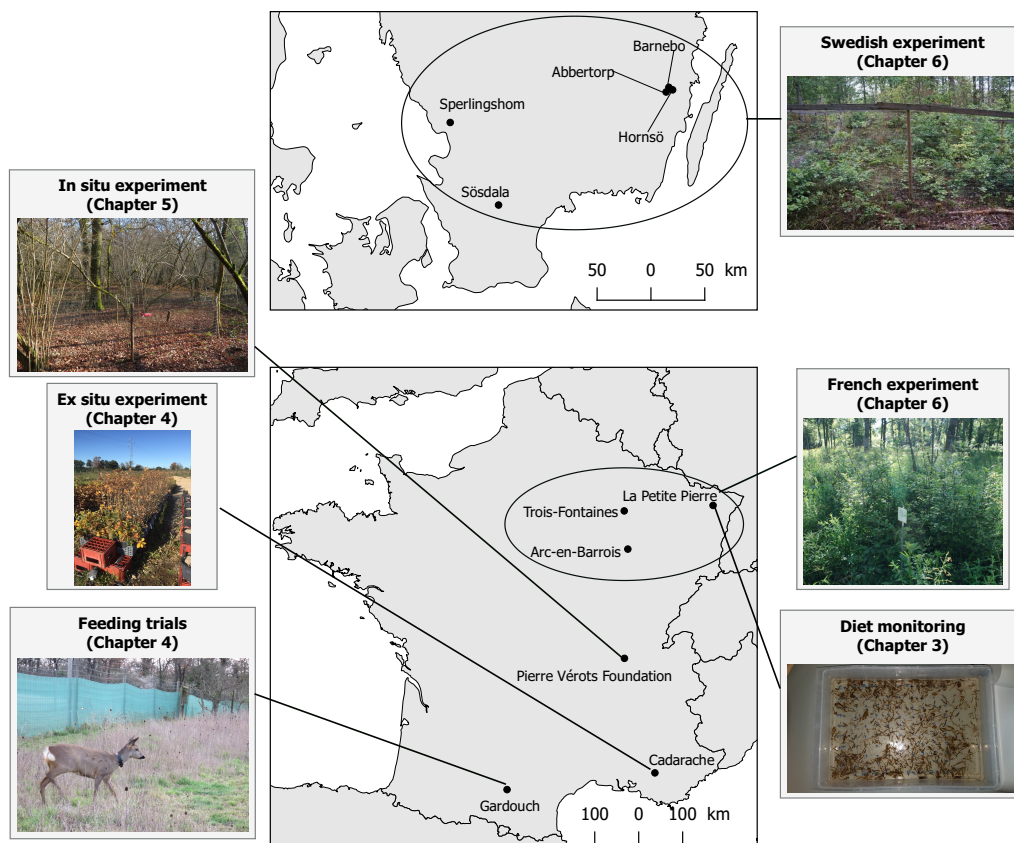


Figure 2.4: Location in Sweden (top) and France (bottom) of the study sites involved in chapters 3, 4, 5 and 6. Since chapter 7 is purely *in silico*, it was not associated with any location. Photo: J. Barrere (chapter 5 and chapter 4 Cadarache), H. Courtines (chapter 4 Gardouch), L. Henry (chapter 3), L. Laurent (chapter 6 France) and L.K. Petersson (chapter 6 Sweden).

for *in silico* studies in forest ecology is more pronounced than in many other sciences. Long before the development of computers, in the 18th century, foresters developed the first yield tables from empirical observations to predict the yields of monospecific stands (see [Johnstone \(1977\)](#) for an example). New objectives other than yield, the increase in computer processing power and a better understanding of the mechanistic processes governing forest growth have led to the development of increasingly complex and powerful computer models ([Porté & Bartelink, 2002](#)). Reviewing all the existing models is an ambitious task far beyond the objectives of this thesis, but see [Marechaux et al. \(2020\)](#), [Porté & Bartelink \(2002\)](#) or [Xi et al. \(2009\)](#) for such reviews. Despite the significant research efforts dedicated to the development of forest-dynamics models, it was only at the very end of the 20th century that some of these models started to include the interactions with large herbivores ([Jorritsma et al., 1999](#); [Kienast et al., 1999](#)). Before then, lower height classes (i.e. below 2m in height) had rarely been included in these quantitative models. This is explained by the fact that (i) the growth of these smaller individuals was not predicted by classic yield tables, and (ii) the processes governing forest regeneration have only relatively recently been identified. In

individual-based forest growth models, the excessive computation time required to model thousands of individuals, most of which will not make it to the adult stage, is an additional constraint (Bugmann, 2001).

The process of herbivory by large mammals in forest ecosystems can be included in three types of models: animal-focused, plant-focused and integrated models (Weisberg *et al.*, 2006). In animal-focused models, the objective is mostly to predict the animal's energy requirements, and vegetation is only an input variable (see Moen *et al.* (1997) for an example). In plant-focused models, the vegetation is modeled while the animal is only an additional factor influencing plant growth or survival (Forsyth *et al.*, 2015; Kienast *et al.*, 1999; Seagle & yuen Liang, 2001). Lastly, integrated models simulate plant growth and animal population dynamics with a comparable level of complexity, along with the interactions between the two processes – *i.e.* the quantity of available plant biomass influences animal population dynamics while animal density influences plant growth (Jager *et al.*, 2017; Kramer *et al.*, 2003; Jorritsma *et al.*, 1999). The majority of these modeling studies aimed to investigate the long-term (*i.e.* from 100 to 500 years) effect of cervid browsing pressure on forest dynamics (Jorritsma *et al.*, 1999; Kienast *et al.*, 1999; Seagle & yuen Liang, 2001; Forsyth *et al.*, 2015; Jager *et al.*, 2017). Some did investigate how this long-term effect interacted with other components of global change such as climate or wildfires (Kramer *et al.*, 2003; Riggs *et al.*, 2015; Bernard, 2018). All of these publications illustrate the potential of *in silico* studies to synthesize data from both observational and experimental studies and to help investigate complex questions relative to deer-forest interactions.

I initiated the last study described in this thesis (chapter 7) for three main reasons. First, some interesting yet poorly known aspects of oak-deer interactions could not be addressed via the other protocols. In particular, testing the effect of specific characteristics of the understory (*i.e.* abundance, palatability, competitiveness) on the constraint exerted by deer browsing on oak sapling growth requires crossing a vast array of initial conditions (density and respective proportion of oak relative competitive species) with a gradient of browsing pressure (Fig. 2.5). Similarly, to decide whether or not to conduct clearing operations depending on the browsing pressure exerted on the understory vegetation, a gradient of deer density must be crossed with different clearing scenarios, while maintaining the other environmental conditions constant. In both cases, this is hardly achievable with experimental or observational approaches, but *in silico* studies can, in theory at least, address such questions. Secondly, a consortium of researchers – *i.e.* Philippe Balandier (INRAE, PIAF), Anders Mårell (INRAE, EFNO), Benoit Courbaud (INRAE, LESSEM) and Gauthier Ligtot (Gembloux Agro-Bio Tech) – wanted to include the process of deer herbivory in forest-dynamics models. However, there was no common project to bring these researchers together on this issue. The third reason is more personal: I was highly motivated to include

this approach in my thesis since I have a strong interest in modeling.

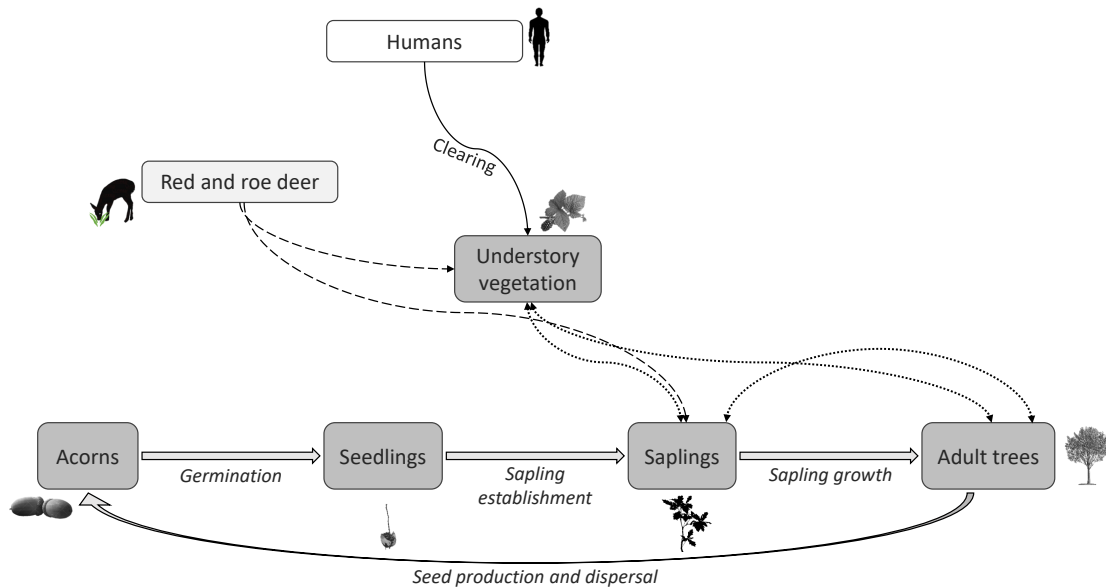


Figure 2.5: Schematic representation of the direct interaction between deer and oak regeneration investigated during chapter 7

Consequently, I initiated the collaboration among the researchers in this consortium around my project aiming to implement deer browsing in a forest-dynamics model while investigating the research questions listed above. I chose to work on the RReShar (Regeneration and Resource Sharing) model, designed by Philippe Balandier, Noémie Gaudio, Nicolas Donès (INRAE PIAF) and François de Coligny (INRAE AMAP). This fifth study included two main tasks: (i) constructing and implementing a deer-browsing extension for the RRE-SHAR based on multi-source data (i.e. the EFFORT protocol, unpublished data and the literature), and (ii) conducting simulations to address the research questions listed above. Because the first methodological task was as important (if not more so) than the simulations, I chose to write the dedicated chapter (Chapter 7) in a hybrid style between methodological report and scientific article.

2.4 Conclusion

The study of the interactions between forest trees and deer can be approached with a wide range of methodologies, depending on the organizational level and the spatio-temporal scale of the studied process (Bergström & Edenius, 2003). Experiments and observations should be seen as complementary approaches to enlighten these interactions. While obser-

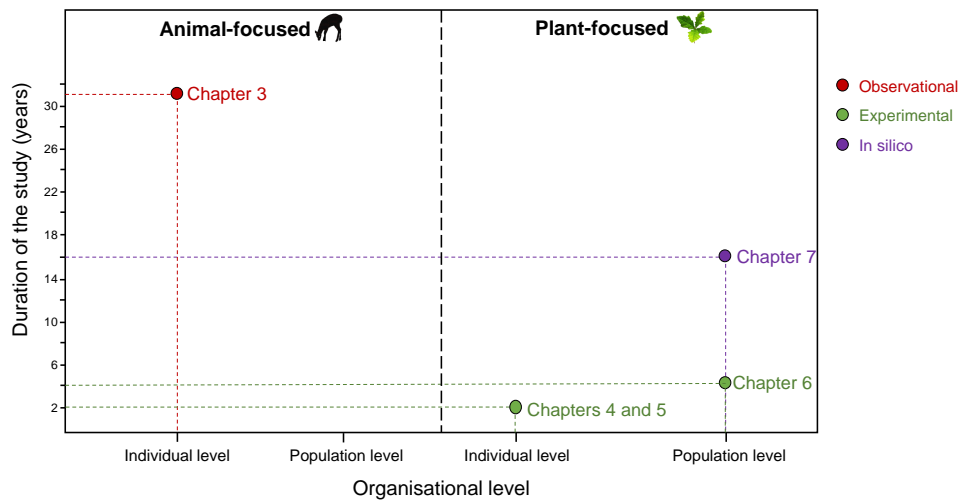


Figure 2.6: Organizational level, duration, and nature (observational, experimental or *in silico*) of the five studies conducted during this thesis.

vations constitute a basis on which to formulate hypotheses about the way ecological processes function, experiments are designed to directly test these hypotheses (Spiegelberger *et al.*, 2012). Furthermore, data from both experiments and observations can be combined to develop theoretical models and investigate complex interactions beyond the scope of simple observational or experimental studies. For this thesis, I exploited two existing sources of data: an observational protocol (chapter 3) to investigate the relation between oak fructification and deer feeding behavior, and an experimental protocol to test the hypothesis that the effects of deer and canopy openness on oak regeneration interact with each other (chapter 6). I also designed two additional experiments to test hypotheses on oak sapling trait responses to browsing, and on the consequences of browsing for subsequent attractiveness (chapters 4 and 5). Lastly, I initiated a modeling approach to combine data from different sources (including the experiment in chapter 6) to investigate the crossed influence of initial species composition and cervid preference on the overall consequences of deer browsing for oak regeneration (chapter 7). These different approaches constitute a complementary set of studies addressing research questions at various organizational and temporal scales through various methodologies (Fig. 2.6).

CHAPTER

3

HOW DOES OAK MAST SEEDING AFFECT THE FEEDING BEHAVIOUR OF SYMPATRIC RED AND ROE DEER ?

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3.1 Abstract

Oak reproduction is characterized by mast seeding with high inter-annual fluctuations in fruit production. Such resource pulses can greatly affect ecosystem functioning and may cause seed consumers to alter their mobility, demography, or diet. Consequences of mast seeding for seed consumers remain poorly understood as their long timescale makes them difficult to study. We investigated impacts of oak mast seeding on the feeding behavior of two sympatric European deer species: red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*). We analyzed their rumen content over a 31-year period in tandem with 10 years of data on oak fructification (i.e. 8 years of field monitoring and two modelled years). Acorn production is strongly correlated with consumption by both deer species. In years of high fructification, acorns represent more than 50% and 35% of red and roe deer diet, respectively, confirming assumptions that deer favor acorns when these are available. Red deer eat more acorns than roe deer both between and within years. High acorn production in mast years appears to saturate the capacity of deer to consume acorns. As the proportion of acorns increase in their diet, red deer eat more grasses and less conifer browse. No dietary shift was found for roe deer. By inducing dietary shifts in consumers, oak mast seeding can have cascading effects on ecosystem processes, notably on the damages on conifers caused by red deer and the consequences for forest dynamics.

Keywords: Deer, Diet, Mast seeding, Resource pulse, *Quercus*, Acorn, *Cervus elaphus*, *Capreolus capreolus*

3.2 Introduction

Resource pulses are events of increased resource availability characterized by low frequency, large magnitude, and short duration relative to the lifespan of their consumers (Yang *et al.*, 2010). Pulsed resources occur in a wide range of ecosystems and have cascading effects at all trophic levels. In terrestrial ecosystems, one of the most documented examples of pulsed resources is the mast seeding of plants (Ostfeld & Keesing, 2000), which is defined as the synchronous and highly variable production of seeds over the years by a population of plants (Janzen, 1976). Initially, mast seeding was mainly interpreted as an evolutionary strategy that aims at satiating seed and fruit predators (Ims, 1990; Janzen, 1971, 1976). The predator satiation hypothesis is still supported by recent studies (Bogdziewicz *et al.*, 2018a; Moreira *et al.*, 2017) and is nowadays regarded as one of the main evolutionary causes of mast seeding, along with an increased pollination efficiency during high flowering years (Lebourgeois *et al.*, 2018; Pearse *et al.*, 2016; Schermer *et al.*, 2018). On a proximate level, recent studies tend to converge on the idea that mast seeding likely results from the combination of internal resource dynamics and weather cues (Bogdziewicz *et al.*, 2019; Pearse *et al.*, 2016). Although it is practiced by some herbaceous species, the mast-seeding strategy has mainly been observed in perennial species that can afford years without reproduction (Kelly, 1994; Waller, 1979). In European temperate forests, this is notably the case of sessile (*Quercus petraea* (Matt.) Liebl.) and pedunculate oak (*Quercus robur* L.) which exhibit a bimodal normal masting (Nussbaumer *et al.*, 2016), i.e. mast and non-mast years can be identified statistically but non-mast years are generally associated with a minimal production of fruits (Kelly, 1994).

In years of high oak fructification, acorns represent a high-quality and easily accessible resource (Kirkpatrick & Pekins, 2003) and are consumed by a wide variety of wildlife species, notably rodents, birds, and ungulates (Herrera, 1995; den Ouden *et al.*, 2005; Steele *et al.*, 1993). Oak mast seeding has been shown to affect the demography (Bieber & Ruf, 2005), abundance (Schnurr *et al.*, 2002), body condition (Harlow *et al.*, 1975), movement (McShea & Schwede, 1993) and diet (den Ouden *et al.*, 2005; Picard *et al.*, 1991) of a wide variety of vertebrates via direct and indirect effects. The effects of mast seeding are strongly dependent on the type of consumer (Ostfeld & Keesing, 2000). For small species with a rapid increase rate – i.e. birds, rodents – mast seeding generally leads to a numerical response, with more individuals following mast years (Bogdziewicz *et al.*, 2016; Schnurr *et al.*, 2002). As the home range of ungulates and birds may exceed the spatial scale of a mast seeding event, these species may also respond by moving towards areas where mast seeding occurs (Lindén *et al.*, 2011; McShea & Schwede, 1993). Lastly, because pulsed resources are only available sporadically, the resource is mostly consumed by generalist species which are able to adapt their diet in the absence of the resource (Ostfeld & Keesing, 2000). Generalist con-

sumers like black bear (*Ursus americanus*) (McDonald & Fuller, 2005) or wild boars (*Sus scrofa*) (Herrero *et al.*, 2005) have been shown to exhibit important dietary shifts in a context of oak mast seeding.

Red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) are amongst the most widespread ungulate species in Europe and often occur in sympatry in temperate forests. The coexistence of the two species is notably allowed by a segregation of their feeding niche (Storms *et al.*, 2008). Red deer is classified as an “intermediate feeder”, able to adapt to fluctuations in resource availability and quality in its environment (Storms *et al.*, 2008). Although the species avoids fibers as much as possible, it is able to consume grass when resources are scarce (Dumont *et al.*, 2005). According to Hofmann’s classification of ruminant feeding types, roe deer has a “moose-type” digestive track (Hofmann, 1989), and is thus characterized by a strong selectivity and an inability to digest fiber-rich food items. This species has been identified as a typical “browser” and it mostly feeds on bramble, buds, forest fruits and cultivated seeds (Felton *et al.*, 2018; Redjadj *et al.*, 2014; Tixier & Duncan, 1996). Due to a more restricted feeding niche, roe deer is more dependent on the resource available in its habitat than red deer (Storms *et al.*, 2008).

Since acorns are characterized by a high energetic content and digestibility, and are available in a period when other resources are scarce for red deer and roe deer (autumn and winter), we may expect these species to shift toward an acorn-enriched diet during years of mast seeding. However, acorns may also be considered as a nutritionally imbalanced food item – *i.e.* food that does not contain the same balance of nutrients as needed by the animal to reach the intake target (Simpson & Raubenheimer, 2011) – due to its low protein content (Kirkpatrick & Pekins, 2003). It has indeed been shown that species that consume a high proportion of acorns may exhibit a negative nitrogen balance (Harlow *et al.*, 1975; Kirkpatrick & Pekins, 2003). The nutrient balancing hypothesis predicts that when sufficient food is available, the animal’s goal is to reach a nutritionally balanced diet (Simpson & Raubenheimer, 2011). Under that perspective, deer would thus have to compensate acorn consumption with complementary food items that are rich in nitrogen. Acorns are also rich in tannins, secondary metabolites known to deter herbivores by lowering the digestibility and nutritional value of plant tissues (Iason, 2005). Cervids have been shown to be relatively tolerant to plant secondary metabolites such as tannins (Iason & Villalba, 2006), notably roe deer due to its salivary proteins that may bind with tannins (Tixier *et al.*, 1997a). However, the ingestion of high levels of tannins comes with a cost (e.g. cost of detoxification) (Iason & Villalba, 2006) and whether this resource is sufficiently beneficial for red and roe deer to induce a dietary shift is still debated. Several studies have documented that acorns may dominate the diet of white-tailed deer (*Odocoileus virginianus*) (Harlow *et al.*, 1975; McShea & Schwede, 1993), red deer (Picard *et al.*, 1991) and roe deer (Abbas *et al.*, 2011) in years

of mast seeding. However, most of these studies were conducted over a period that did not exceed three years and were limited to a binary comparison of mast years vs. non-mast years, without any quantification of the magnitude of oak fructification. To our knowledge, an analysis of the relationship between the magnitude of oak fructification and deer diet is still lacking.

The recent increase of deer populations in most northern hemisphere countries, and especially the damage that they cause on young forest stands is a major issue for sustainable forest management (Beguin *et al.*, 2016; Côté *et al.*, 2004). A modification of red and roe deer diets in years of mast seeding is likely to change their consumption of forest vegetation, both in composition and intensity. Understanding how oak mast seeding shapes red and roe deer diet is thus critical to assess the consequences of this phenomenon on the forest damage caused by the two species. The issue is all the more important as several studies have reported that oak fructification is determined by spring weather conditions: mast-seeding frequency is thus likely to be sensitive to changes in climate conditions (Koenig *et al.*, 1996; Schermer *et al.*, 2018). In the context of a long-term monitoring of red and roe deer rumen content and oak fructification in La Petite Pierre National Hunting and Wildlife Reserve (NHWR), we will examine the following hypotheses:

- *H1*: Because of their high energetic content and digestibility, acorns are highly consumed by both deer species during years of mast seeding, especially in October, at the peak of acorn availability.
- *H2*: Red deer consumes a higher proportion of acorns than roe deer during mast years, due to its better ability to adapt to fluctuating resources.
- *H3*: To compensate for the acorn's low protein content, acorn consumption affects red and roe deer diet in favor of the more nutritious items in autumn and winter – i.e. mainly bramble for roe deer and bramble and grass for red deer (Dumont *et al.*, 2005).

3.3 Materials and methods

3.3.1 Study area

La Petite Pierre National Hunting and Wildlife Reserve (hereinafter referred to as “LPP”) is a 2.674 ha unfenced forest located in the Vosges mountain range, in northeast France (48.5°N, 7.0°E). The climate is continental with oceanic influences, involving cool summers and mild winters: mean January and July temperatures since 1986 at the Phalsbourg weather station, located 10 km from LPP, are respectively 1.35 °C and 19.0 °C (data from

Météo France). Snow accumulation is rare. The mean elevation is 300 m and the topography is characterized by a succession of small hills and steep-sided valleys. The sandstone substrate produces poor acidic soils; the vegetation is thus characterized by a low diversity and low nutritional quality for herbivores. The forest is structured in even-aged clusters of trees, and includes roughly an equal proportion of broadleaved (mainly common beech *Fagus sylvatica* and sessile oak) and coniferous (mainly silver fir *Abies alba*, Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*) tree species. Free-ranging populations of red deer, roe deer and wild boar are present in LPP. The reserve is free of big game predators and ungulate populations are managed through hunting, with an average of 48 (min: 24, max: 102) red deer and 43 (min: 19, max: 88) roe deer harvested per year since 1986. The annual population dynamics of red deer in LPP estimated using the capture-mark-recapture method from 1986 to 2018 are presented in the appendices, section 3.8.2

3.3.2 Diet analysis

We analyzed rumen samples taken from red deer and roe deer shot by hunters in LPP during the legal hunting season (from the beginning of October to the end of January). All samples came from animals tagged with annual hunting quotas delivered by the county prefect in compliance with the French Environmental Code (Art. R425-2 to 425-14113). The animals were not harvested following a protocol specific to this study. From 1986 to 2018, a total of 330 and 231 samples of red and roe deer rumen, respectively, had been collected. The number of rumen analyzed per year for each species is indicated Fig. 1.B. We noted the exact date of harvest for each culled animal. The inter-annual fluctuations in the number of rumen analyzed per year are the results of the management of deer populations in the NHWR that lead to fluctuations in the number of animals shot per year, a shortage of staff to collect and analyze the rumen before 2005, and occasional extreme climatic events (e.g. Lothar storm in December 1999) that could lead to an absence of harvest in some years.

For each culled individual, 500 g of rumen were frozen until analysis. Once defrosted, the samples were washed and sieved through a 5-mm mesh. The material is sieved to avoid an overrepresentation of the larger particles (Chamrad & Box, 1964), that are harder to digest and that occupy more space (note that sieving could however lead to a slight underestimation of certain food items such as lignified fragments). The rumen content was also carefully mixed to ensure that all items were randomly distributed. The material was then sorted macroscopically using a method derived from the point-frame technique developed by (Chamrad & Box, 1964): a portion of the sieved items was mixed with water and placed in a rectangular tray. A grid with 100 intersection points at the bottom of the tray allowed the selection of 100 items (appendices, section 3.8.5), which were identified to the lowest possible taxon using a binocular loupe and a reference collection of the local flora. This pro-

cess was repeated 3 times so that 300 items could be identified per rumen. The proportion of a given taxon in a rumen was computed as a percentage of occurrence of the taxon in the rumen. It has been shown by Dubois (1992) that this percentage of occurrence was not significantly different from the percentage obtained when the whole rumen sample was analyzed, nor from the weighted percentage obtained after drying and weighing the 300 items.

For the purpose of the analysis, we grouped all the taxa in 15 food categories: acorns, shrub leaves, conifer needles, grasses, dry fruits, fern, deciduous leaves, crops, fungi, dicotyledonous herbaceous species, buds, bryophytes, animal fragments, unidentified and others. For each rumen analyzed, the proportion of a given food category in the diet was computed as the sum of the proportions of all the taxa that belonged to the food category. The main taxa of each food category are listed in the appendices, section 3.8.4

As the acorns were partly digested, genetic analyses would have been necessary to identify the oak species (sessile or pedunculate). Although sessile oak is far more abundant than pedunculate oak in the studied forest, the category ‘acorns’ thus includes the fruits of both oak species.

3.3.3 Oak fruit production

3.3.3.1 Direct measurements

Sessile oak fructification was measured in LPP with the “ground-plot counting method” (Touzot *et al.*, 2018), which consists in counting acorns on the ground under the tree crown in quadrats of known area and without protection against seed predators. For each monitored oak tree, 4 quadrats of 0.25 m^2 (0.5 m x 0.5 m) were placed at a distance of 1 m to 4 m from the trunk. Soon after the main acorn drop which generally occurs in the first two weeks of October, we gathered and counted the fruits collected in the four quadrats to obtain a number of acorns sampled per tree. From 2010 to 2017, 30 trees were monitored with this method in LPP. Selected trees were located at a sufficient distance from any other mature oak tree to avoid any potential contamination from any adjacent tree during the counting: they were selected randomly and no criteria on the characteristics of the trees (*e.g.* height, diameter, shape of the tree crown) were taken into account. The fructification f_i for a given year i was computed as the mean number of acorns sampled per tree:

$$f_i = \frac{\sum_{y=1}^{30} t_{y,i}}{30} \quad (3.1)$$

Where $t_{y,i}$ represents the number of acorns sampled for tree y in year i .

This value was divided by the maximum fructification observed at LPP during the study

period to obtain a relative fructification F_i , ranging between zero and 1.

$$F_i = \frac{f_i}{\max[f_{2010}, \dots, f_{2017}]} \quad (3.2)$$

In addition, a categorical variable reflecting relative fructification was created, with three classes corresponding to increasing F_i values: low ($F_i < 0.15$), partial ($0.15 \leq F_i \leq 0.6$) and high ($F_i > 0.6$) relative fructification.

3.3.3.2 Modelling oak mast seeding in LPP

The aim was to complete the eight years of fructification monitoring in LPP by modeling additional years. [Schermer *et al.* \(2018\)](#) identified April temperature and the previous year's fructification as the two main factors explaining oak mast seeding using a long-term monitoring of oak fructification in 30 sites of the European network RENECOFOR from 1993 to 2008 ([Ulrich, 1995](#)). Based on this result, we integrated the fructification data of LPP and of four of the RENECOFOR sites that were located within a 200 km radius in a predictive Bayesian model with April temperature and previous-year fructification as explanatory variables. Note that this model predicts a relative fructification, ranging between zero and 1. As the previous year's fructification was included in the model, the model is considered first order autoregressive – *i.e.* the precision of the prediction decreases for each additional year predicted. For this reason, we only kept for analysis the two first years (2008 and 2009). Finally, a total of 10 years (2 years with modeled fructification and 8 years with observed fructification) were available for the study. The predictive model is presented in detail in the appendices, section 3.8.3.

3.3.4 Data analysis

3.3.4.1 Effect of oak fructification on the mean acorn proportion in red and roe deer diet

We analyzed the relationships between the relative fructification of oak and the mean annual acorn consumption of red deer and roe deer using a linear mixed-effect model (lme4 package) ([Bates *et al.*, 2014](#)) with two fixed effects (fructification and deer species) and one random effect (hunting season). We tested the significance of the effects using a type II Wald χ^2 test using the Anova function in the “car” package of R ([Fox *et al.*, 2012](#)). An interaction between the two fixed effects was included in the model. To fit the assumption of normality for the error distribution, the annual acorn consumption was arcsine square root transformed prior to analysis ([Zar, 1984](#)). For each species, we excluded from this analysis the years with less than 4 individuals. Oak fructification is characterized by significant tem-

poral autocorrelations that we quantified in the Bayesian model (appendices, section 3.8.3, fig. 3.7). We checked that these temporal autocorrelations did not affect our linear model by examining the model residuals.

Intra-annual variations in the proportion of acorns in the diet were analyzed and compared for the two deer species on the month scale. Intra-annual variations were assumed to depend on the total annual amount of available resources, the analyses were thus performed separately for years with low ($n = 6$), partial ($n = 3$) and high ($n = 1$) relative fructification. For each of the three categories of relative fructification, we conducted a two-way ANOVA to test the effect of species (factor with two levels: “red deer” and “roe deer”), month (ordered factor with four levels: “October”, “November”, “December” and “January”) on the proportion of acorns in the diet. For each class of relative fructification, an interaction between the two factors was included. In the case of a significant effect of the month, we tested the differences between the four levels of this factor with Tukey’s HSD test.

3.3.4.2 Effect of acorn consumption on red deer and roe deer feeding behavior

The aim was to investigate whether the main resources consumed by red and roe deer were favored or discriminated against when the proportion of acorns increased in the diet. In a first step, we determined which of the 15 food categories were the most consumed by each deer species. We defined $\gamma[red]_{i,k}$ and $\gamma[roe]_{i,k}$ as the proportion of the food category i ($i \in [1; \dots; 15]$) in the rumen k for red deer and roe deer, respectively. We computed the total proportion of each food category i in the diet of red deer ($\Gamma[red]_i$) and roe deer ($\Gamma[roe]_i$) as:

$$\begin{cases} \Gamma[red]_i = \frac{\sum_{k=1}^{n_{red}=330} \gamma[red]_{i,k}}{\sum_{j=1}^{15} \sum_{k=1}^{n_{red}=330} \gamma[red]_{i,k}} = \frac{\sum_{k=1}^{n_{red}=330} \gamma[red]_{i,k}}{330} \\ \Gamma[roe]_i = \frac{\sum_{k=1}^{n_{roe}=231} \gamma[roe]_{i,k}}{\sum_{j=1}^{15} \sum_{k=1}^{n_{roe}=231} \gamma[roe]_{i,k}} = \frac{\sum_{k=1}^{n_{roe}=231} \gamma[roe]_{i,k}}{231} \end{cases} \quad (3.3)$$

Where n_{red} and n_{roe} are the respective numbers of red and roe deer rumens collected. The computed proportions of each category are presented in the appendices, section 3.8.4, table 3.3. We only selected for this analysis the categories that represented on average more than 5% of the diet of a given deer species ($\Gamma[red] > 5\%$ or $\Gamma[roe] > 5\%$). The categories “others” and “unidentified” were not included, nor was the “acorns” category. N_{red} and N_{roe} food categories represented more than 5% of red and roe deer diet, respectively. To restrict the analysis to these categories, we computed the relative proportions of each selected category i in the rumen k ($\gamma'[red]_{i,k}$ and $\gamma'[roe]_{i,k}$) so that for each rumen, the relative proportions of the N selected categories add up to 1:

$$\begin{cases} \gamma'[\text{red}]_{i,k} = \frac{\gamma[\text{red}]_{i,k}}{\sum_{j=1}^{N_{\text{red}}} \gamma[\text{red}]_{j,k}} \\ \gamma'[\text{roe}]_{i,k} = \frac{\gamma[\text{roe}]_{i,k}}{\sum_{j=1}^{N_{\text{roe}}} \gamma[\text{roe}]_{j,k}} \end{cases} \quad (3.4)$$

Since for each rumen, the relative proportions of the selected food categories add up to 1, we studied the effect of acorn proportion in the diet (γ_{Acorn}) on these proportions with a multinomial Dirichlet regression. We fitted for each deer species the following Dirichlet multinomial regression model on a system with N equations :

$$\begin{cases} \ln(\gamma'_1) = \alpha_1 + \beta_1 * \ln(\gamma_{\text{Acorn}}) \\ \dots \\ \ln(\gamma'_i) = \alpha_i + \beta_i * \ln(\gamma_{\text{Acorn}}) \\ \dots \\ \ln(\gamma'_N) = \alpha_N + \beta_N * \ln(\gamma_{\text{Acorn}}) \end{cases} \quad (3.5)$$

We used the R package “DirichletReg” (Maier, 2014) to run the Dirichlet multinomial regression models. All the analyses were performed with the R statistical framework (RCoreTeam, 2019).

3.4 Results

3.4.1 Inter-annual variations of acorn consumption and oak fructification

From 2008 to 2017, oak fructification in LPP exhibited high inter-annual fluctuations (Fig. 3.1.A). The maximum fructification in the study site occurred during the hunting season 2011/2012 ($109 \text{ acorns.m}^{-2}$, relative fructification = 1). The following year, oak fructification reached a minimum of 0 acorns.m^{-2} (relative fructification = 0). From 1986 to 2017, acorns represented on average 9.4% and 4.2% of the red and roe deer diet, respectively. The peak of oak fructification (hunting season 2011/2012) in LPP matched the peak of acorn consumption for both deer species (Fig. 3.1). In that season, acorns represented on average 52% and 34% of red and roe deer diet, respectively. At the inter-annual scale, the proportion of acorns in the diet was 15% higher on average ($p < 0.001$) in red deer than in roe deer. Mean acorn proportion in the diet significantly increased with oak fructification ($p < 0.001$), with a higher slope for red deer ($p = 0.027$) (appendices, section 3.8.1 fig. 3.6 and section 3.8.6 table 3.4).

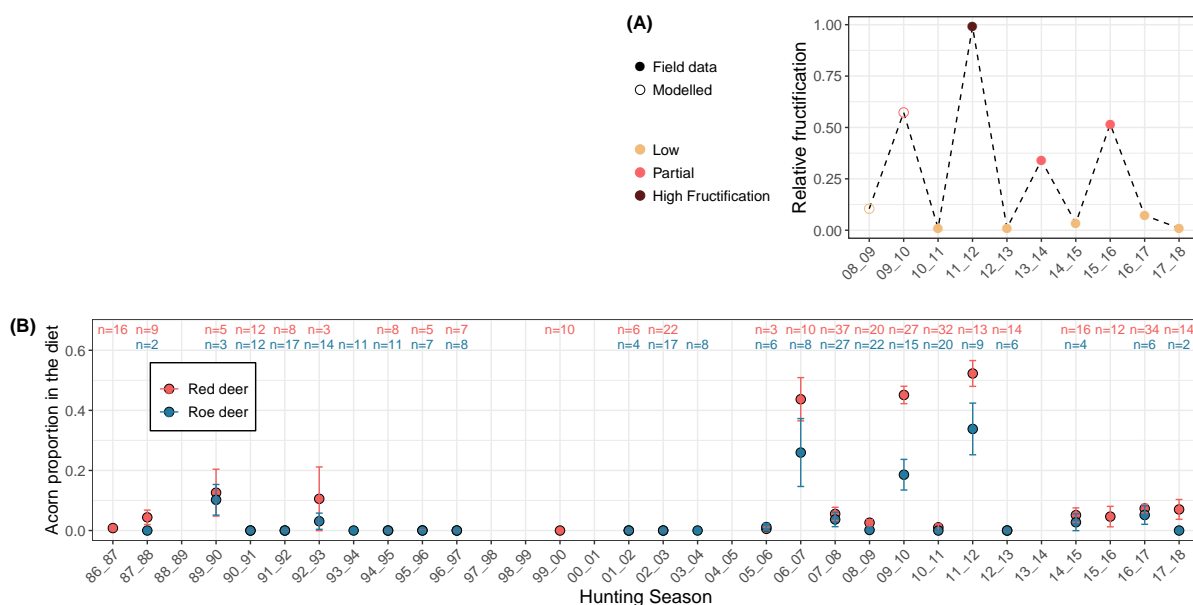


Figure 3.1: Inter-annual variations in (A) oak relative fructification and (B) the proportion of acorn in red deer and roe deer diet. Fructifications values are given as the proportion of acorns counted for a given year with the ground-plot method (Touzot *et al.*, 2018) relative to the maximum ever counted at that site (mean \pm standard error). Years are presented as hunting seasons to allow comparison between the two graphs.

3.4.2 Intra-annual variations in acorn consumption

On the intra-annual scale, the proportion of acorns in the red deer diet was also higher than in the roe deer diet in a context of low ($p = 0.005$), partial ($p = 0.018$) and high ($p = 0.034$) relative fructification (Fig. 3.2; appendices, section 3.8.6, table 3.5). The interaction between deer species and month was not significant in years of low ($p = 0.58$), partial ($p = 0.49$) or high ($p = 0.16$) fructification (appendices, section 3.8.6, table 3.5), which means that for the three classes of relative fructification, red deer consumed a higher proportion of acorns than did roe deer throughout the hunting season. In years of low relative fructification, acorns represented an average of 4% and 1% of red and roe deer diet, respectively, and remained stable from October to January ($p = 0.43$) for both deer species. In years of partial relative fructification, the proportion of acorns in the diet of both deer species was lower in December and January than in October and November ($p < 0.001$). Red and roe deer respectively consumed 47% and 34% of acorns in October, while these proportions decreased to respectively 14% and 15% in January (Fig. 3.2). In the context of high relative fructification, acorn proportion remained stable throughout the hunting season in red and roe deer diet ($p = 0.13$), with an average proportion of 52% and 34%, respectively.

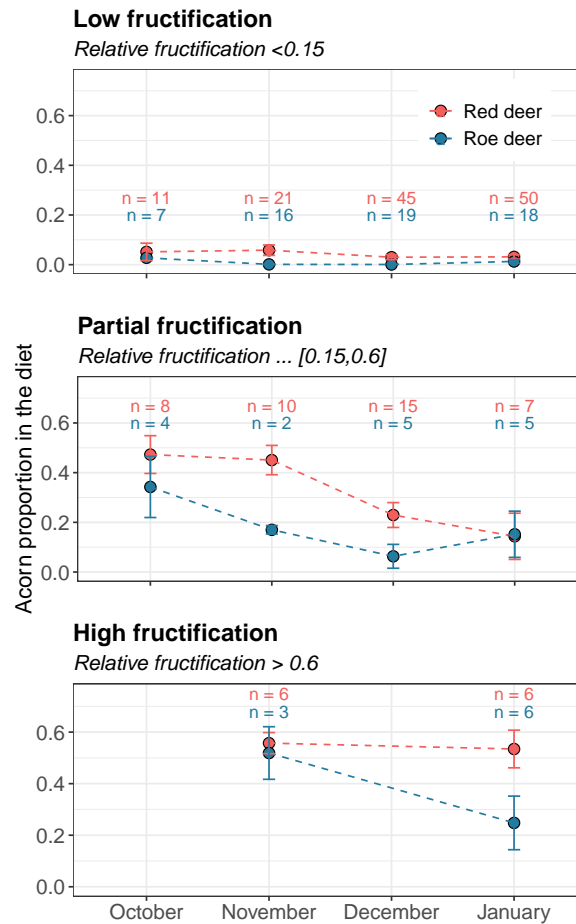


Figure 3.2: Intra-annual variation in the proportion of acorns in red deer and roe deer diet (mean \pm standard error) for different fructification levels. Months with $n < 2$ were removed from the dataset.

3.4.3 Effect of acorn consumption on red and roe deer feeding behavior

For red deer, 4 out of the 14 food categories represented more than 5% of the species' diet, and were therefore selected for the analysis: shrub leaves, conifer needles, grasses, and ferns (appendices, section 3.8.4). Fig. 3.3 shows the relationship between the relative proportion (γ') of these four food categories and the proportion of acorn in the diet, and the fitted Dirichlet regressions. The multinomial Dirichlet regression conducted for red deer indicates that the relative proportion of conifer needles significantly decreased when the proportion of acorns in the diet increased, while the relative proportion of grasses significantly increased (Table 3.1). The fitted model indicated that when acorns were marginal in the diet (acorn proportion $\leq 1\%$), red deer mainly consumed shrub leaves ($\gamma' = 43\%$) and conifer needles ($\gamma' = 29\%$), while ferns ($\gamma' = 12\%$) and grasses ($\gamma' = 16\%$) only represented a minor part of the diet. In contrast, acorn-enriched rumens of red deer contained almost

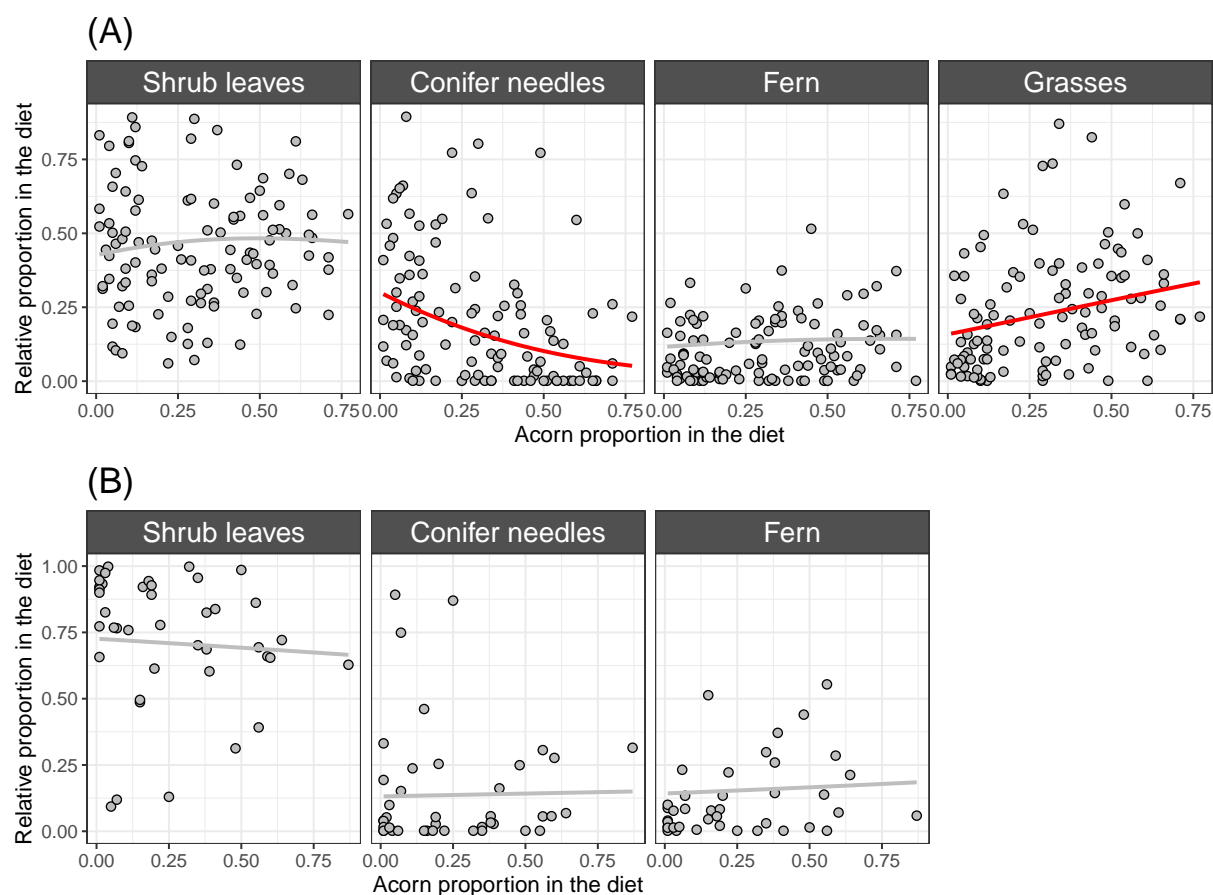


Figure 3.3: Relative proportions of the main food categories consumed, in relationship with the proportion of acorn in the diets of (A) red deer and (B) roe deer. The lines represents the fitted Dirichlet regression model (Eq. 3.5). Red lines indicate significant relationships ($p < 0.05$). Model results for each food category are presented in Table 3.1.

as much grasses ($\gamma' = 34\%$) as shrub leaves ($\gamma' = 47\%$) while conifer needles ($\gamma' = 5\%$) were almost absent from the diet (Fig. 3.3).

3.5 Discussion

3.5.1 Oak fructification as a major determinant of deer diet

Oak mast seeding is a characteristic example of resource pulse that may lead to a significant dietary shift for several generalist consumers (Herrero *et al.*, 2005; McDonald & Fuller, 2005; Sato & Endo, 2006). Although deer are known for consuming mainly plant tissues (Dumont *et al.*, 2005; Storms *et al.*, 2008; Tixier *et al.*, 1997a), our study confirmed that both red and roe deer shifted their diet to an acorn-enriched one in a context of oak mast seeding, consistently with our hypothesis (H1). When the peak of fructification occurred, acorns represented more than half of the red deer diet (52%), which is consistent with the propor-

Table 3.1: α_2 coefficient statistics from Dirichlet regression of the model referring to Eq. 3.5 for estimating the relative proportion of the main resources consumed by red deer and roe deer with the proportion of acorns in the diet.

	Red deer			Roe deer		
	Estimate	SE	p-value	Estimate	SE	p-value
Shrub leaves	0.3772	0.4946	0.45	0.5907	0.8868	0.51
Conifer needles	-2.0366	0.4788	<0.001*	0.8428	0.8405	0.316
Fern	0.5215	0.4604	0.26	0.9886	0.7215	0.171
Grasses	1.2168	0.4456	0.006*			

tions found in the study of [Picard *et al.* \(1991\)](#) in a context of oak mast seeding (50.8%). In addition, it is likely that in both cases, these proportions were underestimated as they were obtained with rumen content analyses, a technique which is known for overestimating poorly digestible items (e.g. grasses, woody shoots or dead leaves) and for underestimating the most digestible portions of the diet (e.g. forbs, acorns) ([McInnis *et al.*, 1983](#)). Our study also provides evidence that in a context of partial fructification, acorns still represent a large part of the red and roe deer diet. This result suggests that this resource is particularly palatable for both deer species. Considering the daily quantity of food ingested by both deer species ([Brown, 1992](#)), the proportions of acorn found in deer diet also indicates that at high densities, red and roe deer may strongly contribute to acorn predation in temperate forests, along with boars, rodents and birds ([den Ouden *et al.*, 2005](#)). Several authors have discussed the potential benefits of an acorn-enriched diet for their consumers. [Pekins & Mautz \(1988\)](#) and [Harlow *et al.* \(1975\)](#) showed that the consumption of acorns by white-tailed deer instead of wintergreen leads to a strong increase in metabolizable energy per gram, resulting in a reduced foraging time and the meeting of energy requirements in winter. [McDonald & Fuller \(2005\)](#) also reported a positive effect of acorn consumption on milk quality for black bear females. In the case of red and roe deer, the consequences of acorn consumption are still poorly documented and deserve further investigation as it could have positive effects on the population dynamics of these species, as reported for wild boar ([Bieber & Ruf, 2005](#)).

In the case of partial fructifications, we observed an intra-annual variability in acorn consumption for both deer species: consistently with our initial hypothesis (H1), acorn proportion in the diet was higher in October and in November, the month of the main acorn drop and the following. The main assumption to explain this pattern is a depletion of the acorn stock from October to January due to predation by deer ([Harlow *et al.*, 1975](#); [Tixier & Duncan, 1996](#)) but also by the other seed consumers such as wild boars ([Herrera, 1995](#)), rodents or jays ([den Ouden *et al.*, 2005](#); [Steele *et al.*, 1993](#)). Under this assumption, this result suggests that a partial fructification is not sufficient to induce a satiation of the seed predators ([Kelly, 1994](#)) and therefore that a large proportion of all acorns available is consumed. Consequently, the low remaining quantity of acorns might not be sufficient to ensure the

regeneration success of oak stands. An alternative hypothesis is that the palatability and/or the nutritional value of acorns decreased from October to January due to a fast degradation of acorn tissues when lying on the soil. [Tejerina et al. \(2011\)](#) showed that in the case of holm oak (*Quercus ilex*) the content in several phenolic compounds increased throughout autumn and winter, probably due to the process of ripening and germination. Acorns are also more likely to be rotten or damaged by pathogens at a more advanced stage of the acorn crop season. Despite this potential decrease in acorn palatability, it is noteworthy that in the case of high fructification, acorn consumption remained stable until January for both species (Fig. 3.2). This observation provides strong support for the resource depletion hypothesis as an explanation for the decrease in the proportion of acorns in the diet observed after November in years of partial fructification. This phenomenon could also be interpreted as a factual argument supporting the predator satiation hypothesis as a possible evolutionary explanation for mast seeding ([Ims, 1990](#); [Kelly, 1994](#)). Indeed, the predator satiation hypothesis assumes that seed predators exhibit a type II or type III functional response, *i.e.* at high seed densities, the proportion of attacked seeds should decrease with increasing seed densities ([Bogdziewicz et al., 2018a](#); [Moreira et al., 2017](#)). In our study, as the main acorn drop occurs in October, the acorn density necessarily decreases from October to January because of predation. Under the assumption that acorn proportion in deer diet reflects the quantity of acorns consumed, a constant acorn consumption throughout this period – as observed in a context of high fructification – would indicate that the proportion of predated acorns decreases with acorn density. Our results therefore seem to confirm that the red and roe deer’s diet modification in response to mast seeding is compatible with the predator satiation hypothesis.

3.5.2 Interspecific differences in acorn consumption

At both the intra-annual (Fig. 3.2) and inter-annual scale (Fig. 3.1 and appendices section 3.8.1 fig. 3.6), we found a higher acorn proportion in the red deer diet than in the roe deer diet, in agreement with our initial hypothesis (H2). This pattern is most likely related to the digestive morphology of the two studied species. As an intermediate feeder, red deer has been shown to be highly adapted to fluctuations in resource availability ([Storms et al., 2008](#)). In winter, in a context of scarce resources, this species switches to a grass-based diet, despite the high fiber content of this resource ([Dumont et al., 2005](#); [Redjadj et al., 2014](#)). In contrast, as a browser, roe deer is far more selective and has a more restricted feeding niche ([Tixier et al., 1998](#)). The higher flexibility of red deer may partly explain why it exploits the sudden increase of resource availability to a greater extent than roe deer. In addition, while although acorn pulp has been shown to be highly digestible, the shell, also ingested by deer, is poorly digestible and rich in fibers ([Kirkpatrick & Pekins, 2003](#)). Since roe deer is unable to feed on poorly digestible items, we may assume that the acorn shell’s nutritional

characteristics prevent roe deer from consuming a high proportion of acorns, while red deer is not limited thanks to its more flexible stomach structure. This result could also be interpreted under the framework of the nutrient balancing hypothesis (Simpson & Raubenheimer, 2011): red deer's consumption of significant portions of grass tissues with a very low secondary metabolites content might balance for acorn high tannin content. On the other hand, due to the high secondary metabolite content in the food items preferred by roe deer (*i.e.* deciduous leaves, dicot herbs), this species would not be able to compensate for the high input of tannins by acorns. Interspecific differences in acorn consumption may also be explained by the nutritional requirements of the two studied species. Indeed, red deer are classified as capital breeders as they rely on fat stored during summer and autumn to face winter; while roe deer are income breeders and are unable to store fat reserves (Brown, 1992). The main nutritional property of acorns is their high energetic content (Kirkpatrick & Pekins, 2003) and this resource is mainly available in autumn. We may therefore assume that consuming acorns may be more beneficial for red deer by providing extra fat reserves for winter.

3.5.3 Consequences of acorn consumption on deer feeding behavior

Our analyses of the composition of red and roe deer diets were consistent with their respective feeding types. Red deer has a diverse diet that included fiber-rich items such as grasses while, as reported in other studies (Storms *et al.*, 2008; Tixier *et al.*, 1997a), roe deer has a poorly diversified bramble-based diet (appendices, section 3.8.4), one of the most digestible species available in winter (Dumont *et al.*, 2005). The proportions of all the items consumed are likely to decrease with an increasing proportion of acorns in the diet. Nevertheless, it is critical to understand whether acorns, due to their nutritional characteristics, change the relative proportions of these resources in deer diet in order to assess whether some plant species will be more affected than others by increased acorn availability.

Our results showed that increased acorn consumption strongly reduced the proportion of conifer shoots in the red deer diet, as they were partly replaced by grasses, in agreement with our hypothesis (H3). Indeed, although the energetic content of acorns is higher than that of most items available in autumn and winter, their protein content is relatively low and animals that consume acorns may exhibit a negative nitrogen balance (Abbas *et al.*, 2011; Kirkpatrick & Pekins, 2003). In winter, grasses have been shown to be more nutritious than the conifer species present in the study area (*i.e.* silver fir, Norway spruce and Scots pine) (Dumont *et al.*, 2005). In the framework of the nutrient balancing hypothesis, grasses and acorns could be seen as nutritionally complementary food items – *i.e.* combination of nutritionally imbalanced foods that jointly enable animals to reach their nutrient

intake target (Simpson & Raubenheimer, 2011). Switching from conifer shoots to grasses would allow red deer to benefit from the energetic content of acorns while maintaining a positive nitrogen balance. This result could thus be interpreted as an argument supporting the nutrient balancing hypothesis, along with similar dietary shifts that have been observed in moose when provided with supplementary feeding (Felton *et al.*, 2016a,b).

Surprisingly, roe deer's diet composition was not affected by acorn consumption. This may be explained by the fact that unlike red deer, acorn proportion rarely exceeded 50% in the roe deer diet, which lowered the risk of a nitrogen imbalance for this species. In addition, the main items consumed by roe deer – i.e. bramble, conifer shoots and ferns – have a relatively similar protein content (Gonzalez-Hernandez & Silva-Pando, 2007), and mostly differ in their digestibility (Dumont *et al.*, 2005). Previous studies have shown that red deer has a more diversified diet and is better able to adapt its feeding behavior in a context of resource scarcity than roe deer due to different digestive physiologies (Richard *et al.*, 2010; Storms *et al.*, 2008). Our results therefore support the idea that in the context of a resource pulse, although both species adapt their feeding behavior, red deer shows more flexibility to benefit from the increased resource availability.

3.6 Conclusion

Resource pulse events such as oak mast seeding are known to have a major influence on ecosystem functioning but these events are inherently difficult to study due to their rare occurrence. Based on oak-deer interactions, we showed that oak mast seeding, by providing a significant alternative forage in a period of low resource availability, induced a dietary shift for both red and roe deer. These two species included large proportions of acorns in their diet whenever this resource was available. We also provided evidence that red deer, owing to its broader feeding niche, showed more flexibility than roe deer in its diet to exploit the resource pulse by including a larger proportion of acorns and by adapting the relative proportion of other resources consumed. Red deer dietary shift from conifer – economically valuable trees – to grass suggests that mast seeding could lead to a short-term reduction of the forest damages caused by deer, which would have significant implications for forest management. Nevertheless, further studies should test whether red deer dietary shift is sufficient to affect the browsing damages caused by this species. In addition, if acorn consumption were to benefit deer reproductive success as it has been shown for wild boar (Bieber & Ruf, 2005), in years following mast seeding, higher damages could be expected to occur due to a combination of resource scarcity and increased deer population. Further studies should thus be carried out to better understand how mast seeding may affect deer populations. More generally, as resource pulses like mast seeding are likely to be sensitive to climate change, there is an increasing need for long-term studies on the consequences of

these events for temperate forest ecosystem functioning.

3.7 Acknowledgments

We thank all the agents of the French Office for Biodiversity (OFB) and of the French National Forest Agency (ONF) who collected or analyzed the rumen content, especially Jean-Luc Hamann. We thank all hunters, wildlife technicians, students and volunteers who helped us in the field and in the laboratory analyses. We are also grateful to Clément Calenge and Samuel Soubeyrand for their help in the development of the Bayesian model and to Catherine Carter for correcting the linguistic mistakes. This study was conducted in the context of a PhD co-funded by the OFB and the ONF under partnership agreement CNV-REC-2018-07. This work was also supported by the Ministry of Agriculture (MAA) [convention E12-2018], and the French National Research Agency (ANR) as part of the "Investissements d'Avenir" program [ANR-11-LABX-0002-01, Laboratory of Excellence AR-BRE].

3.8 Appendices

3.8.1 Relationship between acorn consumption by red deer and roe deer and oak fructification

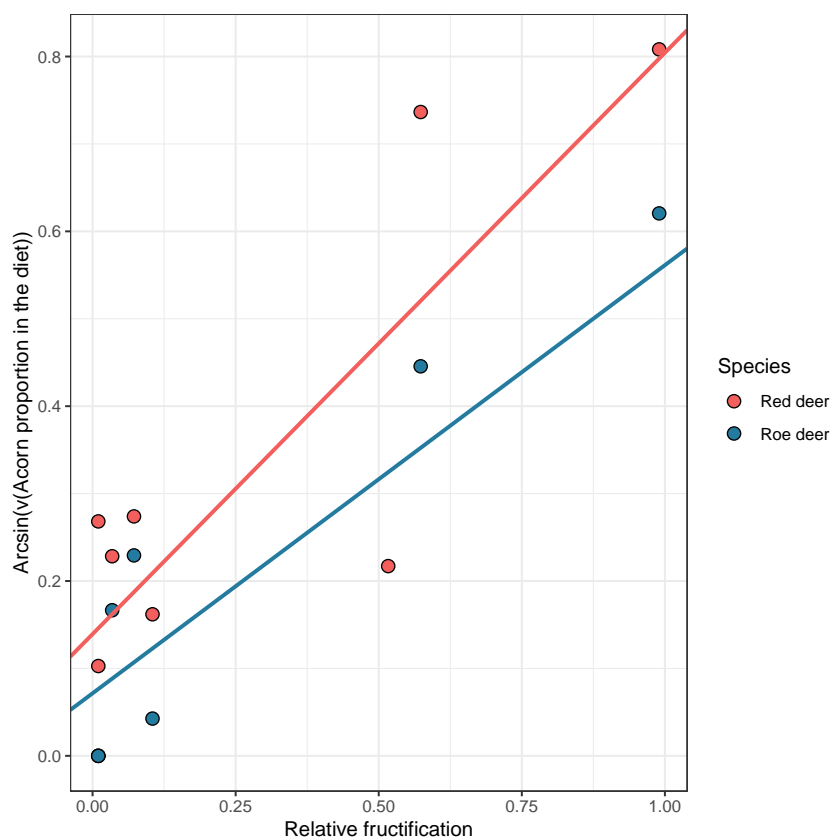


Figure 3.4: Relationship between the mean annual acorn consumption by red deer and roe deer and the relative fruiting intensity. Mean acorn consumption was arcsine square root transformed prior to the analysis. Regression curves were adjusted from the mixed model [Acorn consumption ~ Fructification + Species + (1|Year)].

3.8.2 Population dynamics of red deer in La Petite Pierre NHWR

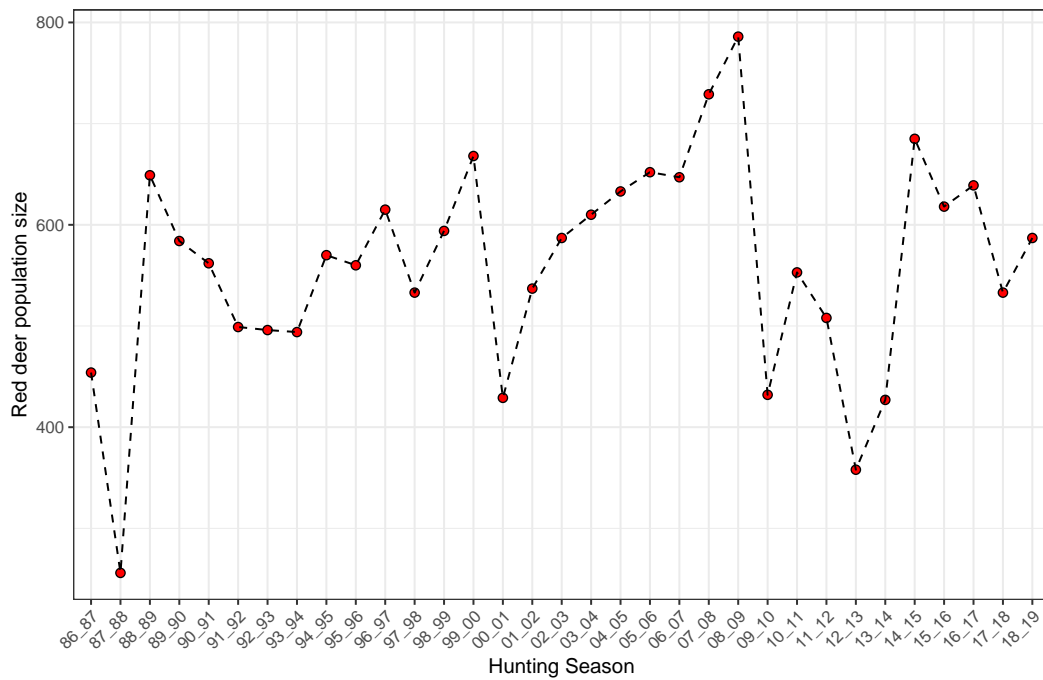


Figure 3.5: Yearly dynamics of red deer population size in LPP from 1986 to 2018. Red deer population size was estimated using the capture-mark-recapture method. Years are expressed in hunting season to facilitate the comparison with the other figures of the paper.

3.8.3 Presentation of the Bayesian model used to predict oak fructification in La Petite Pierre NHWR

3.8.3.1 Observations

Fructification monitoring in LPP is described in the main manuscript (section 3.3.3.1). In each of the RENECOFOR sites (Table C.1), ten non-neighboring sessile oak trees were equipped with a 0.5m² raised litter-fall trap that collected the mature acorns. The acorns collected in these 10 traps were gathered and counted in each site. The number of acorns counted per site from 1993 to 2008 was standardized from 0 to 1 relatively to the maximum number of acorns ever counted at each site (eq. 3.2) in order to allow comparison between the different sites.

Table 3.2: Location of the five RENECOFOR sites included in the Bayesian model.

Site	Altitude	Longitude	Distance from LPP
CHS57B	49°00'59	7°27'45	20 km
CHS88	48°16'17	5°95'40	140 km
CHS51	48°01'36	6°02'24	200 km
CHS68	47°41'33	7°28'06	140 km

Mean April temperature for each RENECOFOR site was extracted from the SAFRAN spatially explicit database (8 x 8 km grid) (Vidal *et al.*, 2010). For the purpose of the analysis, all temperature data were standardized between 0 and 1, relative to the minimum and maximum April temperature ever observed in the 5 sites from 1993 to 2017.

3.8.3.2 Theoretical model

The relative fruiting intensity of a given tree population in the site k the year i ($F_{k,i}$) is driven by the mean April temperature in the year i on this site ($T_{k,i}$) and by the previous-year fructification ($F_{k,i-1}$) through the following model:

$$\begin{cases} F_{k,i} \sim \text{Beta}(\mu_{k,i} * \varphi_k, (1 - \mu_{k,i}) * \varphi_k) \\ \text{logit}(\mu_{k,i}) = \alpha_1 + \alpha_2 * T_{k,i} + \alpha_3 * F_{k,i-1} \end{cases} \quad (3.6)$$

Modeling fructification with a beta distribution is necessary as this variable ranges from 0 to 1 (Cribari-Neto & Zeileis, 2015). In the model, μ and φ respectively represent the mean of the beta distribution and a precision parameter (Ferrari & Cribari-Neto, 2004). Our model relies on the assumption that the beta regression parameters (α_1 , α_2 and α_3), which respectively represent the intercept, the effect of April temperature and the effect of the previous year fructification, are the same for the different study sites. We thus included in the same

model the four RENECOFOR sites and LPP, with the common regression parameters α_1 , α_2 and α_3 but a precision parameter φ_k specific to each site k .

The model was run from 1993 to 2017. Temperature data were available for all sites throughout the study period but, as specified above, fructification data were only available from 1993 to 2008 in the RENECOFOR sites and from 2010 to 2017 in LPP.

3.8.3.3 Model implementation

For the three regression parameters (α_1 , α_2 and α_3), we chose a normal prior distribution $N(0, 10)$. For the precision parameters φ of the five sites included in the model (φ_{57a} , φ_{68} , φ_{88} , φ_{51} and φ_{LPP}), we used an exponential prior $\text{Exp}(0.2)$. The estimation of the parameters and the prediction of fructifications were conducted using the JAGS software ([Plummer, 2003](#)) in the R environment ([RCoreTeam, 2019](#)). We ran three parallel Markov chains with 200000 iterations, a burn-in of 3000 and a thinning rate at 1.

3.8.3.4 Results

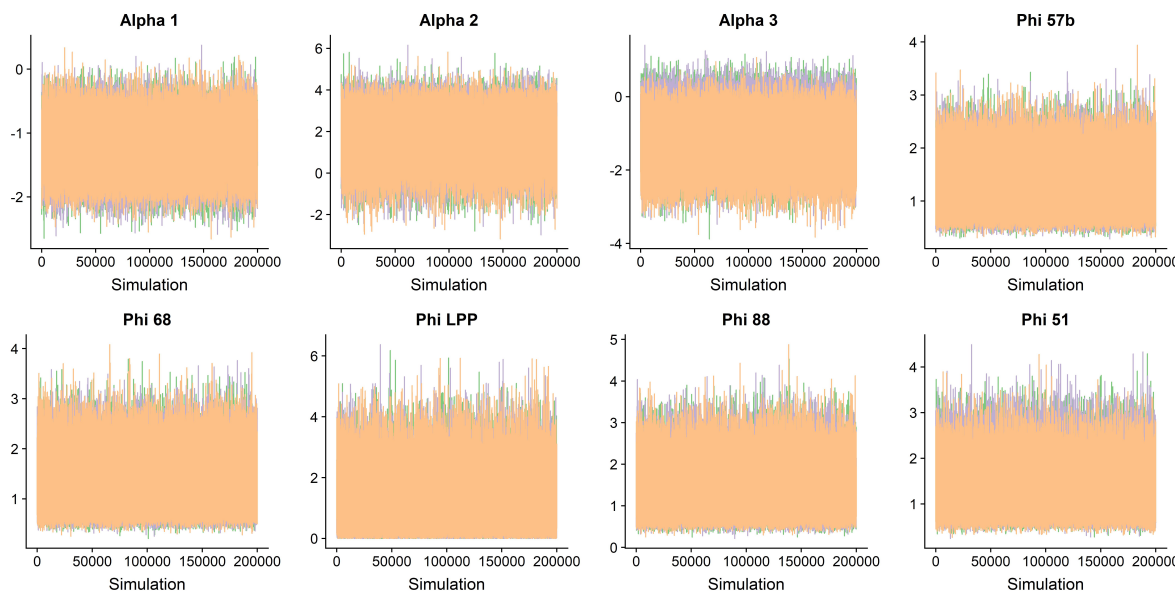


Figure 3.6: Convergence of the three Markov Chains for the eight parameters included in the model

The values of the potential reduction factor (Rhat) ranged between 1 and 1.02, which confirms the convergence of the three Markov chains for the eight parameters (α_1 , α_2 , α_3 , φ_{57a} , φ_{68} , φ_{88} , φ_{51} and φ_{LPP}) of the model (Fig. 3.6). Both of the explanatory factors included in the model (F_{i-1} and T_i) were highly informative and their value was consistent with the literature. α_2 had almost exclusively positive values (Fig. 3.7) which confirms that April temperature had a positive effect on oak fructification (Caignard *et al.*, 2017; Lebourgeois *et al.*, 2018; Schermer *et al.*, 2018). Inversely, α_3 was almost exclusively negative (Fig. 3.7), which indicates that the previous year's fructification had a negative impact on oak fructification (Schermer *et al.*, 2018).

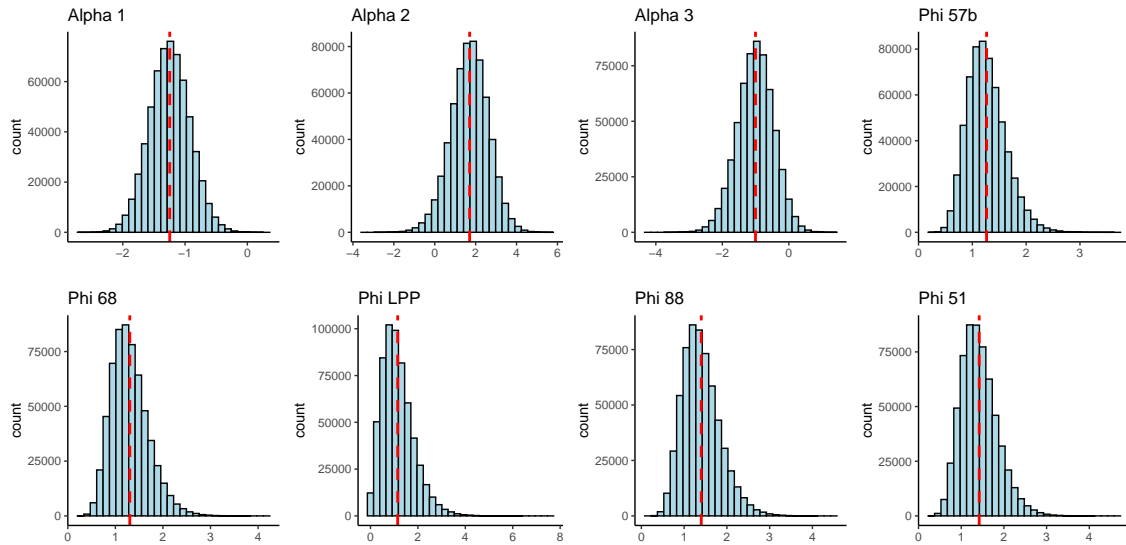


Figure 3.7: A posteriori distribution of the eight parameters of the model. The red dotted lines represent the mean.

The predicted fructifications in LPP in 2008 and 2009 are presented in Fig. 3.8. For each predicted year, the fructification value included in the rest of the analysis of the paper is the median of the predicted values.

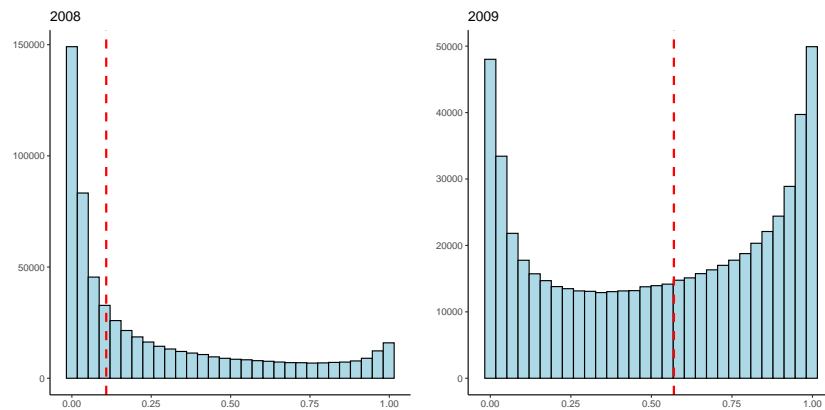


Figure 3.8: Distribution of the fructifications in LPP from 2008 to 2009 predicted by the Bayesian model. The red dotted lines represent the median of the predicted values.

3.8.4 Diet composition of red and roe deer

Table 3.3: Proportion of the different food categories in the diet of red deer and roe deer from 1986 to 2017 in LPP.

Food category	Main components / Species	Red deer	Roe deer
Shrub leaves	<i>Bramble, European Blueberry, common ivy, common mistletoe</i>	28.80%	60.67%
Conifer needles	<i>Silver fir, Norway spruce, Scots pine, Douglas fir</i>	22.26%	17.78%
Grass	<i>Carex species, Festuca species, hair grass</i>	17.50%	0.37%
Acorns		9.42%	4.20%
Fern	<i>Unidentified Filicophyta species</i>	7.93%	5.44%
Deciduous leaves	<i>Beech, birch, oak, hornbeam, maple</i>	1.14%	1.85%
Crops	<i>Corn, apple, chickpea, sugar beat</i>	1.72%	1.13%
Fungi	<i>Lichen, polypores, unidentified fungi</i>	0.32%	2.18%
Other dry fruits	<i>Chestnuts, beechnuts</i>	1.76%	0.56%
Dicot herbaceous species	<i>Oxalise, neetles, sorrels, loosestrife</i>	0.37%	1.57%
Buds		0.20%	0.11%
Bryophyte		0.12%	0.02%
Animal fragments	<i>Feathers, caterpillars, insect legs</i>	0.02%	0.02%
Others	<i>Twigs, woody debris, dead leaves, bark</i>	8.24%	3.81%
Unidentified		0.19%	0.29%

3.8.5 Illustration of the methodology for rumen content analysis



Figure 3.9: Photography of the rectangular tray used to analyze the rumen content (on this photo, the rumen of a roe deer shot in January 2016). 100 Intersection point are drawn at the bottom of the tray: for each point, the closest item is identified. Photo credit: Laurence Henry

3.8.6 Model statistics

Table 3.4: Statistics of the linear mixed model testing the influence of oak relative fructification and of the deer species on the mean annual acorn proportion found in the diet. The acorn proportion in the diet was arcsine square root transformed prior to analysis.

	Estimate	Std. error	p-value
Fructification	0.67	0.15	< 0.001
Species	-0.067	0.034	< 0.001
Fructification:species	-0.18	0.08	0.026

Table 3.5: Statistics of the three 2-way ANOVA testing the effect of the month and of the deer species on the acorn proportion in the diet.

	Low fructification			Partial fructification			High fructification		
	<i>df</i>	<i>F-value</i>	<i>p-value</i>	<i>df</i>	<i>F-value</i>	<i>p-value</i>	<i>df</i>	<i>F-value</i>	<i>p-value</i>
Month	3	0.59	0.62	3	6.94	< 0.001	2	2.33	0.13
Species	1	9.08	0.003	1	4.55	0.038	1	5.02	0.039
Month:species	3	0.65	0.58	3	0.82	0.49	1	2.12	0.16

CHAPTER

4

DO TRAIT RESPONSES TO SIMULATED BROWSING IN QUERCUS ROBUR SAPLINGS AFFECT THEIR ATTRACTIVENESS TO CAPREOLUS CAPREOLUS THE FOLLOWING YEAR?

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4.1 Abstract

With the rise of large herbivore populations in most northern hemisphere forests, browsing is becoming an increasingly important driver of forest regeneration dynamics. Among other processes affecting the regeneration, the concept of plant-herbivore feedback loops holds that browsed saplings are more subject to subsequent herbivory. This phenomenon is interpreted as a consequence of compensatory growth following browsing since fast growth is generally associated with higher digestibility and lower defense against herbivores. However, studies linking browsing-induced trait variations to subsequent attractiveness to herbivores are still lacking, especially in the forest context. In this study, we experimentally examine the existence of a feedback loop between oak (*Quercus robur* L.) and roe deer (*Capreolus capreolus*) and investigate its underlying morphological and chemical traits. We simulated single and repeated roe deer browsing on nursery-grown oak saplings and measured the changes in sapling height growth, lateral branching, leaf traits and winter shoot traits over two years. We conducted winter feeding trials with tame roe deer one year after the first treatment to test the effect of simulated browsing on sapling attractiveness. Simulated browsing reduced sapling height growth but had no effect on branching. Simulated browsing had no effect on leaf traits after half a year, but decreased the phenolic content and increased the fiber content of winter shoots the following winter. Contrary to our predictions, roe deer preferentially browsed control saplings over saplings previously browsed. After two years, repeated browsing promoted fast carbon acquisition leaf traits (high chlorophyll, high specific leaf area and low fiber content), reduced leaf phenolic content and increased leaf digestibility. We showed that a reduction in 1-year-old oak sapling height growth following browsing, combined with increased structural defense at the expense of chemical defense in winter shoots the following winter, was correlated with reduced browsing pressure, thereby challenging the feedback loop hypothesis. However, we also demonstrated that repeated browsing promoted fast carbon acquisition leaf traits in 2.5-year-old saplings, which tend to support the existence of a feedback loop on older and more intensively browsed saplings. As such, our study provides empirical evidence that morphological and physiological trait responses to browsing influence oak sapling attractiveness, but that the direction and magnitude of this effect depend on the ontogenic stage of the sapling and on the number of browsing events.

Key words: Simulated browsing, feeding trial, feeding loop, functional traits, plant-herbivore interactions, browsing lawns

4.2 Introduction

Over the last decades, most northern hemisphere forests have been facing an increasing herbivory pressure due to a globalized increase in wild ungulate populations (Beguin *et al.*, 2016; Lindén *et al.*, 2011). Numerous studies show that the level of browsing damage observed on young saplings in these forests may compromise their ecological and economic value (Clasen *et al.*, 2011; Côté *et al.*, 2004). A better understanding of how young saplings respond to this increasing browsing pressure and of the influence of wild ungulates on forest regeneration dynamics is therefore critical to better manage these ecosystems. In temperate and boreal forests, several studies revealed that individual saplings browsed by ungulates tend to be more frequently browsed the following year (Craig, 2010; Cromsigt & Kuijper, 2011; Mathisen *et al.*, 2017; Moore *et al.*, 2000). This creates a positive “feedback loop” (Burkepile & Parker, 2017; Craig, 2010) between ungulates and saplings, which may decrease the number of saplings able to grow above the reach of ungulates (Bergqvist *et al.*, 2003). In the context of feedback loops, a set of individual saplings undergo browsing almost every year and stay within the reach of cervids, whereas the remaining unbrowsed individuals should rapidly grow above browsing height. Conversely, in the absence of a feedback loop, a greater proportion of saplings are browsed at least once, which should result in a longer regeneration phase but with a higher number of individuals eventually able to grow above browsing height (Bergqvist *et al.*, 2003). As such, feedback loops are likely to be critical for forest ecosystem dynamics, but the mechanisms governing this process remain highly understudied. In particular, it is unclear whether the variation in sapling trait in response to browsing could increase their attractiveness towards ungulates the following year.

Herbivory can induce various plant responses at the tree level, depending on the resistance strategy of the tree species (Boege & Marquis, 2005; Züst & Agrawal, 2017). Tree species that invest in defense strategies divert carbohydrate resource allocation toward structural defense (*e.g.* high fiber content, spines, hairs) (Barrere *et al.*, 2019; Takada *et al.*, 2003) and/or chemical defense (*e.g.* secondary metabolites like phenols) (Iason, 2005) following browsing, thereby reducing the probability of future damage (Bee *et al.*, 2011; Stolter *et al.*, 2005). Tree species that invest in rapid growth strategies allocate their carbohydrate resources toward fast carbon acquisition following browsing in order to compensate for the loss of biomass (Edenius *et al.*, 1993; Palmer & Truscott, 2003). No study to date have investigated how such trait response influences the probability of subsequent browsing, but an investment in rapid growth strategies could in theory increase sapling attractiveness to ungulates via several mechanisms. First, due to the well-documented trade-off between plant growth and defense (Coley, 1988; Herms & Mattson, 1992; Züst & Agrawal, 2017), an investment in compensatory growth implies fewer anti-herbivore defensive compounds in

the leaves (DuToit *et al.*, 1990). Second, an investment in rapid growth following browsing also leads to higher values of fast carbon acquisition traits such as higher specific leaf area (SLA hereafter) (Baraza *et al.*, 2010), or increased leaf chlorophyll content (Danell & Huss-Danell, 1985). These traits are known to positively correlate with leaf nitrogen content (Wright *et al.*, 2004) and digestibility (Cornelissen *et al.*, 2004), which are both important drivers of food selection by ungulates (Bee *et al.*, 2011; Felton *et al.*, 2018; Lloyd *et al.*, 2010). Finally, browsing may increase attractiveness by modifying sapling stature and architecture (Hartley *et al.*, 1997). Common morphological adjustments following browsing include a reduction in height growth and increased lateral branching (Danell *et al.*, 1994; Drexhage & Colin, 2003), which maintains a high number of shoots at the herbivore's optimal browsing height (Cromsigt & Kuijper, 2011).

Chemical trait responses to browsing in deciduous saplings have been detected from 2 hours (Ohse *et al.*, 2017) to several months (Danell & Huss-Danell, 1985; Danell *et al.*, 1994) after the browsing event, but it is not known whether the trait variations related to compensatory growth can persist after a growing season to influence subsequent attractiveness. Furthermore, although the winter shoots of deciduous saplings are more frequently browsed than their leaves (Petersson *et al.*, 2020), studies on sapling physiological response to herbivory are generally focused on leaf traits (Danell & Huss-Danell, 1985; Danell *et al.*, 1994; Woolery & Jacobs, 2014) and rarely on winter shoot traits (but see Ohse *et al.* (2017)). The influence of winter browsing on the chemical composition of shoots the following year is therefore critical to understanding the mechanisms underlying feedback loops, but nevertheless remains highly understudied. Our study aims at unraveling the mechanisms underlying feedback loops by testing the effect of winter browsing on sapling morphology, leaf traits, the chemical composition of shoots the following year and sapling attractiveness the following winter. More precisely, we focused on the interaction between pedunculate oak (*Quercus robur* L., oak hereafter) and roe deer (*Capreolus capreolus*). Oak is a foundational species in European temperate forests since it defines an entire ecological community or ecosystem by virtue of its structural or functional attributes (Ellison *et al.*, 2005). This species is of high value both for economic reasons and for the high level of biodiversity provided by oak-dominated forests (Mölder *et al.*, 2019a). Roe deer are widespread in European forests, and are known to frequently browse on oak sapling shoots (Drexhage & Colin, 2003; Löf *et al.*, 2021), especially in winter (Petersson *et al.*, 2020). We tested the following hypotheses:

H1: Winter browsing promotes leaf traits related to fast carbon acquisition at the expense of defense, and lateral branching over height growth. We thus expect browsed saplings to have higher SLA, chlorophyll content, nitrogen content, digestibility, and lower fiber and phenolic content, but also lower height growth and higher lateral branching than unbrowsed saplings.

H2: Browsing modifies the chemical composition of shoots the following winter, leading to higher nitrogen content and digestibility, and lower phenolic and fiber content.

H3: Winter-browsed saplings are more attractive to roe deer the following winter than un-browsed saplings.

To test these hypotheses, we grew oak saplings from seed in a nursery and performed a standardized simulation of roe deer browsing at the end of winter, keeping half of them as controls. Six leaf traits (leaf chlorophyll, nitrogen, fiber and phenol content, SLA, digestibility) were measured the following summer, and the plant architecture was monitored before and after the growing season (H1). The next winter, four shoot traits (nitrogen, fibers and phenol content, digestibility) were measured (H2), and feeding trials with tame roe deer were performed to estimate the effect of previous browsing on oak attractiveness to roe deer (H3).

4.3 Material and methods

4.3.1 Plant material

In March 2018 acorns collected in the Saône Valley (47°22' N, 5°29' E) in Autumn 2017 were sown in the experimental nursery of the French National Forest Office (ONF) in Saint-Paul-lez-Durance (43°42' N, 5°44' E). Acorns were stored in a cold chamber at a temperature ranging from 2°C to 4°C between collection and sowing. They were planted in 650 individual pots (1120 cm³, 20-cm high x 56 cm² surface area) with a mix of blond peat (50%) and pine bark (50%), and a single application of slow-release Osmocote fertilizer (2 kg/m³, NPK – 15:9:11) and of fast-release fertilizer (1 kg/m³, NPK – 12:12:17). This organic growing media was selected to optimize water retention and aeration, following the study of [Guehl *et al.* \(1989\)](#). The initial nutrient supply was complemented with a fertigation system in summer 2019 (12 applications from August 6 to September 24, NPK – 12:6:8, 2g/L, 5L/m³). Seedlings were grown in a greenhouse the first year. They were watered on a daily basis to maintain the growing media pF (log of the matric potential) between 1 and 1.5, which corresponded to a spray volume ranging between 0.5 to 15 L/m²/day, depending on the season and the amount of precipitation. As part of the experiment, 55 additional oak saplings were also grown in the same conditions and used as a reference for the chemical analyses.

4.3.2 Winter browsing treatment

After one year of growth, the 650 saplings were moved outdoor and organized in two columns of plastic crates (1500 cm², 30 cm x 50 cm) that contained 17 pot each, resulting in an aver-

age density of 113 saplings.m⁻² (see Supplementary Material, Appendix 4.10.2). In March 2019, the crates were assigned to the control or the “browsed” groups, so that crates of the same group were not adjacent to each other (Supplementary Material, Appendix B). The control group (C hereafter, n = 340, split in 20 crates of 17 saplings) did not undergo any treatment, and the “browsed” group (Br hereafter, n = 310, split into 18 crates of 17 saplings and 1 crate of 4 saplings) received a browsing treatment (Fig. 4.1). Browsing was simulated by clipping a 5cm long piece of the apical shoot with scissors and applying 10 µL of roe deer saliva on the clipped section with a pipette (Ohse *et al.*, 2017) (Fig. 4.1.c; and see Supplementary Material, Appendix 4.10.1, for details on saliva collection).

After two years of growth, in March 2020, the simulated browsing treatment was repeated according to the following design: 30 BrBr saplings underwent the browsing treatment in both 2019 and 2020, 30 CBr saplings underwent the treatment only in 2020, and 30 CC saplings did not undergo any browsing treatment (Fig. 4.1.c). The 30 saplings of each treatment were split into one crate of 17 saplings and one crate of 13 saplings (see Supplementary Material, Appendix 4.10.2).

4.3.3 Trait measurements

4.3.3.1 Sapling architecture

To determine the influence of the browsing treatment on sapling height growth and lateral branching (H1), we measured sapling height (distance between the collar and the highest living bud), root-collar diameter (hereafter referred to as “diameter”) and the number of ramifications before the beginning of (March, n=650) and after (December, n=590) the growing season in 2019. All living shoots longer than 1 cm were considered to be ramifications, regardless of whether they stemmed from the apical shoot or from other shoots (Fig. 4.1.a).

4.3.3.2 Leaf traits

Six leaf traits were measured on 30 individual per treatment in August 2019 (treatments C and Br), and in August 2020 (treatments CC, CBr and BrBr) to test the influence of the browsing treatment on leaf traits the following summer over two years (H1) (Fig. 4.1.c).

Three large mature leaves exposed to direct solar radiation and located in the top fourth of the plant were selected per sapling to measure their chlorophyll content (LChl hereafter) and specific leaf area (SLA hereafter). LChl were obtained using a CCM-200 chlorophyll

meter (Opti-Sciences, Tyngsboro, MA, USA) and the equation presented in [Bagard *et al.* \(2008\)](#). The sapling LChl value is the average of six points, made on the upper side of the three leaves, one on each side of the midrib. The leaves were scanned to measure their projected area (using ImageJ software version 1.52a ([Rasband, 2012](#))) and oven-dried to measure their dry mass. The saplings SLA value is the average the ratios between the leaf area and their dry mass (mm^2/mg) ([Pérez-Harguindeguy *et al.*, 2013](#)).

Leaf biochemical composition was estimated using near-infrared spectroscopy (NIRS). All leaves from each individual sapling were harvested and pooled with the three leaves selected for LChl and SLA measurements. They were then oven-dried (60°C for 24 h) and ground in a cutting mill (Retsch SM100, Retsch GmbH, Hann, Germany) equipped with a 1-mm sieve. A reflectance monochromator (FOSS NIRsystems 6500, Laurel, MD, USA) was used to scan the samples placed in small circular cups (50 mm) with a quartz glass cover. Spectral data were collected every 2 nm between 400 nm and 2500 nm. Each sample was scanned twice (with different cup fillings) and the two values were averaged for each sapling. We predicted the values of leaf fiber content (Neutral Detergent Fibers, LNDF hereafter), nitrogen content (LNC hereafter), dry matter digestibility (LDMD hereafter) and total phenols (LPhenol hereafter) ([Singleton *et al.*, 1999](#)) from these NIRS spectra (table 4.1). We used an existing calibration from CIRAD (Center for International Cooperation in Agronomic Research), combined with direct measurements on 55 additional oak saplings grown in the nursery (calibration R2 ranging from 0.91 to 0.94 for the 4 traits measured). Calibration was performed using modified partial least square regression with WINISI software (version 4, Infrasoft International, Port Matilda, PA, USA). The oak leaf used for the calibration were oven-dried (60°C for 24 h) and ground. We used a Kjeldahl procedure to measure nitrogen, the Folin Ciocalteu colorimetric method ([Singleton *et al.*, 1999](#)) for total phenols, the pepsin-cellulase method ([Aufrère *et al.*, 2007](#)) for dry matter digestibility, and sequential fractionation ([Soest *et al.*, 1991](#)) for fiber contents. Some studies reported that air-drying underestimates some phenolic compounds ([Eichenberg *et al.*, 2014](#); [Julkunen-Tiitto & Sorsa, 2001](#)), whereas other studies did not reveal any biases ([Couture *et al.*, 2016](#); [Makkar & Singh, 1991](#)), but it has not been shown to affect the hierarchy between the different individuals sampled in either cases.

4.3.3.3 Winter shoot traits

In March 2020, the shoots clipped after the second browsing treatment (applied on 30 C and 30 Br saplings, Fig. 4.1.c) were oven-dried and ground following the same methodology as that was used for the leaves (H2). For methodological requirements of the NIRS methods, the shoots of three saplings from the same treatment were pooled obtain ten samples of shoots per treatment. Shoot fiber content (SNDF), nitrogen content (SNC), dry matter digestibility (SDMD) and total phenolic content (SPhenol) were estimated using the same

procedures as described for the leaves, and with the same calibration spectra.

Table 4.1: Abbreviation, full name and unit of the different leaf and shoot traits measured on oak saplings.

Trait	Fullname	Organizational level	Method	Unit
<i>Leaf traits</i>				
LChl	Leaf chlorophyll content	Individual (average of three leaves per individual)	CCM-200 chlorophyll meter	mm ² .mg ⁻¹
LNC	Leaf nitrogen content	Individual (all leaves pooled together)	NIRS	% of dry matter
LNDF	Leaf neutral detergent fiber	Individual (all leaves pooled together)	NIRS	% of dry matter
Lphenol	Leaf phenolic content	Individual (all leaves pooled together)	NIRS	% of dry matter
SLA	Specific leaf area	Individual (average of three leaves per individual)		g.m ⁻²
LDMD	Leaf dry matter digestibility	Individual (all leaves pooled together)	NIRS	% of dry matter
<i>Winter shoot traits</i>				
SNC	Shoot nitrogen content	Browsing treatment (shoots of three individuals pooled)	NIRS	% of dry matter
SNDF	Shoot neutral detergent fiber	Browsing treatment (shoots of three individuals pooled)	NIRS	% of dry matter
Sphenol	Shoot phenolic content	Browsing treatment (shoots of three individuals pooled)	NIRS	% of dry matter
SDMD	Shoot dry matter digestibility	Browsing treatment (shoots of three individuals pooled)	NIRS	% of dry matter

4.3.4 Feeding trials

In December 2019, 500 saplings (250 C and 250 Br) not used for any leaf and shoot trait measurement were transferred to the experimental unit of the French National Institute for Agricultural and Environment Research (INRAE) in Gardouch (43°22' N, 1°40' E) to test the influence of the treatment on oak sapling attractiveness to tame roe deer (H3) (Fig. 4.1.c). Feeding trials were conducted at the end of winter (February 2020), on leafless saplings before budburst. The tests took place in three enclosures of approximately 0.5 ha that each

hosted a birth cohort of two or three adult female roe deer. The captive roe deer were fed with pelleted food *ad libitum* and had access to the natural vegetation available in their enclosure (mainly grasses and forbs). The deer were used to feeding on browse as they were regularly given fresh branches of deciduous tree species to supplement their diet (*i.e.*, *Prunus domestica*, *Quercus sp.*, *Cornus sanguinea*, *Ulmus carpinifolia*, *Crataegus monogyna*, and *Acer campestre*).

For each feeding trial, 24 saplings were placed in the center of the enclosure, in pre-dug holes in the soil, to form two groups of 12 saplings per treatment (Br vs C) (Fig. 4.1.b). The aggregation of saplings of the same treatments helps the animal to detect differences between the treatments (see [Verheyden-Tixier & Duncan \(2000\)](#); [Tixier *et al.* \(1998\)](#) or [Rea *et al.* \(2017\)](#) for similar approaches). Saplings were spaced by 50 cm, which is sufficiently large to enable the animal to move between saplings, but sufficiently small so that it can easily switch from one group of saplings (*i.e.* treatment) to the other. (H. Verheyden, pers. obs.). The position of the groups (C and Br) was systematically switched between two consecutive tests to avoid any bias due to the positioning of the sapling groups. During the three weeks preceding the feeding trials, the animals were acclimated to the experiment by placing 24 oak saplings with morphological characteristics similar to the saplings in the experiment in each enclosure one day per week. All the tests began between 8.45 and 9 a.m. A minimum period of two days was left between two tests in the same enclosure. Two types of tests were conducted over a period of four weeks from the 3rd to the 26th of February 2020.

1. The immediate selection patterns were tested using 1 hour feeding trials (“1-h tests” hereafter). Eight tests consisted in filming three roe deer (consuming the plant or not) until half of the sapling were browsed at least once using a Canon SX60HS Power Shot camera (Fig. 4.1.b). We used this method to avoid a bias due to resource depletion (*i.e.*, if all the saplings were browsed down, it might have altered the deer’s initial food choice). The number of saplings browsed in each treatment was recorded. The shoot length that has been consumed was also estimated as the difference between total shoot lengths (including the plant height and all ramifications) measured before and after the test. The video recordings were analyzed with version 6.3 of the Behavioral Observation Research Interactive Software ([Friard & Gamba, 2016](#)). In the video analysis, the total amount of time the roe deer spent sniffing and consuming the saplings of each treatment was counted.
2. Eleven longer feeding trials (“24-h tests” hereafter) were performed to assess consumption preferences in two other enclosures containing two and three deer, respectively. For each test, the saplings were left in place for 24 hours under the surveillance of two camera traps, one facing the C saplings and the other facing the Br saplings,

to ensure that the animals consumed the saplings within the 24 h period. Again, we counted the number of browsed saplings and the shoot length that has been consumed after each test.

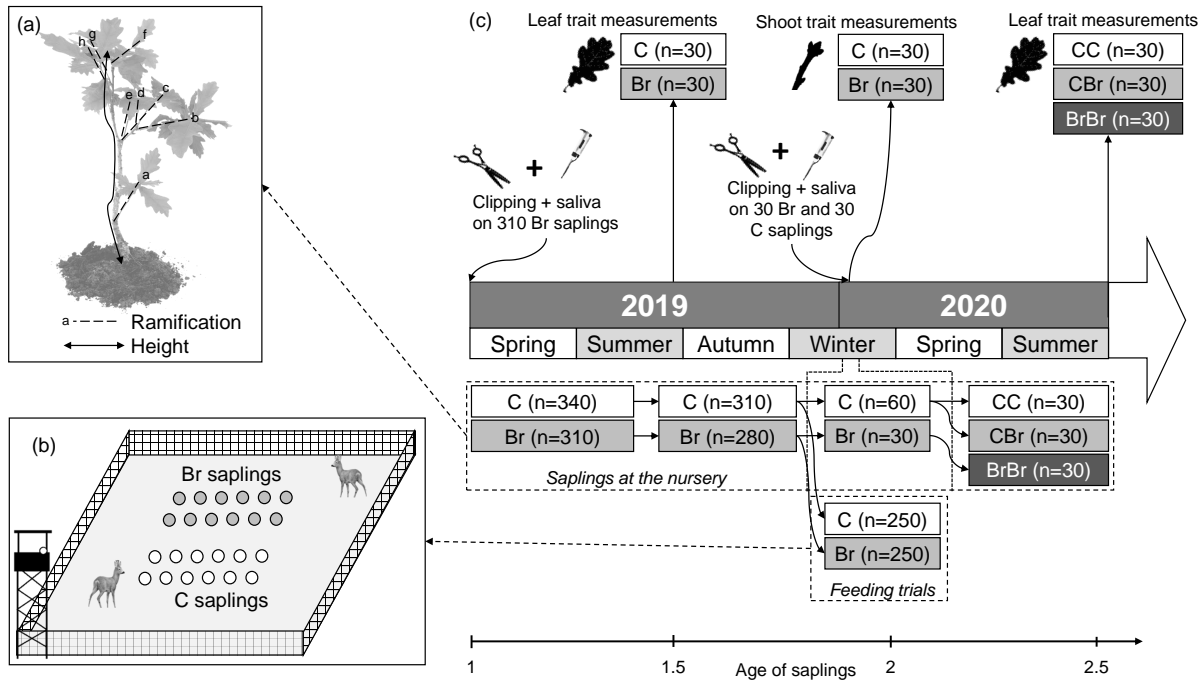


Figure 4.1: Overview of the experimental approach: (a) chronology of the experiment and (b) simplified representation of a feeding trial.

4.3.5 Data analyses

4.3.5.1 Effect of simulated browsing on sapling height growth, lateral branching and leaf traits (H1)

To compare height growth between treatments, we estimated a standardized measurement of height increment between March and December 2019 that accounts for sapling root-collar diameter. Indeed, both initial height and diameter accounted for a significant part of the variability in final height (see Supplementary Material, Appendix 4.10.3). Therefore, the standardized height growth is the residuals of a linear model that predicted the final height from initial height, initial diameter and their interaction. Differences between standardized height growth were tested using Student's t-test. Similarly, a standardized branching was computed as the residuals of a generalized linear model with a Poisson error distribution that predicted the number of ramifications in December 2019 as a function of the number of ramifications and diameter in March 2019. These two models are presented in detail in the Supplementary Material, Appendix 4.10.3.

The effect of the treatment on leaf traits was tested using a redundancy analysis (RDA). Although describing different leaf functions and properties, the selected traits are often found to be correlated (see [Coley \(1988\)](#); [Wright *et al.* \(2004\)](#); [Sterck *et al.* \(2006\)](#); [Díaz *et al.* \(2016\)](#)) (Fig. 4.3.b). This analysis shows the major axes of differentiation in leaf traits between treatments in a multivariate space accounting for the correlation structure between traits. We constructed a unique multivariate space using traits values from both years (2019 and 2020) and the coordinates of individual saplings on the first RDA axis were compared between treatments using an ANOVA, followed by Tukey's post-hoc test, for each year separately. All traits were centered and scaled prior the analysis and LChl was log-transformed to fulfill normality assumptions. Univariate analyses were also performed for each trait separately and are presented in detail in the Supplementary Material, Appendix 4.10.4.

4.3.5.2 Effect of simulated browsing on winter shoot traits (H2)

The effect of the simulated browsing was tested on all shoot traits simultaneously (SNC, SDMD, SPhenol and SNDF) using a RDA. All shoot traits were centered and scaled prior to the analysis. The coordinates on the first RDA axis of C and Br individuals were compared using an ANOVA, followed by Tukey's post-hoc test. Univariate analyses were also performed for shoot traits and are presented in detail in the Supplementary Material, Appendix 4.10.4.

4.3.5.3 Effect of simulated browsing on attractiveness for roe deer (H3)

For each test type separately (1 h or 24 h), paired Wilcoxon signed-rank tests were used to analyze the effect of the simulated browsing on the number of saplings browsed and on the shoot length consumed per treatment. In the 1-h tests, it was found that one individual roe deer accounted for more than 90% of the total time spent both consuming and sniffing saplings in all of the tests, the statistical analyses of these two variables was restricted to this individual only. Paired Wilcoxon signed-rank tests were used to compare the time spent by the animal consuming and sniffing C and Br saplings in each 1-h test.

All statistical analyses were conducted with R statistical software, version 3.6.3 ([RCoreTeam, 2019](#)). Redundancy analyses were performed with the 'vegan' R package ([Oksanen, 2017](#)).

4.4 Results

4.4.1 Effect of simulated browsing on sapling height growth, branching, and leaf traits (H1)

The first year of the experiment, simulated browsing significantly reduced sapling standardized height growth (Student's t-test, $t_{582} = 3.06$, $p < 0.01$) (Fig. 4.2.a) – *i.e.*, for a given initial height and diameter, C saplings grew an average of 4 cm. year^{-1} faster than Br saplings. Simulated browsing did not influence lateral branching (Student's t-test, $t_{576} = 0.95$, $p = 0.34$) (Fig. 4.2.b).

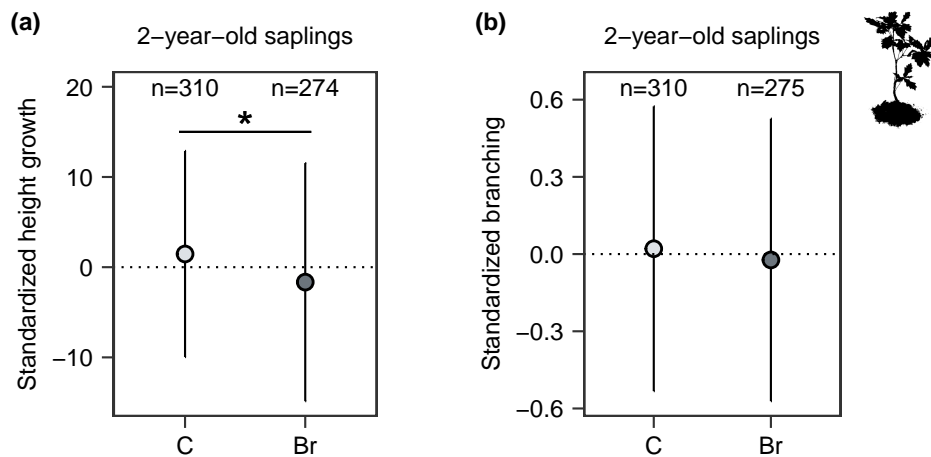


Figure 4.2: (a) Standardized height growth and (b) branching (mean \pm standard deviation) during the growing season 2019 for the different treatments of simulated browsing. The symbol “*” indicates that the two treatments are significantly different from each other ($\alpha = 0.05$).

The first axis (RDA1) of the RDA conducted on six leaf traits explained 15% of the differences in trait values between groups, and mainly contrasted traits related to fast carbon acquisition (*i.e.* LDMD and SLA) and to defense traits (*i.e.* LPhenol and LNDF), while LNC and LChl had weak score values on RDA1 (Fig. 4.3.b, and Supplementary Material, Appendix 4.10.5). Simulated browsing had no effect on 1.5-year-old sapling leaf traits (ANOVA, $F_{1,57} = 1.91$, $p = 0.17$). However, simulated browsing significantly influenced 2.5-year-old sapling leaf traits (ANOVA, $F_{2,80} = 3.91$, $p = 0.02$): BrBr saplings had higher values of fast carbon acquisition traits, while CC saplings had higher values of defense traits (Fig. 4.3.a). The univariate analysis showed that simulated browsing reduced 1.5-year-old sapling SLA and increased 2.5-year-old sapling LNC and LChl (Supplementary Material, Appendix 4.10.4).

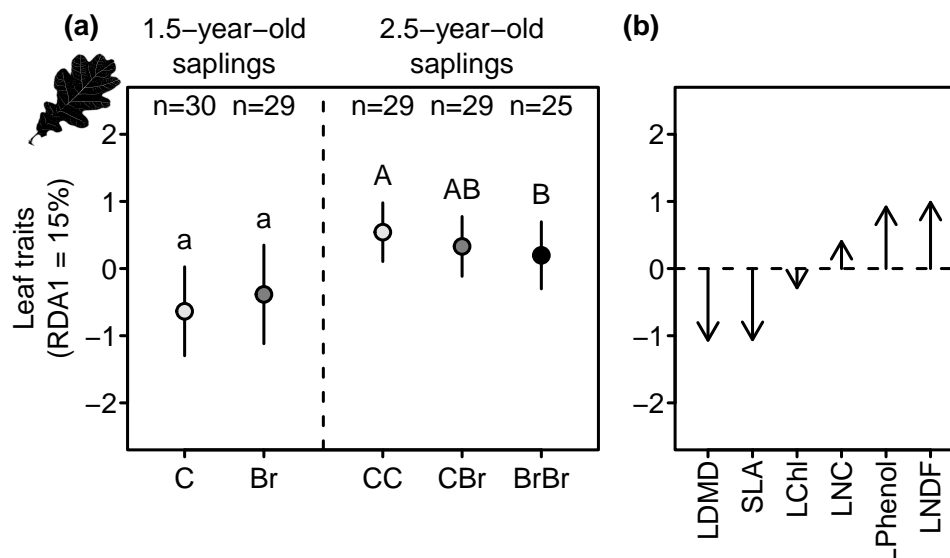


Figure 4.3: (a) Coordinates of the individual saplings per treatment on the first component (RDA1) of the redundancy analysis conducted on six leaf traits (*i.e.* LPhenol, LNDF, SLA, LChl, LDMD and LNC). Treatments with no letters in common are statistically significantly different from each other ($\alpha = 0.05$). (b) Value of the correlation between each trait and RDA1.

4.4.2 Effect of simulated browsing on winter shoot traits

The first axis of the RDA conducted on four shoot traits (SNC, SDMD, SPhenol and SNDF) of 2-year-old saplings explained 14% of the differences in trait values between treatments, and contrasted shoots with high phenolic content to shoots with high fiber content (Fig. 4.4.b, and Supplementary Material, Appendix 4.10.5). The simulated browsing treatment significantly influenced shoot traits (ANOVA, $F_{1,18} = 14.26$, $p < 0.01$): Br saplings had lower SPhenol and higher SNDF compared to C saplings (Fig. 4.4.a). The univariate analysis also showed that simulated browsing reduced SPhenol in 2-year-old oak saplings (Supplementary Material, Appendix 4.10.4).

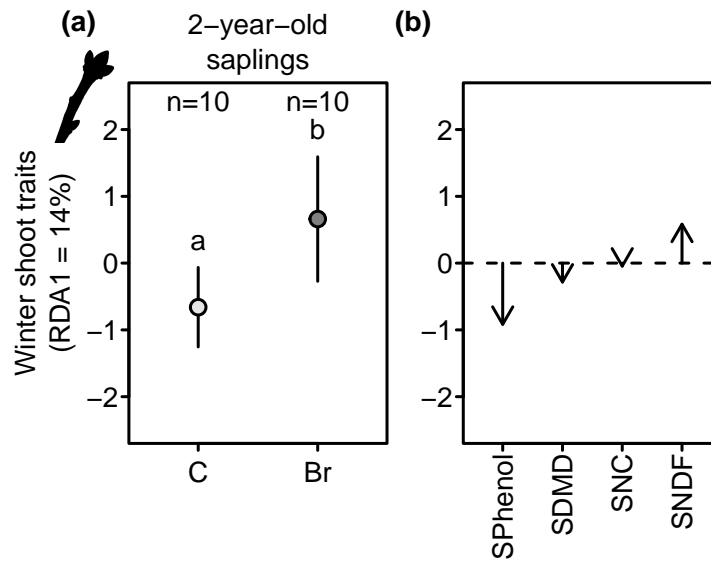


Figure 4.4: (a) Coordinates of the individual saplings per treatment on the first component (RDA1) of the redundancy analysis conducted on six shoot traits (*i.e.* SPhenol, SNDF, SDMD and SNC). Treatments with no letters in common are significantly different from each other ($\alpha = 0.05$). (b) Value of the correlation between each trait and RDA1.

4.4.3 Effect of simulated browsing on attractiveness for roe deer

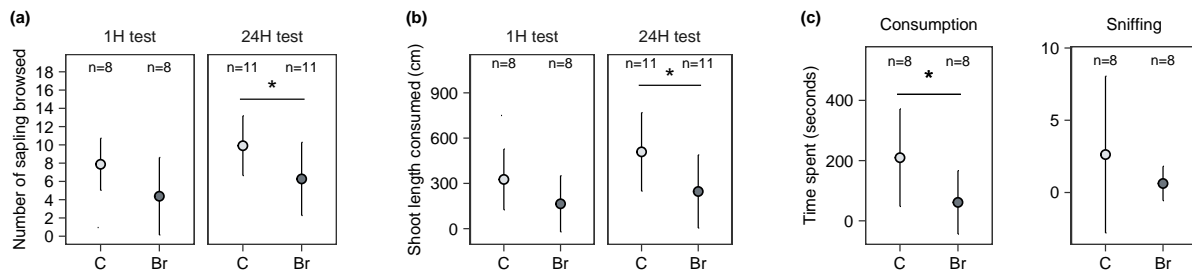


Figure 4.5: (a) Number of sapling browsed per test and per treatment, (b) shoot length consumed and (c) time spent by the roe deer consuming and sniffing the saplings (bottom) for treatments C and Br. “*” indicates a statistically significant difference between treatments C and Br at $\alpha = 0.05$.

During the 1-h tests, simulated browsing significantly reduced sapling attractiveness: roe deer browsed an average of 7.88 C saplings compared to 4.38 Br saplings out of 12 saplings per treatment, but the trend was not significant (Wilcoxon signed rank, $V_7 = 24$, $p = 0.12$). The same trend was significant for the 24-h tests: 9.91 saplings browsed on average for C, vs. 6.27 for Br (Wilcoxon signed rank, $V_{10} = 45$, $p < 0.01$) (Fig. 4.5.a). Similarly, simulated browsing reduced the shoot length browsed by roe deer (Fig. 4.5.b) both in the 1-h tests (Wilcoxon signed rank, $V_7 = 31$, $p = 0.078$) and in the 24-h tests (Wilcoxon signed rank, V_{10}

= 24, $p < 0.01$), but the trend was only significant for the 24-h tests. During the 1-h tests, high inter-individual variability was observed among the three female roe deer present in the enclosure: one individual was responsible for 93% of the total time spent consuming. In six out of the eight 1-h tests, this individual spent more time consuming C than Br saplings, which resulted in a significant negative effect of the simulated browsing treatment on the time spent consuming (Wilcoxon signed rank, $V_7 = 34$, $p = 0.02$) (Fig. 4.5.c). However, the treatment did not influence the time spent sniffing the saplings (Wilcoxon signed rank, $V_7 = 5$, $p = 0.42$) (Fig. 4.5.c).

4.5 Discussion

4.5.1 Effect of simulated browsing on sapling height growth, lateral branching, and leaf traits (H1)

Simulating apical bud browsing in winter was found to be sufficient to reduce oak sapling height growth. While other species like beech (*Fagus sylvatica*) (Frank *et al.*, 2019) or Scots pine (*Pinus sylvestris*) (Edenius *et al.*, 1993) have been found to compensate for the loss of the apical bud by increasing their annual growth rate, our results indicate that one-year-old oak saplings are not capable of such a response. A reduction in sapling height growth following browsing of the apical shoot was found in similar studies conducted on sessile oak (*Quercus petraea* (Matt.) Liebl.) saplings, but this decrease in height growth was compensated for by an increase in the number of ramifications (Chaar *et al.*, 1997; Drexhage & Colin, 2003). This response is interpreted as a biomass allocation strategy to promote a plurality of competitive growth axes, which could increase resilience in the eventuality of future browsing events (Drexhage & Colin, 2003). In our study, simulated browsing did not influence the production of new ramifications. The ability of saplings to develop more ramifications following browsing has been shown to increase with the number of shoots browsed (Bergström & Danell, 1987; Frank *et al.*, 2019), and to increase with sapling age (Hóðar *et al.*, 2008). Thus, the absence of response to browsing in our study is probably likely due to the young age of the saplings (*i.e.*, browsed at one year of age), and to the fact that only one shoot was browsed. Alternatively, it cannot be excluded that the saplings in our study responded to browsing by allocating their biomass to plant parts that we did not measure. For instance, birch saplings (*Betula pubescens* and *B. pendula*) have been shown to increase the growth of their existing lateral shoots following browsing (Bergström & Danell, 1987), which tends to prevent large herbivores from accessing the internal parts of the sapling (Archibald & Bond, 2003). Similarly, Hóðar *et al.* (2008) found that Scots pine saplings responded to browsing by allocating more biomass to roots, which protect carbon resources from aboveground herbivores. Overall, our results indicate that young oak saplings do not seem to show any morphological plasticity in response to browsing.

Browsed and unbrowsed 1.5-year-old saplings had similar values of leaf traits, whereas we expected browsed saplings to have higher values of traits related to fast carbon acquisition (LNC, SLA, LChl) and digestibility (LDMD), and lower values of defense traits (LPhenol and LNDF). At this ontogenic stage, saplings have a very limited amount of stored reserves and rely predominantly on carbon acquisition via photosynthesis to grow (Boege & Marquis, 2005). As a result, if saplings do not respond to herbivory by investing in traits related to fast carbon acquisition, the removal of photosynthetic organs by herbivores will necessarily result in lower carbon acquisition and, therefore, in reduced growth. Our observation that browsing reduces height growth and does not influence branching tends to support this, although a measurement of the plant biomass would be necessary to draw any conclusion on the effect of browsing on primary productivity. A possible explanation for the absence of browsing-induced leaf trait variation could be an insufficient intensity or frequency of the simulated browsing. In this study, we only removed 5 cm of the apical shoot, whereas other studies found that several winter browsing events within a year were necessary to induce changes in leaf nutrient content of *Betula pubescens* saplings (Danell *et al.*, 1994). Nosko & Embury (2018) even found a threshold of biomass removal in early summer that induced changes in the phenolic content of balsam fir (*Abies balsamea*) sapling leaves.

Interestingly, 2.5-year-old oak saplings responded to the treatment: compared to unbrowsed saplings, saplings browsed for two consecutive years had higher values of SLA and LDMD, and lower values of LPhenol and LNDF, two traits related to chemical and structural defense, respectively. Although LDMD is known to be an important driver of food selection by large herbivores (Bee *et al.*, 2011; Felton *et al.*, 2018; Lloyd *et al.*, 2010), studies on the influence of browsing on this trait are surprisingly scarce (Danell & Huss-Danell, 1985). Digestibility tends to be positively related to fast carbon acquisition traits such as SLA or chlorophyll content (Cornelissen *et al.*, 2004): an investment in fast carbon acquisition in response to browsing should therefore also result in increased LDMD. Our study confirms this hypothesis, thereby supporting the assumption that browsing can promote traits that increase further attractiveness. While defense is often seen as the only mechanism used by woody species to deal with herbivory, our study corroborates the less documented assumption that woody species may also invest in growth rather than in defense to compensate for the loss of tissues to herbivores (Haukioja & Koricheva, 2000). It is noteworthy that these changes only occurred for 2.5-year-old saplings and not for 1.5-year-old saplings. This finding provides strong empirical support for the theory that the ability of saplings to change their resource allocation in response to herbivory depends on their ontogenic stage (Barton, 2013; Elger *et al.*, 2009). In particular, this theory predicts that the root:shoot ratio decreases throughout the sapling stage, and that plants acquire an increasing amount of resources that can be either stored, or allocated to resist herbivory via compensatory growth or defense (Boege & Marquis, 2005).

4.5.2 Influence of the simulated browsing treatment on winter shoot traits (H2)

In our study, one year after the application of the simulated browsing treatment (at the end of winter and before budburst), the shoots of the browsed saplings had a lower phenolic content and a higher fiber content than the controls. To our knowledge, this is the first evidence that a winter browsing event modifies shoot chemical composition the following winter. These results suggest a trade-off between the investment in different types of defense, notably chemical vs. physical defense. [Palo *et al.* \(1992\)](#) showed that as the thickness of birch winter shoots increased, their phenolic content decreased and their fiber content increased, which is interpreted as a positive correlation between the thickness of cell walls and shoot diameter. Under this perspective, winter browsing would have induced an increase in shoot thickness at the expense of their phenolic content, which would also be consistent with the findings of [Bergström & Danell \(1987\)](#) who showed that simulated browsing enhanced the radial growth of birch sapling lateral shoots.

Although both phenolic and fiber content tend to decrease attractiveness by reducing the nutritional value of plant tissues ([Iason, 2005](#)), their relative efficiency depends on the herbivore species. In the case of cervids, high fiber content is known to deter herbivory ([Bee *et al.*, 2011](#)), but a few species, including roe deer, digest tannins relatively well since some of the proteins contained in their saliva are able to bind with tannins. Roe deer are even known to select for a certain level of hydrolysable tannin in their diet ([Verheyden-Tixier & Duncan, 2000](#)). Although hydrolysable tannins are not the only component of total phenols, it could be expected that phenol-rich shoots of unbrowsed seedlings are more palatable for roe deer than fiber-rich shoots of previously browsed saplings.

In this study, leaves and winter shoots did not respond similarly to browsing, which is consistent with the recent findings of [Ohse *et al.* \(2017\)](#) who reported that simulated browsing decreased phenolic acid content in beech sapling buds but not in their leaves. These differential responses could be due to different constraints in the functioning of these organs. In leaves, investment in defense trade-offs with the capacity of carbon acquisition ([Herms & Mattson, 1992](#); [Züst & Agrawal, 2017](#)), and different browsing-induced chemical changes are found across species, ranging from low defense associated with high carbon acquisition traits (e.g., oak in this study, birch in [Danell & Huss-Danell \(1985\)](#)) to high chemical defense but low carbon acquisition rate (e.g., *Acer pseudoplatanus* in [Ohse *et al.* \(2017\)](#) and *Pinus strobus* in [Champagne *et al.* \(2021\)](#)). Conversely, no function clearly trade-offs with defense in winter shoots, which likely explains the consistent response to browsing

across tree species (see [Ohse *et al.* \(2017\)](#) for beech, [Danell & Huss-Danell \(1985\)](#) for birch or [Keefover-Ring *et al.* \(2016\)](#) for *Populus tremuloides*).

4.5.3 Influence of the simulated browsing treatment on roe deer feeding preference (H3)

In the feeding trials conducted on 2-year-old saplings, a consistent trend in roe deer preference appeared in both type of tests, although the results of the 1h-test must be cautiously interpreted since they rely on the decision of only one individual. While it was expected that roe deer would prefer saplings browsed the previous winter, the animals preferentially fed on unbrowsed oak saplings. Whereas similar findings have been found in other feeding trials conducted with red deer (*Cervus elaphus*) ([Duncan *et al.*, 1998a](#)) and moose ([Edeinius *et al.*, 1993](#)), most studies conducted in field conditions found the opposite: cervids tend to prefer previously browsed saplings ([Bergqvist *et al.*, 2018](#); [Makhabu & Skarpe, 2006](#); [Mathisen *et al.*, 2017](#); [Moore *et al.*, 2000](#)). The preferences for unbrowsed individuals in our study could be the consequence of the lower fiber content in their winter shoots, which would be consistent with previous observations that roe deer tend to select plants with low fiber content despite high levels of hydrolysable tannins ([Verheyden-Tixier & Duncan, 2000](#)).

The preference of roe deer for unbrowsed saplings could also be linked to differences in architecture since these saplings were generally higher and more ramified compared to previously browsed saplings (Supplementary Material, Appendix 4.10.6). Several studies have shown that sapling morphology, particularly the distribution of biomass in 3D space, influences attractiveness to deer ([Hartley *et al.*, 1997](#); [Renaud *et al.*, 2003](#)). According to the optimal foraging theory, deer make their foraging decisions to maximize their net energy gain ([Stephens & Krebs, 1986](#)). The animal's energy gain depends on its feeding rate – which is the product of bite size (biomass available at each bite) and bite rate – and on plant chemical composition ([Charles-Dominique *et al.*, 2020](#)). It has been shown that the production of a high number of ramifications leads to the formation of a 'cage-like' structure that decreases the feeding rate ([Charles-Dominique *et al.*, 2020](#)), and, consequently, saplings attractiveness to large herbivores ([Archibald & Bond, 2003](#)). Despite the fact that sapling height has a rather weak influence on feeding rate ([Renaud *et al.*, 2003](#)), studies show that deer preferentially browse near their shoulder height ([Duncan *et al.*, 1998a](#); [Nichols *et al.*, 2015](#)). As a consequence, deer browsing often prevents saplings from growing above their maximum browsing height, thus maintaining a high density of saplings at their optimal browsing height – around 75 cm for roe deer ([Duncan *et al.*, 1998a](#)). [Cromsigt & Kuijper \(2011\)](#) showed that palatable trees were maintained at a constant height of 80 cm, which

corresponds to the optimal browsing height for red deer (Nichols *et al.*, 2015). In that regard, our findings support the assumption that height, rather than the number of ramifications, is the main morphological factor undermining roe deer preferences.

4.5.4 Is there any evidence of feeding loops between oak and roe deer?

The theory of feedback loops presumes that the trait response of saplings to browsing increases their subsequent attractiveness to herbivores, thereby trapping them within the reach of large herbivores through repeated browsing (Cromsigt & Kuijper, 2011; Craig, 2010; Mathisen *et al.*, 2017). At first glance, the fact that roe deer in our study preferred unbrowsed saplings conflicts with the existence of any feedback loops between oak and roe deer. On the other hand, several results in our study also tend to support this theory. Indeed, roe deer preferred the tallest saplings, and browsing reduced sapling height growth, which support the idea that through feedback loops, roe deer actively prevent taller plants from growing beyond their reach and therefore maintain the saplings at their optimal browsing height (Cromsigt & Kuijper, 2011). In addition, we showed that repeated browsing over two years increased leaf digestibility at the expense of fiber content. Although not tested in our study, higher leaf digestibility has been shown to positively influence deer preferences (Felton *et al.*, 2018; Lloyd *et al.*, 2010), while leaf fiber content tends to deter herbivory by cervids (Bee *et al.*, 2011). Finally, browsing increased the fiber content and decreased the phenolic content of winter shoots. Our results therefore show that the trait response of oak saplings to browsing modifies their subsequent attractiveness to roe deer, but that the magnitude and direction of this effect is likely to depend on the sapling phenological and ontogenic stage, but also on the browsing intensity. Our findings thus shed light on the factors driving feedback loops by showing that trait plasticity at the plant level (*i.e.*, height growth) but also organ levels (leaf and winter shoots chemical composition) affected sapling attractiveness.

Whereas this trait plasticity in response to browsing seems consistent across species in winter shoots, as confirmed by our study, there is a high interspecific variability in leaf responses. Interestingly, the species known to exhibit a tolerance response to browsing in their leaf traits (higher digestibility, lower defense) – *i.e.*, oak in this study, birch (Danell & Huss-Danell, 1985) or aspen (Keefover-Ring *et al.*, 2016) – share the common feature of being relatively palatable for large herbivores (Boulanger *et al.*, 2009; Hjältén *et al.*, 1993). Conversely, unpalatable species such as spruce or beech tend to show limited leaf trait plasticity following browsing (Barrere *et al.*, 2019; Duncan *et al.*, 1998a; Ohse *et al.*, 2017), which suggest that the tree species inherent palatability could determine the strength of its plasticity in response to browsing. Testing this hypothesis with an experiment comparing the

traits of browsed and unbrowsed saplings for tree species of contrasted palatability would constitute a first step towards a more general and multi-specific understanding of the relationship between browsing and subsequent attractiveness for herbivores.

4.6 Conclusions

We showed that (i) winter browsing reduced sapling height growth and modified the chemical composition of shoots the following winter, resulting in an increase in fiber content and a decrease in phenol content, and that (ii) these changes decreased the probability of subsequent herbivory by roe deer. This study is, to our knowledge, the first to connect browsing-induced sapling trait variations to subsequent browsing. We also showed that older and more intensively browsed saplings were able to respond to browsing by investing in fast carbon acquisition traits at the expense of defense traits, thereby supporting the assumption that browsing can promote leaf traits known to increase attractiveness (*i.e.*, high digestibility and low phenolic content). These changes in leaf traits, along with the browsing-induced reduction in height growth and roe deer preference for higher saplings tend to support the theory that large herbivores can maintain trees at their optimal browsing height by repeated browsing. However, we suggest that further studies verify the existence of these possible feedback loops between oak and deer in field conditions, and investigate their consequences on oak dynamics at the population level to assess how they may influence forest management. This is all the more necessary given that the regeneration of oak populations in the presence of high deer densities is an increasingly critical issue for forest management and conservation ([Barrere *et al.*, 2021](#); [Pettersson, 2019](#)).

4.7 Funding

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4.8 Authorship

JB, CC, SS, HV and VB designed the study. JB and VB monitored sapling morphology and collected leaf and shoot samples at the nursery. DB supervised the chemical analyses. JB,

HV, HC and AB conducted the feeding trials. JB and SS collected roe deer saliva. JB and JS conducted the statistical analyses. JB led the writing of the manuscript. All authors critically contributed to the draft and approved the final version of the manuscript.

4.9 Acknowledgments

We thank Nicolas Cebe and Jean-Luc Rames (INRAE) for their help during the feeding trials, Elodie Baby and Laurent Bonnal (CIRAD) for conducting the chemical analyses, and Patrice Brahic, Baptiste Delor, Jerome Reilhan and Marie De Castro (ONF) for their essential contribution to sapling growth, maintenance and transportation. We are grateful to the wildlife technicians (Stephane Chabot, Mario Bottacio, Marc Marchi and Eveline Nivois) and the many volunteers who helped capture roe deer at Trois-Fontaines. Finally, we thank François Débias (CNRS) for his contribution to saliva collection, Didier Le Thiec for helping and loaning material for the chlorophyll measurements, and Victoria Moore and Gail Wagman for correcting the English manuscript.

4.10 Appendices

4.10.1 Appendix A - Protocol for roe deer saliva collection

The timing, frequency and intensity of deer browsing are extremely difficult to control in the field so, in order to standardize the treatment applied to all our saplings, we chose to simulate deer browsing (Baldwin, 1990). Ohse *et al.* (2017) showed that, for several tree species, applying deer saliva and clipping shoots provoked a different plant chemical response than when browsing was only simulated by clipping shoots. Therefore, we chose to simulate roe deer browsing in the same way (clipping and saliva application). We applied the simulated browsing treatment before budburst at the end of winter, since oak is most frequently browsed at that time of year (Petersson *et al.*, 2020).



Figure 4.6: Saliva collection on a wild roe deer in Trois-Fontaines. Photo: Julien Barrere.

We collected saliva on wild roe deer caught in driving nets in the experimental territory of Trois-Fontaines (48°41' N, 4°55' E) during the winters in 2018 and 2019. We placed one extremity of a 125mm SalivaBio's Children's swab (Salimetrics) in the roe deer's mouth for 30 seconds to 1 min, depending on the chewing frequency of the animal. We immediately centrifuged the swabs at 3700 rpm (2000 g) for 10 minutes using in a Hettich EBA-20 centrifuge to extract the saliva. We froze the saliva until it was applied during the simulated browsing treatment. At the end of winter in 2019 and 2020, we simulated browsing by clipping the apical shoot with scissors and applying 10 μ L of roe deer saliva on the clipped section with a pipette (Fig. 4.6). We took-off a 5-cm-long portion of shoot, based on the length of the shoots found in roe deer rumen.

4.10.2 Appendix B - Spatial organization of the saplings at the nursery.

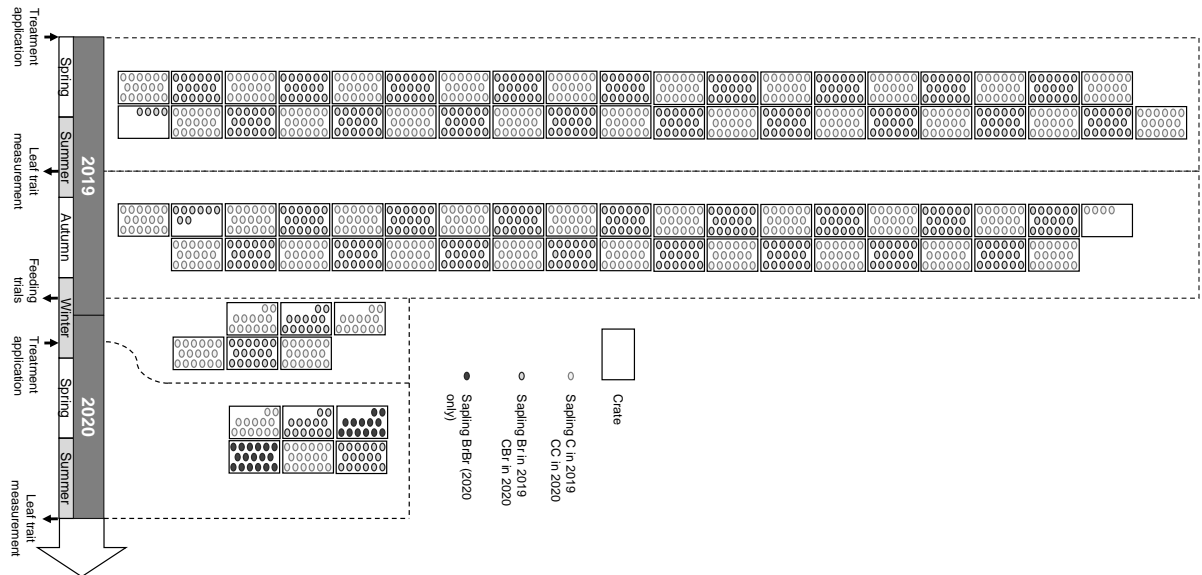


Figure 4.7: Spatial organization of the saplings of each treatment per block at the nursery throughout the experiment.

4.10.3 Appendix C - Standardization of height growth and branching

4.10.3.1 Height growth

To account for sapling morphological variability before testing the effect of the simulated browsing on height growth, we first modeled height in December 2019 (*i.e.* after the second growth season) (H) as a function of sapling height (H_0) and diameter (D_0) in March 2019 with a linear model (Eq.4.1). The residuals of this model are hereafter referred to as standardized height growth (SHG).

$$H = \alpha_1 + \alpha_2 * H_0 + \alpha_3 * D_0 + \alpha_4 * H_0 * D_0 + SHG \quad (4.1)$$

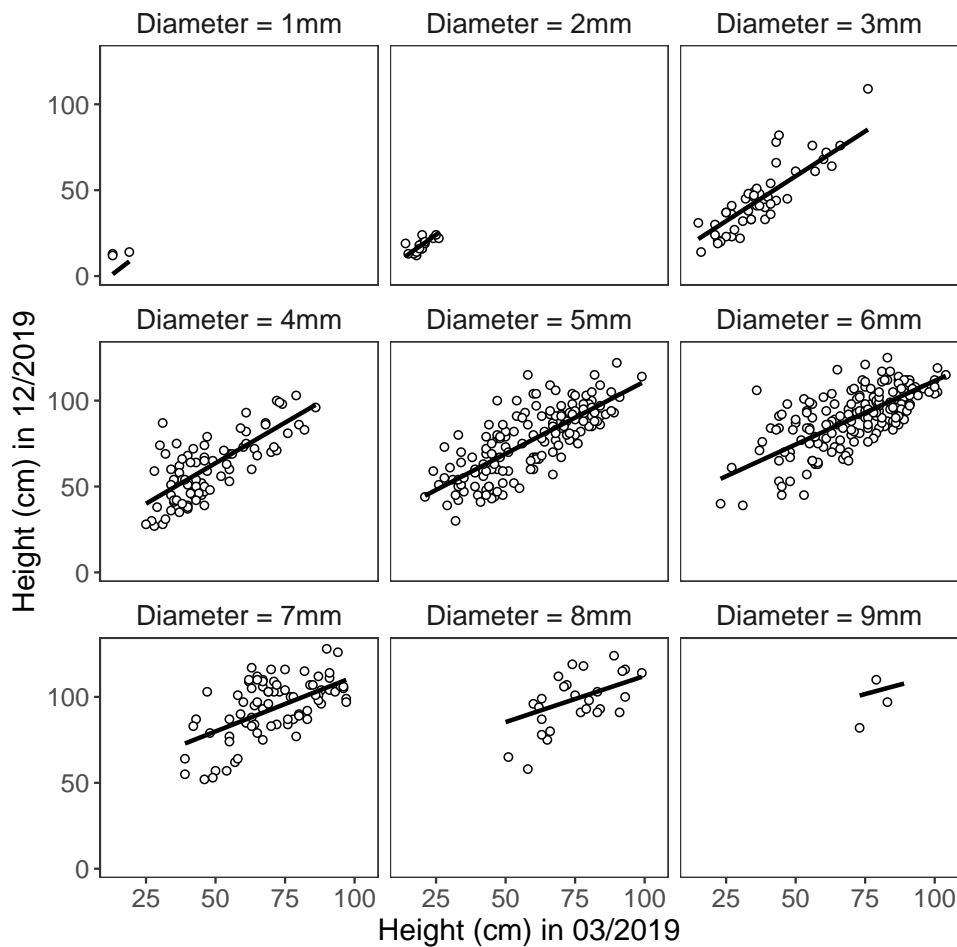


Figure 4.8: Fit of the linear model predicting sapling height in 12/2019 as a function of sapling height and diameter in 03/2019 (Eq. 4.1).

The model explained 77% of the variability in height. The estimates of the parameters are presented in Table 4.2.

4.10.3.2 Branching

We also modeled using a generalized linear model with a Poisson error distribution the number of ramifications in December 2019 (R) as a function of the number of ramifications (R_0) and diameter in March 2019 (D_0) (Eq. 4.2). The residuals of this model are hereafter referred to as standardized branching (SB).

$$\log(R) = \beta_1 + \beta_2 * R_0 + \beta_3 * D_0 + \beta_4 * R_0 * D_0 + SB \tag{4.2}$$

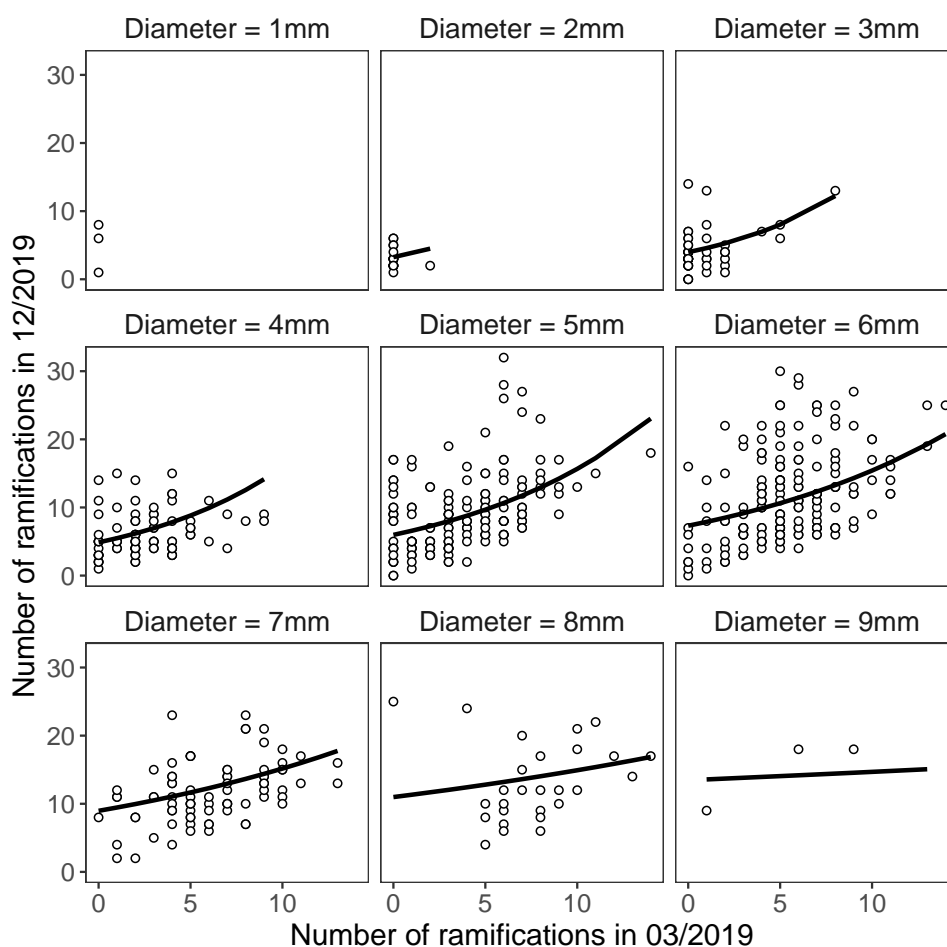


Figure 4.9: Fit of the generalized linear model predicting the number of ramification in 12/2019 as a function of sapling height and diameter in 03/2019 (Eq. 4.2).

The estimates of the model parameters are presented in Table 4.2.

Table 4.2: Estimate and standard error of the parameters of the two models presented in Eq. 4.1 and Eq. 4.2

Parameter	Estimate	Standard error
<i>Height model</i>		
α_1	-25.65	4.66
α_2	1.35	0.09
α_3	10.52	1.00
α_4	-0.10	0.02
<i>Branching model</i>		
β_1	0.77	-0.09
β_2	0.20	0.02
β_3	0.21	0.02
β_4	-0.02	0.003

4.10.4 Appendix D - Analysis of the effect of the simulated browsing treatment on each trait separately.

Because C and Br saplings were likely to differ from CC, CBr and BrBr for various reasons independent of the simulated browsing treatment (sapling age, leaf size, climate, timing and conditions of leaf collection), we analyzed the two study years separately. For each leaf trait (SLA, LChl, LNC, LDMD, LPhenol and LNDF), we used an unpaired Wilcoxon signed-rank test to compare C and Br saplings and a Wilcoxon rank-sum test followed by post-hoc Dunn's multiple comparisons test to compare CC, CBr and BrBr. We also used unpaired Wilcoxon signed-rank tests to compare the shoot traits (SNC, SDMD, SPhenol and SNDF) of the C and Br saplings.

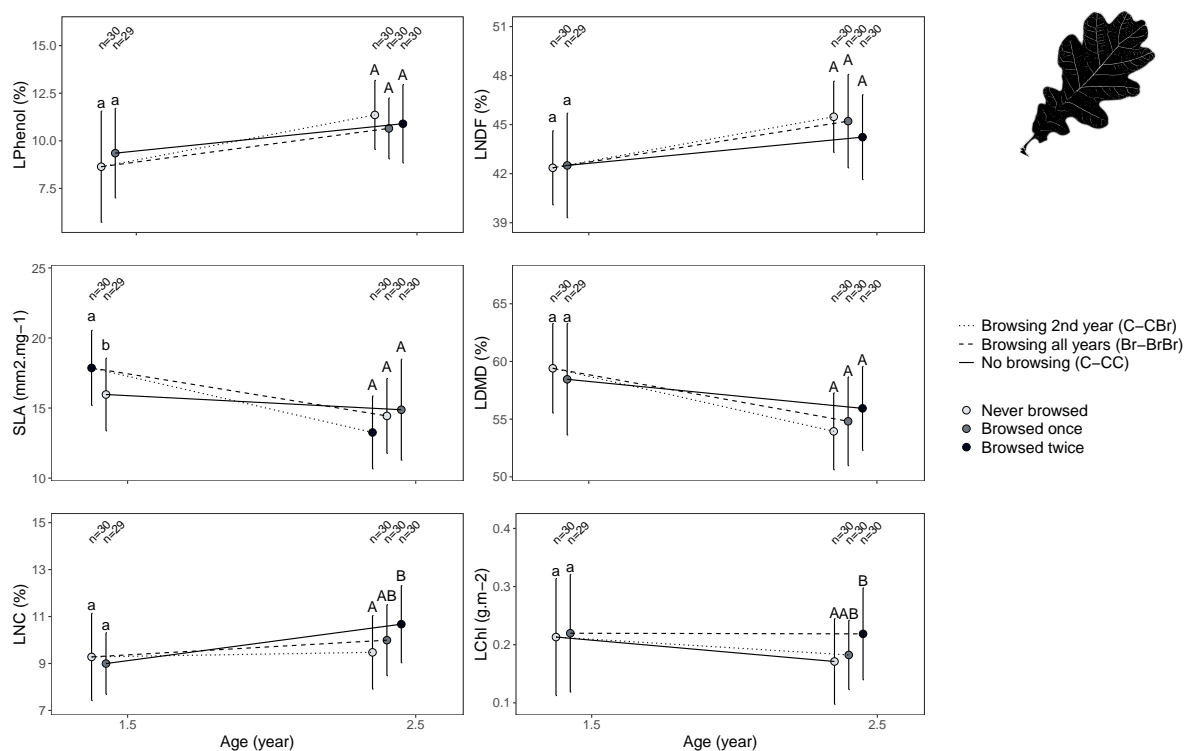


Figure 4.10: Leaf trait values (mean ± standard deviation) measured in summer 2019 and 2020 for the different treatments of simulated browsing. For a given trait, treatments with no letters in common are significantly different from each other at a significance level of $\alpha=0.05$.

At the end of the first year of the experiment, SLA was the only leaf trait significantly affected by the simulated browsing treatment: C saplings had a significantly higher SLA than did Br saplings (Table 4.3). For all the other leaf traits, C saplings were not significantly different from Br saplings. Before the second growing season, when the feeding trials were run, C sapling shoots had a higher phenolic content than did BR saplings (Table 4.3, Fig. 4.9).

Table 4.3: Results of the models testing the effect of the simulated browsing treatment on leaf traits the first (2019) and second (2020) year of the experiment. We analyzed the effect of the treatment with Wilcoxon rank-sum test and Wilcoxon signed-rank test for 2019 and 2020 respectively. The symbol * indicates a significant effect of the treatment with a significance level of 5%.

	2019 (C vs Br)		2020 (CC vs CBr vs BrBr)	
	W	p-value	Chi-square	p-value
<i>Leaf traits</i>				
LDMD	394	0.5	4.2	0.1
LNDF	442	0.9	3.1	0.2
LPhenol	369	0.2	2.2	0.3
LNC	468	0.8	6.7	0.04*
LChl	426	0.7	7.5	0.02*
SLA	609	0.02*	3.6	0.2
<i>Shoot traits</i>				
SDMD	35	0.3		
SNDF	72	0.1		
SPhenol	15	< 0.01*		
SNC	46	0.8		

The second year of the experiment, simulated browsing significantly influenced two leaf traits: LNC and LChl (Table 4.3). CC saplings leaves had a lower LNC (Dunn's test, $p = 0.01$) and LChl (Dunn's test, $p < 0.01$) than did BrBr leaves (Fig. 4.10). Finally, CC leaves tended to have a higher LNDF and a lower LDMD than BrBr saplings (Fig. 4.10) but these differences were non-significant at $\alpha = 5\%$ (Table 4.3).

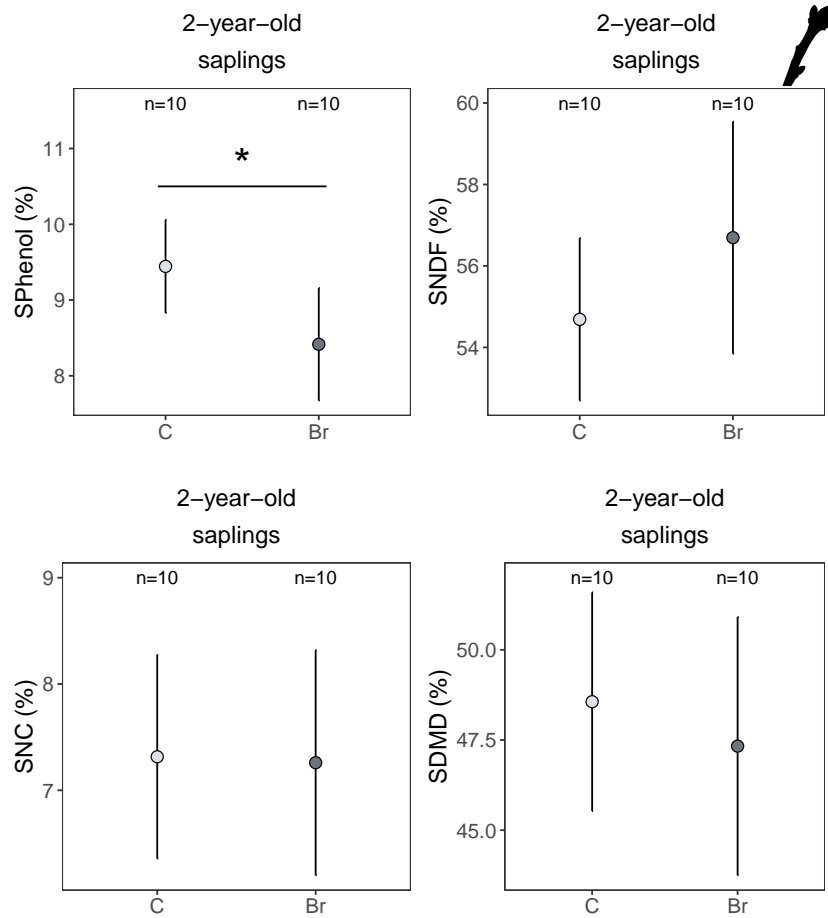


Figure 4.11: Shoot trait values (mean \pm standard deviation) measured in winter 2019/2020 for the different treatments of simulated browsing. The symbol “*” indicates that the two treatments are significantly different from each other at a significance level of $\alpha=0.05$.

4.10.5 Appendix E –Redundancy analysis scores for leaf and shoot traits

Table 4.4: Scores of the six leaf traits on the four constrained axes showing differences between treatments and years (see Fig. 4.3 in the main text). The proportion of constrained and total inertias explained by each axis is also given.

	RDA1	RDA2	RDA3	RDA4	
LChl	-0.286	-0.336	-0.197	-0.043	
SLA	-1.058	-0.157	0.212	0.040	
LNC	0.403	-0.623	0.059	0.009	
LNDF	0.987	0.001	0.187	-0.032	
LDMD	-1.067	-0.011	-0.061	0.022	
LPhenol	0.916	-0.026	-0.114	0.089	Total
Proportion of constrained inertia	0.864	0.105	0.028	0.003	1
Proportion of total inertia	0.148	0.018	0.005	0.000	0.172

LChl: leaf chlorophyll content; *SLA*: specific leaf area; *LNC*: leaf nitrogen content; *LNDF*: leaf fiber content; *LDMD*: leaf dry matter digestibility; *LPhenol*: leaf phenolic content

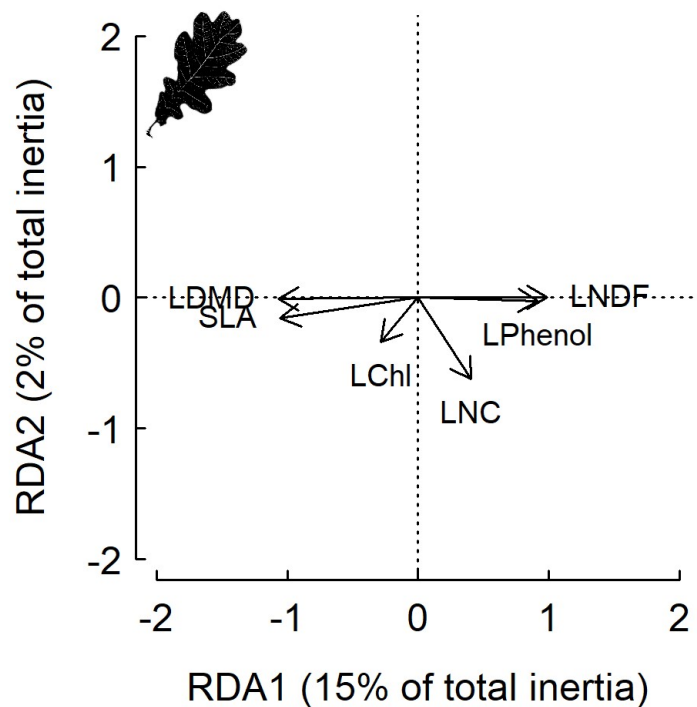


Figure 4.12: Scores of the six leaf traits on the two first constrained axes showing differences between treatments and years (see Fig. 4.3 in the main text).

4.10.6 Appendix F - Morphology of the saplings included in the feeding trials.

We compared the height and the number of ramifications of the C and Br saplings ($n = 250$ per treatment) that were included in the feeding trials in December 2019 with Student's two sample t-tests.

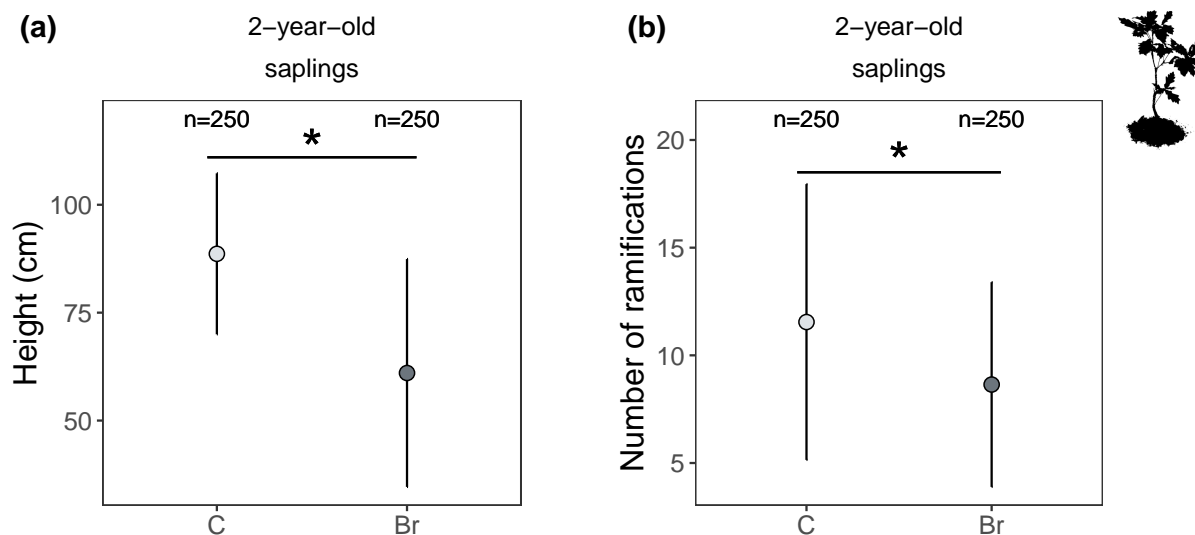


Figure 4.13: (a) Height (cm) and (b) number of ramifications (mean \pm standard deviation) measured in December on the C and Br saplings included in the feeding trials. The symbol “*” indicates that the two treatments are significantly different from each other at a significance level of $\alpha = 0.05$.

We found that individuals of treatment C were higher (Student's t-test, $t = 13$, $df = 436$, $p < 0.01$) and had more ramifications (Student's t-test, $t = 6$, $df = 460$, $p < 0.01$) compared to the individuals of treatment Br. The lateral span was not statistically different between the two treatments (Student's t-test, $t = 0.3$, $df = 442$, $p = 0.74$) (Fig. 4.11).

CHAPTER

5

OAK RESPONSES TO BROWSING IN FIELD CONDITIONS

5.1 Context and objective

This study was designed to investigate the same research questions as in chapter 4 but in field conditions. The aim was to assess the effect of simulated browsing on (i) oak sapling growth and leaf traits, (ii) winter shoot chemical composition and (iii) subsequent attractiveness to roe deer. Since the theoretical context has already been presented in the previous chapter (see section 4.2), this chapter will mostly focus on the methodology planned for this experiment. I will also briefly present and discuss the results obtained.

5.2 Overview of the methodology

5.2.1 Study area

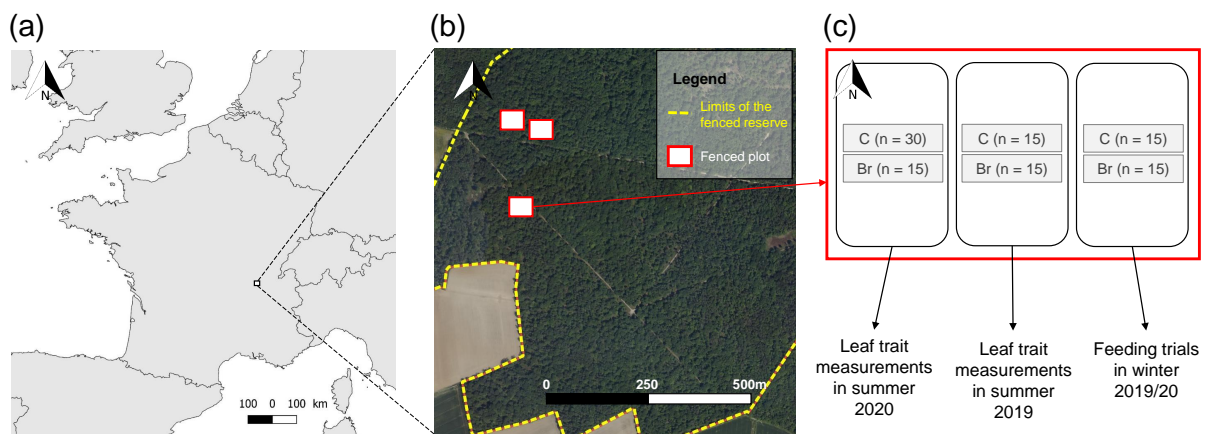


Figure 5.1: (a) Location of the Pierre Vérots Foundation in France, (b) of the three fenced plots inside the Foundation and (c) spatial organization of the 105 seedlings selected in each fenced plot.

This study was conducted in a 148ha fenced private reserve belonging to the Pierre Vérots Foundation (4°55' 30'E, 45°57' N), located in the Dombes region (Eastern France) (Fig. 5.1.a). The forested habitat of this fenced reserve is an uneven-aged pedunculate oak-dominated forest, where hornbeam, poplar (*Populus tremula*), and birch (*Betula pubescens*) are also common. When the experiment was set up in December 2018, the fenced area hosted a population of ten fallow deer, which hunting reduced to one individual by the end of 2019;

a replacement population of ten roe deer were introduced in December 2019. Wild boar were abundant throughout the experiment.

5.2.2 Experimental set-up

In December 2018, we erected 1.5m-high fences around three regeneration sites (Fig. 5.1.b) of 12 to 17m² hosting dense cohorts of one-year-old oak saplings and where competitive understory vegetation was scarce. We selected, tagged and mapped 105 oak saplings presenting similar morphological characteristics (no lateral shoots, height ranging from 18 to 30cm) per fenced plot (for a total of 315 saplings in the experiment). All the other oak seedlings and saplings present in the fenced plots were removed. In March 2019, 45 saplings per fenced plot underwent a simulated browsing treatment (5cm of the apical shoot were clipped off and roe deer saliva was applied: treatment Br hereafter), while the remaining 60 saplings were left untouched as controls (treatment C hereafter).

5.2.3 Planned chronology of the experiment

Thirty saplings (15 per treatment) per fenced plot were to be sampled for leaf-trait measurements in August 2019 (Fig. 5.2). From a spatial point of view, these saplings were located at the center of each fenced plot, leaving two remaining groups: 30 saplings (15 per treatment) at the eastern side of the fenced plot, and 45 saplings (30 C and 15 Br) at the western side of the fenced plots (Fig. 5.1.c). In December 2019, the 30 saplings located at the eastern side of each fenced plot were to be “unfenced” to expose them to the recently introduced roe deer population. Camera traps were to be set up to verify the animals’ movements, and browsing damage was to be monitored on a weekly basis throughout winter and spring. For the 45 saplings remaining in each fenced plot, we planned to apply the simulated browsing treatment in March 2020 to 15 Br and 15 C saplings, leaving three treatments for the second year of the experiment: CC (no simulated browsing applied), CBr (simulated browsing in March 2020 only) and BrBr (simulated browsing in March 2019 and 2020). The clipped shoots were to be kept for chemical analysis, while the 45 saplings per fenced plots were to be sampled in August 2020 for leaf-trait measurements (Fig. 5.2).

5.2.4 Actual chronology of the experiment

In summer 2019, an unexpected drought combined with the relatively poor canopy openness in each fenced plot caused significant mortality among the monitored saplings (69% of mortality in September 2019). The number of remaining sapling was insufficient to conduct the experiment as planned: no leaf traits were measured, nor were feeding trials actually performed. Survival rate and the height of each remaining sapling were measured in

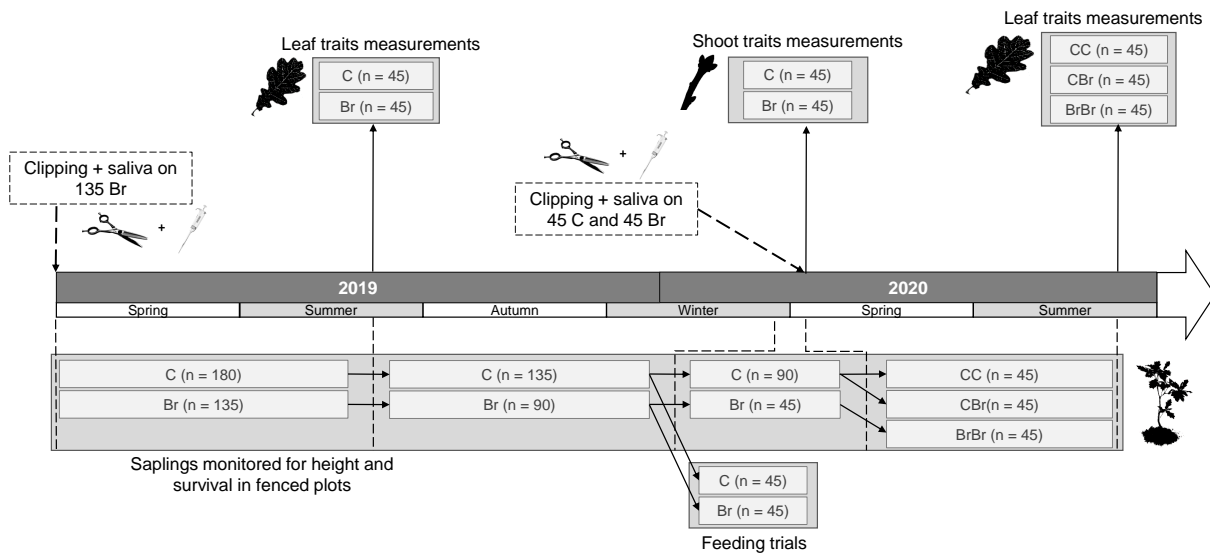


Figure 5.2: Chronology planned for the experiment. Due to the high mortality rate in summer 2019, no leaf traits measurements nor feeding trials were conducted, and the experiment was stopped at the end of 2019.

March, May, July and September. In December 2019, a final survey of sapling survival was conducted, and the experiment was stopped.

5.3 Results

The only data available for analysis were the height and survival data for the year 2019. These data are at the population level (with $n=3$ fenced plots), though most of the data from the experiment (leaf- and shoot-trait measurements) were originally to be analyzed at the individual level. Due to the relatively low number of fenced plots, I did not conduct any statistical analyses and chose to show only the global trends emerging from the limited available data (Fig. 5.3).

Height growth was negligible: C saplings did not gain in height from March to September 2019, while Br saplings lost 5cm of height on average following the simulated browsing treatment (Fig. 5.3.b). Survival was equivalent between the two treatments until July but in September and December, a sharp difference between the two treatments emerged: survival rate for C sapling was twice as high as for Br saplings (Fig. 5.3.a).

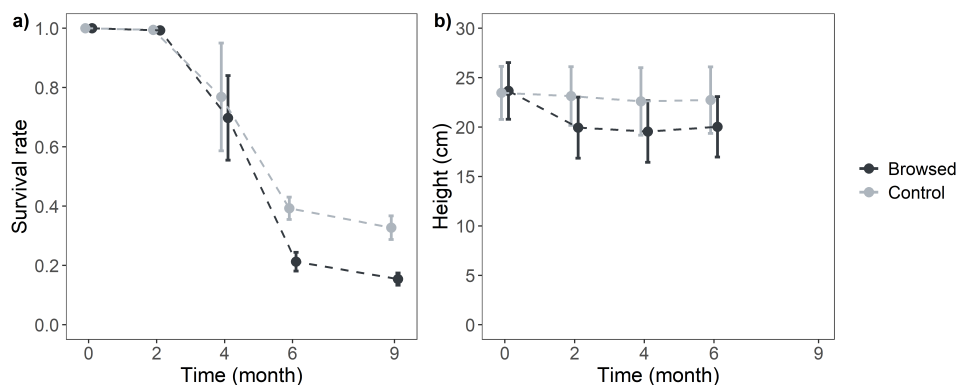


Figure 5.3: Oak seedling survival rate (mean \pm standard deviation) (a) and height (mean \pm standard deviation) (b) from the application of simulated browsing (March 2019, time = 0 in the x-axis) to the end of the experiment (December 2019). Only survival was monitored in December 2019 since height growth was null from September to December.

5.4 Conclusion

This short study highlighted the fact that experiments conducted *in situ* may be subject to field-related hazards that can compromise the study. Nevertheless, an interesting trend emerged from these limited results. Deer browsing has not been documented as a significant mortality factor for oak saplings in the literature (Drexhage & Colin, 2003; Götmark *et al.*, 2014), but our results suggest that it could actually increase mortality for young oak saplings already exposed to environmental stress (*i.e.* drought in this experiment). However, considering the low number of replicates in this experiment, further study of this potential interaction between drought and browsing would be necessary to confirm this hypothesis.

CHAPTER

6

CANOPY OPENNESS AND EXCLUSION OF WILD UNGULATES ACT SYNERGISTICALLY TO IMPROVE OAK NATURAL REGENERATION

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6.1 Abstract

The recruitment of forest trees is driven by both bottom-up processes (the acquisition of resources) and top-down processes (herbivory). To initiate stand regeneration, foresters commonly reduce tree density to increase light levels for seedlings and enhance primary productivity. These changes in vegetation dynamics, however, could also influence effects of ungulate browsing, resulting in unintended consequences for forest management. Here, we assessed how effects of ungulate exclusion and canopy opening interacted to affect the regeneration of two oak species: *Quercus robur* and *Quercus petraea*. We monitored the growth and survival of oak seedlings for two to three growth seasons in paired fenced and unfenced plots under contrasting conditions of canopy openness (8% to 52%) at five sites in southern Sweden and three sites in northeastern France. We scored browsing in the unfenced plots by the four cervids occurring in these areas (*Alces alces*, *Capreolus capreolus*, *Cervus elaphus* and *Dama dama*). Fencing increased the growth of (mostly taller) seedlings occurring in Sweden and the survival of (mostly smaller) seedlings in France. Both effects increased as canopies became more open. Browsing reduced oak seedling growth in both countries, independently of canopy openness. Canopy openness increased browsing levels in Sweden. Cervid densities did not appear to modify how fencing affected oak seedling growth and survival. In both contrasting forest environments, creating gaps tended to enhance ungulate damage on young forest stands as browsing frequency increased. We conclude that net forest regeneration reflects a subtle equilibrium between enhancing resource availability, boosting seedling growth, and limiting herbivory, which curtails seedling growth and survival.

Keywords: Plant-herbivore interactions, red deer, roe deer, moose, fallow deer, herbivory

6.2 Introduction

The development of most living communities is driven by both bottom-up and top-down processes. A bottom-up process is the regulation of communities by lower trophic levels – e.g. limited nutrients for plants or prey for predators – while a top-down process is the impact of a higher trophic level on lower levels – e.g. predation (Hairston *et al.*, 1960; Power, 1992). For decades, scientists have focused on the respective importance of these two types of mechanisms to regulate populations (Dyer & Letourneau, 1999; Hairston *et al.*, 1960), and on the factors influencing resource acquisition (bottom-up) and predation (top-down) (Power, 1992). In recent years, there has been a growing interest in the interactions between bottom-up and top-down processes, observed in a wide range of ecosystems (Churski *et al.*, 2017; Collar *et al.*, 2017; Lynam *et al.*, 2017; Wieters, 2005). For instance, both in marine communities (Hillebrand, 2005) and in cultivated fields (Moran & Scheidler, 2002), it has been shown that increasing resource availability does not necessarily benefit the organism consuming the resource as it may also enhance the importance of predation. This type of interaction may have major implications for ecosystem management, as it questions the efficiency of an anthropogenic increase in resource availability to promote organisms of high ecological or economic value such as, for instance, forest trees.

Light is a crucial resource for plants as it provides them the energy required to assimilate carbon and grow, defend and store nutrients (Ericsson *et al.*, 1996; Giertych *et al.*, 2015) while ungulate browsing is a major top-down force regulating the production of plant biomass (Martin *et al.*, 2010). In forest ecosystems, because the canopy of mature trees intercepts most of the solar irradiance, tree seedlings often need an opening of the canopy to be recruited into adult trees (Watt, 1947; Yamamoto, 2000). The natural formation of gaps through the senescence and decay of old trees or natural disturbances such as fire or storms can take a very long time. In forestry, the harvesting of adult trees at their economic optimum hastens canopy opening and initiates the process of forest natural regeneration. Though many studies acknowledge that the creation of canopy gaps enhances seedling growth and biomass production (Cannell *et al.*, 1988; Lu *et al.*, 2018), surprisingly little is known about how this sudden increase in resource availability influences top-down processes such as ungulate browsing.

A high degree of canopy openness often leads to an increase in ground cover (Willms *et al.*, 2017) and species richness (Alexander & Mack, 2017) in the forest understory. An increase in canopy openness may also, however, increase browsing pressure in forest gaps by providing a higher quantity and diversity of forages (Kuijper *et al.*, 2009; Mangas & Rodríguez-Estival, 2010). Other studies have documented that plants growing under canopy gaps may have a different chemical composition than plants growing in the shade (Agrell *et al.*, 2000;

Giertych *et al.*, 2015), and hence a different palatability for ungulates (Tucker *et al.*, 1976). For instance, light-demanding species are believed to be more palatable than shade-tolerant species due to a higher nutrient content and fewer chemical defenses (e.g. phenolic compounds) (Giertych *et al.*, 2015; Kitajima *et al.*, 2012). Lastly, canopy openness may influence the ability of individual seedlings to recover and/or respond to browsing in terms of growth, morphology or chemistry. No common response across tree species has been found, however: light availability may improve or worsen seedling growth response to deer browsing in field conditions, depending on tree species (Baraza *et al.*, 2010; Kupferschmid *et al.*, 2014).

Petersson *et al.* (2019) showed that the accelerating decline in pedunculate (*Quercus robur* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.) regeneration observed in Sweden over the last 60 years was due to the increased abundance of wild ungulates, but also to changes in forestry practice that led to denser forests and insufficient light availability for seedlings (Lüpke, 1998). This increase in ungulate populations follows a global trend observed in the Northern Hemisphere (Beguin *et al.*, 2016; Côté *et al.*, 2004). In most temperate European forests, pedunculate and sessile oak (hereinafter referred to as oak) are classified as highly palatable species (Bergqvist *et al.*, 2018; Kullberg & Bergström, 2010). Browsing by wild ungulates may therefore be an important limiting factor for growth during the first stages of oak regeneration (Braithwaite & Mayhead, 1996; Harmer, 2001). Browsing may also reduce oak seedling survival, though to a lower extent than growth, due to the high sprouting ability of oak seedlings (Drexhage & Colin, 2003). Several field studies in Europe have confirmed that fencing to exclude wild ungulates could greatly benefit oak natural regeneration by protecting the seedlings from browsing (Leonardsson *et al.*, 2015; Petersson *et al.*, 2020). Oak is also particularly shade-intolerant at the beginning of the regeneration phase and cannot survive low light availability (Lüpke, 1998). In forest environments, opening the canopy is often necessary to achieve the successful regeneration of these oak species (Ligot *et al.*, 2013; Petersson *et al.*, 2020).

Because its regeneration is highly influenced by both ungulates browsing and canopy openness (Leonardsson *et al.*, 2015; Petersson *et al.*, 2020; Tinya *et al.*, 2020; Lüpke, 1998), a case study of oak is relevant when investigating the interactive effects of these two factors on the first stages of natural regeneration – *i.e.* seedling development and survival. Although many studies investigated the effects of canopy openness and browsing on oak regeneration, the interactive effect of these two factors and the mechanisms driving this interaction are poorly understood. In this paper, we used the data from two comparable studies, conducted over similar periods in forests in southern Sweden and northeastern France. Both studies monitored the growth and survival of oak seedlings in pairs of fenced and unfenced plots located under different levels of canopy openness ranging from 8% to 52%. We tested for the existence of common patterns in the contrasted environments (*i.e.* in terms of ungulate

species, soil or climate) considering the following predictions:

- *P1*: Both ungulate exclusion and canopy openness increase oak seedling height growth (P1.a) and survival (P1.b).
- *P2*: Oak seedlings growing under an open canopy are more likely to be browsed by ungulates than seedlings growing under closed canopy.
- *P3*: Annual height growth is reduced less by browsing for oak seedlings growing under an open canopy than for seedlings under a closed canopy.

The development of understory vegetation – e.g. shrubs, forbs, vines – is also highly conditioned by canopy openness (Gaudio *et al.*, 2008) and may influence seedling growth (Jensen & Löf, 2017), or browsing probability (Harmer *et al.*, 2010; Jensen *et al.*, 2012). Therefore, we also tested whether understory competition influenced oak growth, and browsing probability. Lastly, as we conducted the study at different study sites characterized by different ungulate densities, we tested whether the effect of fencing on oak seedling growth and survival increased with ungulate density.

6.3 Material and methods

6.3.1 Study area

Five study sites were located in southern Sweden and three in northeastern France (Fig. 6.1). All eight sites were located at low elevations (45 to 400m above sea level) in forests where both pedunculate and sessile oak were abundant. Because the two species occurred in sympatry at every site and present very similar morphological characteristics during the regeneration phase (Bacilieri *et al.*, 1995) we made no distinction between the two species, hereinafter referred to as oak (*i.e.* *Quercus sp.*). Due to the strong overlap in the distribution of these species in Europe, this simplification is relatively common in studies on oak regeneration (Annighöfer *et al.*, 2015; Petersson *et al.*, 2020). Oak, Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) were dominant in the Swedish sites (Table 6.1). In France, most of the study sites were dominated by oak, beech (*Fagus sylvatica*) and hornbeam (*Carpinus betulus*) (Table 6.1). Although moose (*Alces alces*) and roe deer (*Capreolus capreolus*) were most abundant in southern Sweden, red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) were also present (Table 6.1). Roe deer occurred at all three French sites and red deer was present at two of the sites. Wild boar (*Sus scrofa*) was abundant in both countries. We did not apply any herbicide neither in the French, nor in the Swedish sites. We did not observe the occurrence of fire in any of the stands included in the experiment

throughout the study. A snow cover reaching 10 to 30 cm depth occasionally persisted up to 30 consecutive days in some of the Swedish sites, while snow accumulation was negligible in the French sites.

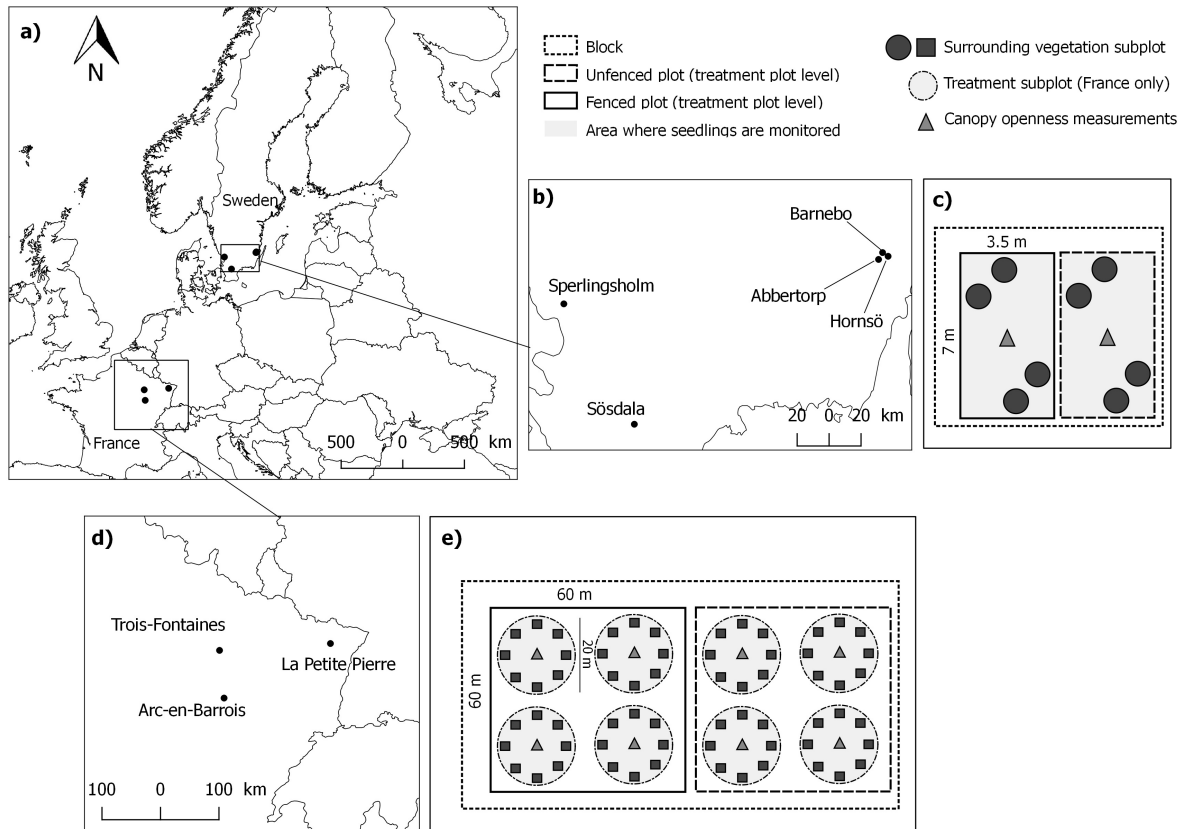


Figure 6.1: a) Location of the eight study sites in Europe, b) location of the 5 study sites in southern Sweden, c) experimental design in Sweden, d) location of the three study sites in northeastern France and e) experimental design in France.

6.3.2 Experimental design and site preparation

At each Swedish site, there were two pairs of fenced (without browsing) and unfenced (with browsing) plots (*i.e.* total of 10 pairs in Sweden). Hereinafter, a pair of fenced-unfenced plots will be referred to as a block and a treatment plot will designate either a fenced or an unfenced plot (thus making two treatment plots per block) (Fig. 6.1.c). We erected a 2-m-high steel wire fence (mesh size: 5 x 5 cm) around one treatment plot per block to protect the seedlings from ungulates and hares, but not from rodents. In one block per site, we cut out a circular canopy gap of around 400 m². Each site therefore contained two blocks associated with two different levels of canopy openness. The treatment plots were 24.5 m² (3.5 x 7m) Fig. 6.1.c). At each site, we set up the blocks in April 2016 and monitored the seedlings every year from 2016 to 2018 (Table 6.1).

In France, there were between four and nine pairs of fenced-*unfenced* plots – *i.e.* blocks – at each site (total of 19 pairs in France). We erected a 2-m-high steel wire fence around one treatment plot per block (mesh size: 10 x 10cm) to protect the vegetation from ungulates, but not from hares or rodents. The same year, we performed partial cutting in each treatment plot, which resulted in contrasted canopy openness conditions both between and within blocks. We also removed all shrubs, seedlings and saplings – except oak – on each treatment plot. The treatment plots were 3600 m² (60 x 60m or 30 x 120m depending on the position of the seed trees) and were divided into four circular treatment subplots with a 10m radius (*i.e.* 314 m²) (Fig. 6.1.e). Table 6.1 presents the dates the blocks were set up, the seedling monitoring period and the number of blocks at each site.

6.3.3 Monitoring the oak seedlings

In Sweden, at the beginning of the study, we marked all the available seedlings in each treatment plot. If the number of available seedlings was higher than 100 in a given treatment plot, a random subset of at least 50 seedlings was selected for measurements (*i.e.* no selection criteria based on the seedling characteristics were applied). An available seedling was defined as any oak individual less than 3m in height since moose can browse trees up to 3m high (Nichols *et al.*, 2015). The year following the beginning of the study, we did not select any additional seedling to compensate for dead or missing seedlings.

In France, we selected seedlings less than 2 m in height – *i.e.* maximum browsing for red deer (Nichols *et al.*, 2015). At the beginning of the study, we selected ten oak seedlings per treatment subplot (*i.e.* 40 per treatment plot), or fewer when the number of oak seedlings in the treatment subplot was less than ten. In later measurements, if a seedling was found dead or missing, we selected a new seedling in the treatment subplot to maintain the number of seedlings monitored constant. As far as possible, we targeted one-year-old seedlings when selecting new individuals.

Table 6.1: Date of treatment installation, monitoring period (first and last year), main canopy tree and main cervid species, range of canopy openness (%) and understory cover index (%) and understory height index (cm) for the eight study sites in Sweden and France. In La Petite Pierre, though the experiment was set up earlier (2012), we restricted the analysis to the 2016-2019 period to ensure uniformity between the French sites. For description of the indices, see text.

Site	Date of Treatment installation	Monitoring period	Tree species	Cervid species	Number of blocks	Canopy openness (%)		Understory cover index	Understory height index
						min	max		
Abbertop	2016	2016-2018	Oak, Scots pine, Norway spruce	Red deer, roe deer, fallow deer, moose	2	18.1	23.4	59%	18cm
Barnebo	2016	2016-2018	Oak, Scots pine, Norway spruce	Red deer, roe deer, fallow deer, moose	2	17.3	22.9	43%	20cm
Hornsö	2016	2016-2018	Oak, Scots pine, Norway spruce	Red deer, roe deer, fallow deer, moose	2	15.4	25.7	44%	20cm
Sperlingsholm	2016	2016-2018	Oak, Scots pine, Norway spruce	Red deer, roe deer, fallow deer, moose	2	12.7	25.5	68%	25cm
Sösdala	2016	2016-2018	Oak, Scots pine, Norway spruce	Red deer, roe deer, fallow deer, moose	2	10.6	30.9	38%	18cm
Arc en Barrois	2014-2015	2016-2019	Oak, beech, hornbeam	Red deer, roe deer	9	8.8	52.4	15%	33cm
Trois Fontaines	2015	2016-2019	Oak, beech, hornbeam	Roe deer	9	8.1	41.9	15%	17cm
La Petite Pierre	2012	2016-2019	Oak, beech, silver fir, Norway spruce	Red deer, roe deer	6	7.8	39.5	4%	8cm

For our final analysis, we removed all seedlings higher than 2 m from the dataset to ensure compatibility between the two countries. We selected a total of 1163 seedlings in Sweden and 2761 in France (the number of selected seedlings in France is higher because we selected additional seedlings throughout the experiment to replace dead or missing ones). We measured the height of each selected seedling once a year, after the growing season in Sweden (August) and before the growing season in France (March). We also noted whether the current year shoots presented marks of browsing by ungulates (binary data, with no distinction between winter and summer browsing). Marks of ungulate browsing were identified using the same criteria as [Kullberg & Bergström \(2001\)](#). From the height measurements, we computed the annual growth rate of a seedling i in year y_1 (GR_{i,y_1}) as:

$$GR_{i,y_1} = \frac{H_{i,y_2} - H_{i,y_1}}{y_2 - y_1} \quad (6.1)$$

where H_{i,y_1} and H_{i,y_2} are the height of seedling i measured in year y_1 and y_2 respectively. We used the growth rate instead of the relative growth rate (*i.e.* growth rate divided by the initial height) because initial height had to be included in the statistical analyses anyway to account for possible interactions with other explanatory variables. The relative growth rate also assumes a linear relationship between the growth rate and initial height, which is not always true for oak ([Ligot *et al.*, 2013](#)). Years y_1 and y_2 were always two consecutive years, except in the case of a data gap – *i.e.* a seedling was first lost, then found alive one or two years later.

6.3.4 Understory competition

In Sweden, we monitored understory competition in four circular $2m^2$ vegetation subplots randomly placed inside each treatment plot (Fig. 6.1.c). Once a year in August, we estimated the cover (percentage of the soil surface occupied by the vertical projection of the leaves $\pm 10\%$) and mean height ($\pm 1cm$) of the different understory species – *i.e.* shrubs, forbs and vines – in each vegetation subplot.

In France, we monitored understory competition in eight vegetation subplots of $1m^2$ (1 x 1m) arranged in a circle (5m radius) around the center of each treatment subplot (Fig. 6.1.e). In each vegetation subplot and each year, in spring, we estimated the cover class (0-5%, 5-25%, 25-50%, 50-75% and 75-100%) of every understory species per vegetation layer (three vegetation layers: below 50cm, 50-130cm and 130-300cm). To ensure that the data were comparable between the two countries, we first converted the cover classes into a percentage using median values (*e.g.* if a species was in the 25-50% cover class, its median cover was 37.5%). We combined the median cover values of the three layers to obtain the total cover for each understory species per vegetation subplot (values ranged between 0 and

100%) following the method proposed by Fischer (2015). We computed the cover ($Cover_{i,k}$) of understory species i in vegetation subplot k as:

$$Cover_{i,k} = 1 - \prod_{l=1}^3 (1 - c_{i,l,k}) \quad (6.2)$$

where $c_{i,l,k}$ is the median cover of understory species i in layer l of vegetation subplot k . Similarly, we computed the mean height $H_{i,k}$ of understory species i in vegetation subplot k as the mean of the median heights (e.g. the median height of the vegetation layer 0-50cm was 25cm) weighted by the cover values of the species in each vegetation layer:

$$H_{i,k} = \frac{\sum_{l=1}^3 (c_{i,l,k} * h_l)}{\sum_{l=1}^3 c_{i,l,k}} \quad (6.3)$$

where h_l is the median height for vegetation layer l .

From the mean height and cover of each understory species, we computed an understory height index (UHI_k) and an understory cover index (UCI_k) in both countries, specific to each vegetation subplot k , as follows:

$$UHI_k = \frac{\sum_{i=1}^{n_k} (c_{i,k} * H_{i,k})}{\sum_{i=1}^{n_k} c_{i,k}} \quad (6.4)$$

$$UCI_k = 1 - \prod_{i=1}^{n_k} (1 - C_{i,k}) \quad (6.5)$$

where n_k is the number of understory species in vegetation subplot k . We averaged the values of the understory height index and understory cover index to obtain an index at the treatment-plot scale in Sweden, and at the treatment-subplot scale in France. The main understory species were bilberry (*Vaccinium myrtillus*) in Sweden and bramble (*Rubus fruticosus*) and raspberry (*Rubus idaeus*) in France.

6.3.5 Canopy openness

In Sweden, we measured canopy openness in the summer of every sampling year by taking one hemispherical photograph (Canon Coolpix 8800VR, fisheye lens LC-ER2) in the middle of each treatment plot (Fig. 6.1.c) during an overcast day. We took the photograph at a height of 160 cm above ground level, with the lens perpendicular to the forest floor. The north was automatically referenced in the image. We thresholded the images in the blue color plane, and computed the percentage of canopy openness with the Gap Light Analyzer software (Frazer *et al.*, 1999).

In France, in the summer of 2019, we measured canopy openness at the center of each treatment subplot (*i.e.* four measurements per treatment plot) (Fig. 6.1.e) at a height of approximately 130 cm above the ground with a spherical convex densiometer following the protocol of [Baudry *et al.* \(2014\)](#). We assumed that canopy openness was constant throughout the different sampling years. [Baudry *et al.* \(2014\)](#) includes a regression analysis of the relationship between canopy openness percentage measured with hemispherical photographs (*CO_f*) and with a densiometer (*CO_d*) ($R^2 = 0.60$), as follows:

$$CO_d = -6.75 + 1.77 * CO_f \Leftrightarrow CO_f = 3.81 + 0.57 * CO_d \quad (6.6)$$

We used this regression equation to convert the French measurements, originally expressed in *CO_d*, to *CO_f* to ensure that the data were comparable between the two countries. Hereinafter, this percentage is referred to as “canopy openness” for both countries.

In this study, canopy openness never exceeded 60%. Indeed, during the first stages of oak natural regeneration, it is common practice to maintain adult trees in the stand to ensure a minimal flow of seeds in case the regeneration fails. Foresters harvest these remaining trees (*i.e.* final cut) only when there is a sufficient density of saplings above 3m high, which was not the case yet in neither of the two protocols (France and Sweden).

6.3.6 Cervid density

In Sweden, we computed a moose density index and a deer density index (red deer, roe deer and fallow deer were all included in the same index, but roe deer was by far the most common deer species) for each site based on data from dung pellet counts. This count is performed on an intermediate landscape scale and is designed to assess the average density of ungulates frequenting that landscape wintertime ([Bergström *et al.*, 2011](#)). We collected pellet-count data in 20 circular sample plots located every 200 m along the side of a 1x1 km square transect (= 4 km transect) laid out in the landscape around each site, following protocol described in [Månsson *et al.* \(2011\)](#). Moose sample plots were 100 m^2 and deer sample plots were 10 m^2 . Every year from 2016 to 2018, the sample plots were cleaned in autumn (all fecal pellets were removed) and surveyed the following spring. We only took into account pellet groups with at least 20 single moose and 10 single deer pellets, with the majority of the pellets located within the boundaries of the plots. The density index $DI_{i,j}$ for species i (deer or moose), and year j was computed as:

$$DI_{i,j} = \frac{PG_{i,j} * k_i}{NP * D_i * T_j} \quad (6.7)$$

where $PG_{i,j}$ is the number of pellet groups found for species i during year j , k_i is an area

scaling factor per species ($k_{deer} = 100000$, $k_{moose} = 10000$). NP is the number of surveyed sample plots (20 excluding exceptions). D_i is an index correlated to the defecation rate of each species ($D_{deer} = 22$, $D_{moose} = 17$) and T_j is the number of days between the previous autumn clearing and the spring survey during year j . In addition to the deer and moose indices, we also computed a cervid density index, the sum of moose density index and of deer density index for each site. For the rest of the analysis, we averaged each of the three indices over the three years to obtain a mean density index per species (deer, moose) and for all cervids for each site.

In France, we computed abundance indices for red deer and roe deer at each site (Appendices, Table 6.3). However, because of the limited number of sites in France, and the difficulty to compare these indices among sites, we only used the Swedish data for the analysis.

6.3.7 Statistical analysis

In a first approach, we analyzed the data from the two countries in a single model. However, the country effect interacted with all the other variables and, in order to obtain model equations that are easy to interpret, we fitted the data separately for the two countries, using the same explanatory variables.

To study the effect of fencing and canopy openness on oak seedling growth (P1.a), we explained the growth rate of individual seedlings using a linear mixed model with three fixed effects: initial seedling height (H_{i,y_1} in eq. 6.1, added as a control variable), canopy openness and fencing. To account for the hierarchical structure of the experimental design, and the fact that there were several measurements per individual (one per growing season), we included a nested random effect (Site/Block/Individual). To study the effect of fencing and canopy openness on survival (P1.b), we used as a response variable the survival of the oak seedlings after two years (binary variable: 1 = alive, 0 = dead), in order to have comparable data between the two countries. We analyzed this variable using a generalized linear mixed model with a binomial error distribution and a logit link function. We included three fixed effects: initial seedling height (*i.e.* height of the seedling the year of its selection), canopy openness and fencing, and a nested random effect (Site/Block).

We analyzed browsing occurrence (binary data, measured for each individual seedling once a year) using unfenced plot data only. We studied the effect of canopy openness on browsing occurrence (P2) through a generalized linear mixed model with a binomial error distribution and a logit link function. In addition to canopy openness, we included a previous browsing factor (with two modalities: previously browsed or not) and seedling height as fixed effects as these variables may influence browsing occurrence (Mathisen *et al.*, 2017;

Moore *et al.*, 2000) and must be controlled for to assess the effect of canopy openness. To account for repeated measurements on the same sample, we used a “Site/Block/Year” random effect that allowed us to compare all the individuals within a block for a given year, which is closer to the experimental design of feeding trials, and thus more appropriate for studying browsing likelihood.

To test the effect of canopy openness on the growth response following browsing (P3), we analyzed individual seedlings’ growth rate with a linear mixed model with three fixed effects: initial seedling height (H_{i,y_1} in eq. 6.1, added as a control variable), canopy openness and browsing (factor with two modalities, “browsed” or “unbrowsed”), and a nested random effect (Site/Block/Individual).

We proceeded to the same model selection process for the test of each prediction in both countries. We first included all possible interactions between the fixed effects in the model, then non-significant interactions were removed one by one to select the most parsimonious model (i.e. with the lowest number of terms). To take into account understory competition, we tested whether adding understory cover index and/or shrub height index as additional fixed effects improved the model, based on the Akaike’s Information Criterion (AIC) values. For all the selected models (presented in Table 6.2), we visually checked that the histogram of the model residuals was consistent with the error distribution assumed in the model. We verified the assumption of homogeneity of variance by plotting the residuals against the predictors and the predicted values.

Table 6.2: Selected model for each prediction in France and in Sweden. The complete model selection and the statistics of the selected models are included in the Appendices 6.8.2 and 6.8.4 respectively. The factors included are canopy openness (Ca), initial height (Hi), fencing (Fen), browsing (Br), understory cover index (UCI), understory height index (UHI) and previous browsing (PreB).

Prediction	Response variable	Selected model
<i>Sweden</i>		
P.1.a	Growth rate (<i>cm/year</i>)	Ca+Hi+Fen+Ca*Hi+Hi*Fen+Ca*Fen+Ca*Hi*Fen
P.1.b	Survival (binary)	Ca+Hi+Fen
P.2	Browsing (binary)	Ca+Hi+PreB+UCI
P.3	Growth rate (<i>cm/year</i>)	Ca+Hi+Br+Ca*Hi
<i>France</i>		
P.1.a	Growth rate (<i>cm/year</i>)	Ca+Hi+Fen+Ca*Hi+Hi*Fen
P.1.b	Survival (binary)	Ca+Hi+Fen+Ca*Fen
P.2	Browsing (binary)	Ca+Hi+PreB++Hi*PreB*UCI
P.3	Growth rate (<i>cm/year</i>)	Ca+Hi+Br+Ca*Hi+Hi*Br+UCI+UHI

We computed two indices centered in zero that represented the magnitude of the “deer ef-

fect” on oak growth and survival at each study site in Sweden. The complete calculation of these indices is presented in the Appendix 6.8.4. We fitted simple linear regressions to study the relationship between the impact of deer on growth or survival and the average values over the three years of the three density indices (deer, moose and cervid).

We conducted all the data analyses with the statistical software R version 3.6.3 (RCoreTeam, 2019). We fitted mixed models with the ‘lme4’ package (Bates *et al.*, 2014) and tested the significance of the fixed effects by performing post-analyses of deviance (Wald χ^2 , type II) with the ‘Anova’ function of the ‘car’ package (Fox *et al.*, 2012). We bootstrapped each selected generalized linear mixed model 500 times with the ‘bootMer’ function of the ‘lme4’ package (Bates *et al.*, 2014) to obtain a 95% confidence interval around the model prediction.

6.4 Results

6.4.1 Effect of fencing and canopy openness on oak seedlings growth (P1.a)

In Sweden, both canopy openness ($p = 0.02$) and fencing ($p < 0.01$) increased individual seedlings growth rate, and the interaction between the two variables was significant ($p < 0.01$): the positive effect of fencing was higher under a relatively open canopy (Fig. 6.2.a). When canopy openness was above 25%, growth rate was on average three times higher in fenced plots than in unfenced plots, while below 15% of canopy openness, seedlings in fenced and unfenced plots had the same average growth rate (Fig. 6.2.a).

In France, fencing did not increase growth rate ($p = 0.48$). There was a significant interaction between canopy openness and initial height ($p < 0.01$; Appendix 6.8.4, Table 6.8): canopy openness had a positive effect on the growth rate only for intermediate and tall seedlings (*i.e.* higher than 20 cm) (Fig. 6.2.b).

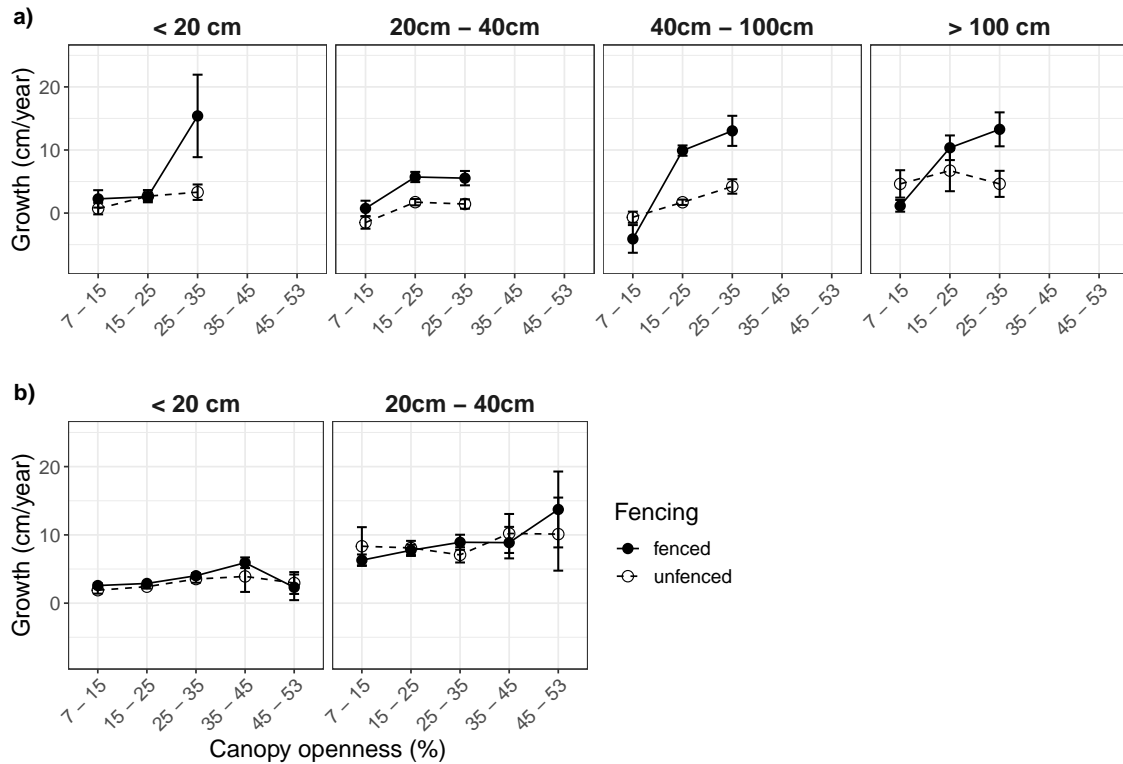


Figure 6.2: Annual seedling growth rate ($cm \cdot year^{-1}$) according to initial height and canopy openness (%) in fenced and unfenced plots, in Sweden (a) and France (b). Error bars show the standard error. Values for initial height and canopy openness classes were chosen for each country based on the distribution of each variable in each country (Appendix 6.8.5).

In both countries, adding understory cover index and/or understory height index to the most parsimonious models did not improve the models, based on the AIC. These variables were therefore not included in the final model (Appendix 6.8.2, Table 6.4).

6.4.2 Effect of fencing and canopy openness on oak seedlings survival (P1.b)

In Sweden, survival after two years increased with canopy openness ($p = 0.03$) (Appendix 6.8.4, Table 6.9). Survival was slightly higher in fenced plots (Fig. 6.3.a.) but the trend was not significant ($p = 0.11$).

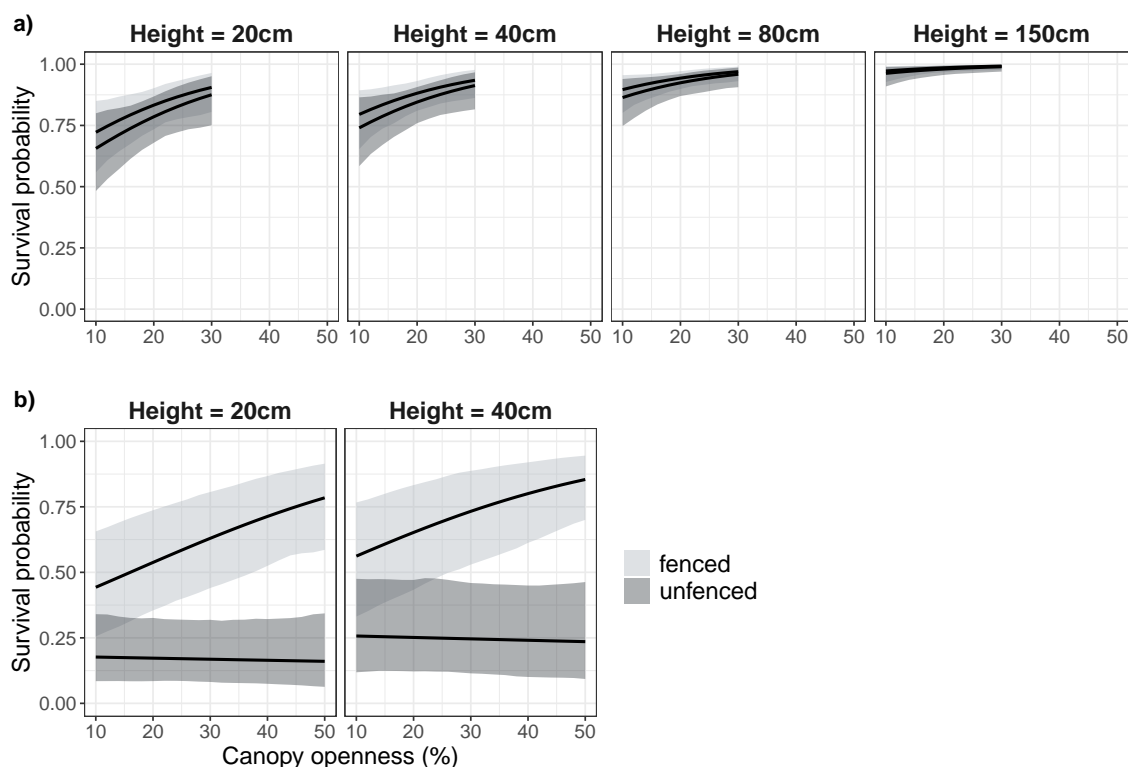


Figure 6.3: Predicted values and 95% confidence intervals from the generalized mixed models for seedling survival probability after 2 years as a function of canopy openness, fencing and initial height in (a) Sweden and (b) France, using models presented in Table 6.2. Initial height values and the range of canopy openness per country were chosen based on the distribution of each variable in each country (cf. Appendix 6.8.5)

In France, both fencing ($p < 0.01$), and canopy openness ($p < 0.01$) increased survival, and the interaction between the two variables was significant ($p < 0.01$; Appendix 6.8.4, Table 6.9). Canopy openness increased survival only in fenced plots (Fig. 6.3.b). Seedlings located in unfenced plots had a very low survival after two years (e.g. 25% for a 40-cm seedling), regardless of canopy openness. Overall, survival after two years was much higher in Sweden than in France (Fig 6.3).

6.4.3 Effect of canopy openness on browsing likelihood (P2)

Canopy openness ($p < 0.01$) increased the likelihood of seedlings being browsed in Sweden but not in France (Appendix 6.8.4, Table 6.10) (Fig. 6.4). In France, the AIC test supported the inclusion of the shrub height index in the final model (Appendix 6.8.2, Table 6.6), but the factor was not statistically significant ($p = 0.06$). In Sweden, the AIC also supported the inclusion of the shrub height index in the final model (Appendix 6.8.2, Table 6.6) that significantly decreased browsing ($p < 0.01$).

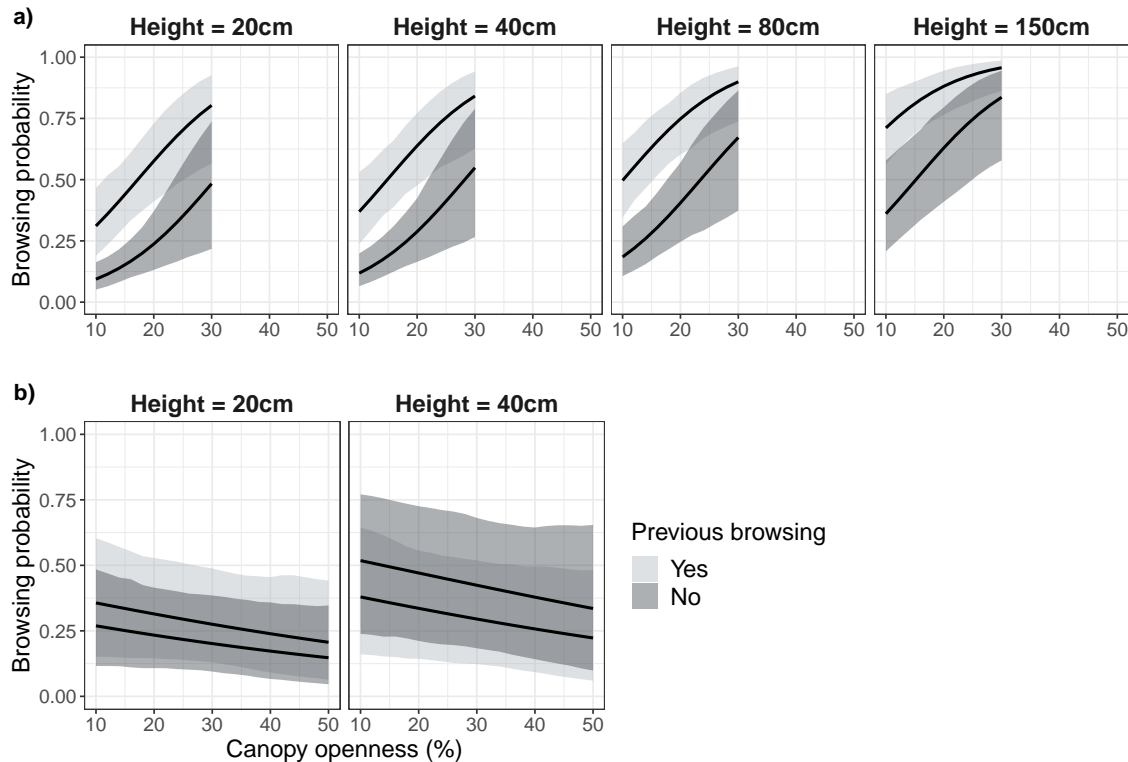


Figure 6.4: Predicted values and 95% confidence interval from the generalized mixed models for browsing probability as a function of canopy openness, previous browsing, and initial height in (a) Sweden and in (b) France using models presented in Table 2. Initial height values and the range of canopy openness per country were chosen based on the distribution of each variable in each country (cf. Appendix 6.8.5)

6.4.4 Effect of canopy openness on the reduction in growth rate induced by browsing (P3)

Browsing had a negative effect on growth rate both in Sweden ($p < 0.01$) and in France ($p < 0.01$) (Appendix 6.8.4, Table 6.11) but the model selection did not support the inclusion of an interaction between canopy openness and browsing in the final models (Appendix 6.8.2, Table 6.7) (Fig. 6.5). This means that the negative effect of browsing on growth rate was independent of canopy openness. Overall, the negative effect of browsing on growth rate was much higher in France than in Sweden – *e.g.* for seedlings between 20 and 40cm, browsing reduced the average growth rate by 5.94 $\text{cm}\cdot\text{year}^{-1}$ in France, and only by 1.23 $\text{cm}\cdot\text{year}^{-1}$ in Sweden. In France only, the AIC supported the inclusion of understory competition indices in the model, and both the understory height index ($p < 0.01$) and the understory cover index ($p = 0.04$) were positively correlated to the growth rate (Appendix 6.8.4, Table 6.11).

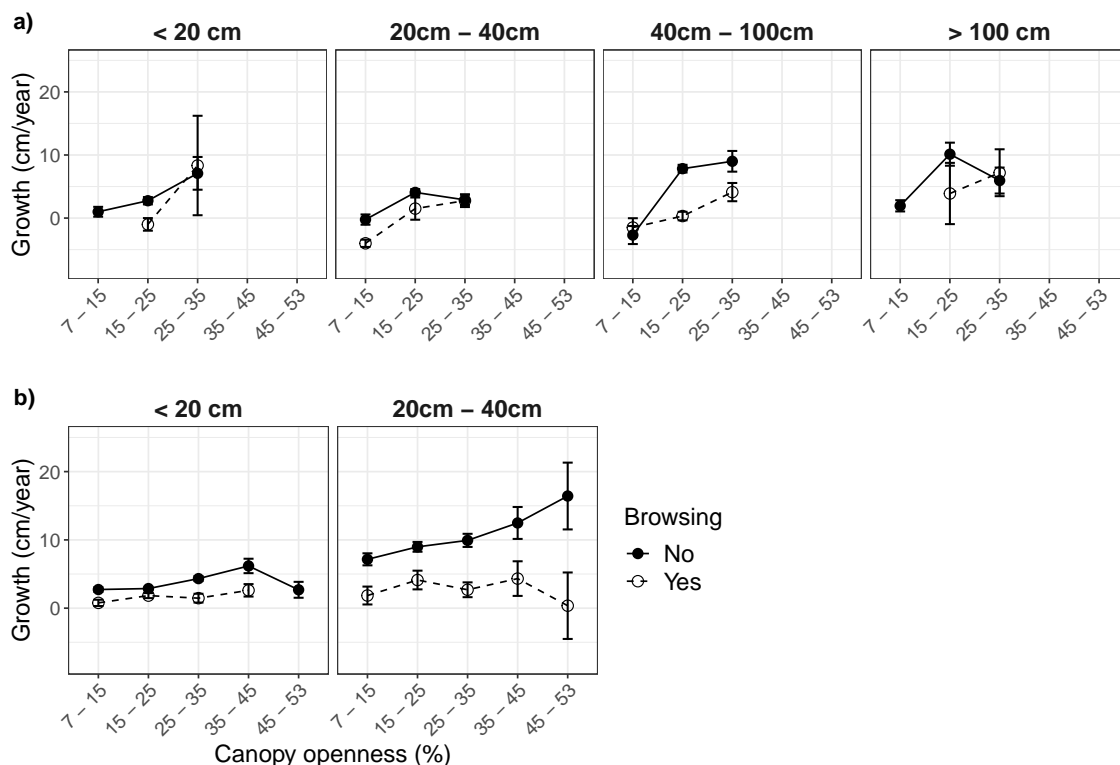


Figure 6.5: Annual seedling growth rate ($cm \cdot year^{-1}$) according to browsing, initial height and canopy openness (%), in Sweden (a) and France (b). Error bars show the standard error. Values for initial height and canopy openness classes were chosen for each country based on the distribution of each variable in each country (Appendix 6.8.5).

6.4.5 Relationship between cervid density and the impact of cervids on oak growth and survival in Sweden.

Neither the impact of cervids on growth ($p = 0.48$) nor their impact on survival ($p = 0.59$) were correlated to our cervid density index (Fig. 6.6). Results were similar when we compared the impact of cervid on growth and survival with the more narrowly defined density indices (moose and deer density indices) (Appendix 6.8.6).

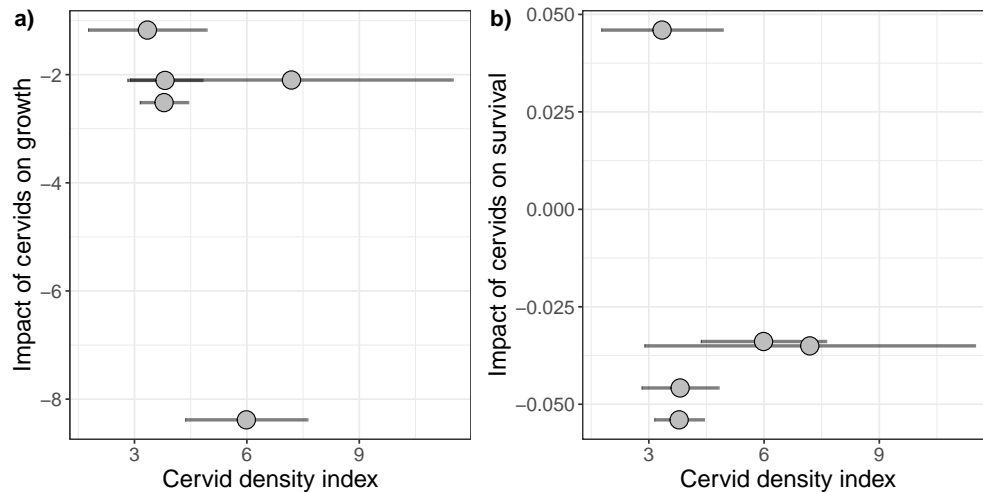


Figure 6.6: Variations in the impact of cervids on growth and survival with cervid density index ($animal.km^{-2}$) in Sweden. Negative values of the impact of cervids on growth and survival indicate a negative effect of deer on seedling growth and survival respectively. Horizontal error bars show the standard error of the cervid density index.

6.5 Discussion

6.5.1 How do canopy openness and fencing affect oak seedlings growth and survival?

Our observation that oak seedling growth (Fig. 6.2) and survival (Fig. 6.3) increase with canopy openness corroborates our first prediction (P1). This result supports the already well-documented finding, applied in everyday use by foresters, that high canopy openness promotes the regeneration of oak (Ligot *et al.*, 2013; Petersson *et al.*, 2020) and more generally of shade-intolerant tree species, by increasing understory light availability (Iverson *et al.*, 2017; Lu *et al.*, 2018). We also showed that fencing improved oak seedling growth in Sweden and survival in France, which is consistent with many studies where the exclusion of wild ungulates improved the natural regeneration of oak (Leonardsson *et al.*, 2015; Petersson *et al.*, 2020), and of other palatable tree species (Kumar *et al.*, 2006; Rhodes *et al.*, 2018). Overall, these findings confirm that opening the canopy, through thinning or natural disturbance, and excluding wild ungulates through fencing may effectively assist oak seedlings during the first stages of the natural regeneration. Although forest managers commonly control wild ungulates and manipulate canopy openness, the interaction between the effects of these two disturbances on forest dynamics has received little research attention so far.

Two recent studies showed that the exclusion of wild ungulates enhanced the positive effect of gap creation on understory species richness and cover (Sabo *et al.*, 2019) and on the abundance of several tree species (van Gundy *et al.*, 2014). In our study, we show that, in two contrasted forest regions, the effects of canopy openness and fencing also acted in synergy to improve oak natural regeneration: the positive effect of fencing on oak seedling growth or survival increased with canopy openness both in France and in Sweden. Different mechanisms could explain the observed pattern. A first assumption would be that ungulates browse more frequently and/or intensively on oak seedlings when canopy openness increases, which would be consistent with our second hypothesis. A second possibility is that oak responds differently to browsing depending on light availability, with a stronger reduction in growth under high light availability. Such pattern could relate to the higher growth rates of seedlings growing under open canopies, leading to a greater height difference between browsed and unbrowsed seedlings in the absence of compensatory growth. Although it has been observed in holm oak (*Quercus ilex*) (Baraza *et al.*, 2010) in controlled conditions, this would, however, go against our third prediction (P3), and most results found in the literature for other tree species (Baraza *et al.*, 2010; Kupferschmid *et al.*, 2014).

It is noteworthy that fencing did not significantly influence seedling growth in France. This may be the result of a lower browsing pressure exerted on the understory vegetation and/or more specifically on oak seedlings. Cervids have species-specific browsing height that generally corresponds to their shoulder height (Duncan *et al.*, 1998b; Nichols *et al.*, 2015) and our results, along with other similar studies, confirmed that height positively influences the probability of browsing (Hartley *et al.*, 1997; Renaud *et al.*, 2003). Because the regeneration was more advanced in Sweden, seedlings and other understory vegetation were on average much higher than in France (Appendix 6.8.5, Fig. 6.7), and this could have resulted in an overall higher browsing pressure in the Swedish plots. The observed pattern could also be the result of a difference in the palatability of oak relative to the other woody species present in the two countries. Indeed, cervid browsing preference for a given plant species – and the associated damages – is not only dependent on the plant species' palatability and availability, but also on the palatability of the alternative forage available (Bee *et al.*, 2009; Milligan & Koricheva, 2013; Ohse *et al.*, 2017). The 'attractant-decoy hypothesis' predicts that, within a patch, an individual plant that grows among more palatable plants will be somewhat protected from herbivores, as their attention is on the preferred neighbors (Hjältén *et al.*, 1993). In Sweden, studies on cervid selectivity show that oak is one of the most palatable species (Bergqvist *et al.*, 2018; Kullberg & Bergström, 2010). At the French sites, several of the co-occurring woody (hornbeam) and shrub (bramble) species (see Appendix 6.8.7, Fig. 6.12 for the height and cover of the main understory species) have been shown to be more often selected by red deer and roe deer than oak (Boulanger *et al.*, 2009; Tixier *et al.*, 1997b). The high availability of these more palatable species in the French sites may have contributed to the fact that fencing did not affect oak seedling growth. In addition, the alternative forages present may also influence the timing of herbivory – e.g. cervids browse evergreen species

in winter when deciduous species are scarce. Since oak responds differently to summer or winter browsing (Woolery & Jacobs, 2014), the existence of differences in the seasonality of browsing between the two countries could also explain the observed pattern.

6.5.2 Do cervids preferentially browse seedlings growing under open canopies?

In Sweden, consistent with our second prediction (P2), seedlings growing under an open canopy were more likely to be browsed than those growing under a closed canopy (Fig. 6.4). This pattern is consistent with other studies documenting a higher frequentation of wild ungulates in canopy gaps (Kuijper *et al.*, 2009; Mangas & Rodríguez-Estival, 2010), and is likely driven by a combination of several mechanisms. First, increasing canopy openness may lead to a higher abundance, biomass and diversity of herbs, shrubs and tree species in the forest understory (Alexander & Mack, 2017; Burton *et al.*, 2014; Sabo *et al.*, 2019; Willms *et al.*, 2017), all of which influence the browsing probability of a given individual seedling (Milligan & Koricheva, 2013; WallisDeVries, 1996). Second, canopy gaps also modify the species composition of the understory in favor of light demanding species (Lu *et al.*, 2018). Studies linking browse quality for cervids and plant shade-tolerance have shown that light demanding species generally have lower leaf toughness, fewer chemical defenses (e.g. phenolic compounds) and higher nutritional content (Giertych *et al.*, 2015; Kitajima *et al.*, 2012), and may therefore be more palatable to cervids. By increasing the quantity, quality and diversity of the surrounding vegetation, canopy gaps may therefore create better foraging conditions for herbivores, hence increasing the likelihood for oak to be browsed (Hjältén *et al.*, 1993). At the intra-specific scale, an increase in light availability can also influence plant chemical composition, though it remains unclear how these changes actually affect plant palatability. Nutrient content or digestibility are considered good proxies for plant nutritional value for cervids, and are often drivers of food selection (Felton *et al.*, 2018; Soest, 1996). It has been shown that at the intra-specific scale, light availability may increase the digestibility of several woody species (Agrell *et al.*, 2000), though it may also decrease the leaf nutrient content (Giertych *et al.*, 2015). More knowledge on the consequences of increased light availability on plant nutritional properties is therefore necessary before drawing any conclusions on this issue.

The fact that canopy openness did not influence browsing likelihood in France could relate to the importance of the understory – especially shrubs – in the French sites. Indeed, understory height is relatively similar between the two countries (Table 6.1) while seedlings are higher in Sweden, thus suggesting that the understory competition is developing rapidly in France. It is thus likely that in most French sites, oak seedlings are still growing beneath

the shrub layer. Our results confirm that the understory protects the seedlings from browsing (Jensen *et al.*, 2012), as understory height or cover decreased the browsing probability in both countries. However, several species that dominate the shrub layer in France – e.g. bramble, raspberry – are highly competitive regarding light interception (Balandier *et al.*, 2013). Because light availability also promotes growth for these shrub species (Appendix 6.8.4, Fig. 6.12) (Gaudio *et al.*, 2008), a higher canopy openness may not necessarily increase light availability for seedlings growing beneath the shrub layer, and therefore may not influence their palatability. The fact that in France, canopy openness only improved the growth of higher seedlings tend to support this hypothesis.

6.5.3 Does the impact of browsing on growth vary with canopy openness?

The ability of trees to recover from browsing may depend on the available light (Kupferschmid *et al.*, 2014) but this relationship is highly variable among different tree species (Baraza *et al.*, 2010). In our study, we observed a consistent trend in both countries: browsing significantly reduced seedling annual growth rate, but contrary to our third prediction (P3), the effect was independent of canopy openness (Fig. 6.5). This is even more notable, as the short duration of the study in most sites (2-3 years), along with the relatively shady conditions, could have limited the possibility to detect differences in growth rates. This finding confirms that the synergy between the effects of fencing and canopy openness on oak seedling growth observed in Sweden is related to a higher browsing frequency in canopy gaps (result of P2) rather than to a light-mediated response to browsing.

At the individual seedling level, reduction in growth rate induced by browsing seems to be higher in France than in Sweden. This pattern could be related to differences in site conditions that we did not measure - e.g. soil composition, moisture, or climate; factors that have interacted with the effect of browsing on understory vegetation dynamic (Danell *et al.*, 1991; Randall & Walters, 2011). These inter-site differences could therefore explain differences in tree species' tolerance to browsing between French and Swedish sites. This pattern could also be related to different cervid compositions between the two countries. Indeed, the effect of browsing on seedlings growth is conditioned by both the timing and intensity of herbivory (Danell *et al.*, 1994; Woolery & Jacobs, 2014), and these two factors are known to vary depending on the cervid species (Nichols *et al.*, 2015). The identification of the relative effect of each cervid species, as has been done in recent studies (Barasona *et al.*, 2013; van Beeck Calkoen *et al.*, 2019), would be necessary to confirm this hypothesis. Lastly, we may assume that because oak is under higher browsing pressure in Sweden, it has developed local genetic adaptations to better tolerate browsing as has been shown for the Japanese

nettle (*Urtica thunbergiana*) (Kato *et al.*, 2008), or the orange jewelweed (*Impatiens capensis*) (Martin *et al.*, 2015). Strong inter-specific differences are known to exist in the ability of trees to recover from herbivory (Baraza *et al.*, 2010; Kupferschmid & Heiri, 2019) but the existence of such differences at the intra-specific scale has been far less documented. A study by Mann *et al.* (2012) showed that two distinct populations of *Eucalyptus morrisbyi* were not equally tolerant to browsing, through differences in chemical and physical leaf traits. Vourc'h *et al.* (2002) also found that the ability of western red cedar (*Thuja plicata*) to tolerate deer browsing varies between populations, and more specifically with the browsing history of each population. However, several recent studies conducted in temperate forests for Scots pine (O'Reilly-Wapstra *et al.*, 2014) and for beech (Frank *et al.*, 2019) do not support population-specific responses to browsing. Our results suggest that this question should be investigated for oak, as it could have major management implications.

6.5.4 Does the impact of cervids on growth and survival correlate with cervid density?

Our results did not show any correlation between cervids density indices and the impact of these animals on oak seedlings' growth or survival (Fig. 6.6). A weak statistical relationship between cervid population density and browsing impact on trees is not an unusual finding, due to the multitude of other factors influencing the foraging choices of free-ranging animals (e.g. Jarnemo *et al.* (2014); Putman *et al.* (2011); Reimoser & Putman (2011)) and to the difficulty to accurately estimate cervid density (Pfeffer *et al.*, 2018). Indeed, it is possible that the variation in deer densities among our sites was insufficient to enable us to identify a differential impact on seedling growth and survival. Also, while dung pellet counts have been found to accurately predict winter habitat use by moose (Månsson *et al.*, 2011), the method may under-estimate population densities of roe deer (Pfeffer *et al.*, 2018). In addition, our study was of relatively short duration, compared to most of the studies that show significant correlations between deer densities and forest regeneration (Horsley *et al.*, 2003; Kuijper *et al.*, 2010).

6.5.5 Top-down and bottom-up processes in managed forests

Many recent studies converge on the idea that the relative importance of the effects of bottom-up and top-down processes on the development of living organisms is highly dependent on the environmental conditions – e.g. resource availability (Gilliam, 2006; Hillebrand, 2005; Moran & Scheidler, 2002) or climate (Lynam *et al.*, 2017; Rosenblatt & Schmitz, 2016). In this study, we show that under closed canopies, oak seedling growth and survival were constrained by low light availability (bottom-up control), but were not influenced by the presence of ungulates. Inversely, under open canopies, seedlings were more frequently

browsed (top-down control), leading to a strong effect of fencing on growth and survival. As resource availability increased, the regulation of seedlings development thus shifted from a bottom-up to a top-down control. In the context of a managed forest, the review by Gilliam (2006) revealed a similar pattern: N fertilization to increase nutrient availability for the understory vegetation also tended to increase the importance of insect herbivory. In a study of deer and their predators, (Crête, 1999) also reached the conclusion that top-down effects are more pronounced in high productivity systems than in systems with low resource availability. Our results support the hypothesis that net outcome for forest regeneration is the result of a balance between enhanced resource availability for primary productivity and limitation of predation. From a more general perspective, our findings support the pattern already observed in marine communities (Hillebrand, 2005) or in cultivated fields (Moran & Scheidler, 2002): an increase in resource acquisition does not always benefit the organism consuming the resource as it may also increase predation.

6.6 Conclusion

Based on consistent patterns in two contrasted European forest regions, our results contributed to improve our understanding of the interaction between the effects of wild ungulates and canopy openness on oak regeneration. We have thus provided new insights into how these top-down and bottom-up processes can interact with each other to influence the development of forest trees. Fencing only improved oak growth or survival when the canopy was sufficiently open, this was explained by a higher browsing frequency in canopy gaps. Gap creation is generally necessary to achieve successful oak regeneration, but our results show that moderate canopy operations may increase the damage caused by ungulates. From a management point of view, these findings suggest that in forests with high ungulate densities, gap creation alone may be insufficient to successfully regenerate oak stands if it is not combined with protection from browsing. As anthropogenically increasing resource availability to promote organisms of high ecological or economic value is common in ecosystem management, our study highlights the importance of considering the interactions between bottom-up and top-down processes before implementing measures.

6.7 Acknowledgments

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6.8 Appendices

6.8.1 Deer abundance index in France

Table 6.3: Mean number of red and roe deer observed per km at the three French sites from 2017 to 2019. Two types of indices were used: the pedestrian kilometric index (IKP) (Vincent *et al.*, 1991) and spotlight counts (IN) (Garel *et al.*, 2010)

	La-Petite-Pierre		Arc-en-Barrois		Trois Fontaines	
	Index	Value	Index	Value	Index	Value
	<i>Roe deer</i>		<i>Roe deer</i>		<i>Roe deer</i>	
2017	IKP	0.10			IKP	0.556
2018	IKP	0.12	IN	0.789	IKP	0.556
2019	IKP	0.10	IN	0.683	IKP	0.461
	<i>Red deer</i>		<i>Red deer</i>			
2017	IN	0.888				
2018	IN	0.973	IN	1.717		
2019	IN	0.745	IN	1.332		

6.8.2 Presentation of the model selection for each prediction

Table 6.4: Selection based on the Akaike's Information Criterion (AIC) of the linear mixed models predicting the growth rate as a function of canopy openness (Ca), initial height (Hi), fencing (Fen), understory cover index (UCI) and understory height index (UHI) in France and in Sweden. Np represents the number of parameters included in the model. The $|\Delta_{AIC}|$ is the absolute value of the difference between the Akaike's Information Criterion (AIC) of the model and of the selected model, shown in bold for each country.

Parameters	Np	AIC	$ \Delta_{AIC} $
<i>Sweden</i>			
Ca + Hi + Fen + Ca*Hi + Ca*Fen + Hi*Fen + Ca*Hi*Fen	7	16056	0
Ca+Hi+Fen+Ca*Hi+Ca*Fen+Hi*Fen+Ca*Hi*Fen+UCI+UHI	9	32270	16214
Ca + Hi + Fen + Ca*Hi + Ca*Fen + Hi*Fen + Ca*Hi*Fen + UCI	8	32314	16258
Ca + Hi + Fen + Ca*Hi + Ca*Fen + Hi*Fen + Ca*Hi*Fen + UHI	8	32272	16216
<i>France</i>			
Ca + Hi + Fen + Ca*Hi + Ca*Fen + Hi*Fen + Ca*Hi*Fen	7	17461	2
Ca + Hi + Fen + Ca*Hi + Ca*Fen + Hi*Fen	6	17461	2
Ca + Hi + Fen + Ca*Hi + Hi*Fen	5	17459	0
Ca + Hi + Fen + Ca*Hi	4	17463	4
Ca + Hi + Fen + Ca*Hi + UCI + UHI	6	32322	1486
Ca + Hi + Fen + Ca*Hi + UCI	5	32362	14902
Ca + Hi + Fen + Ca*Hi + UHI	5	32323	14864

Table 6.5: Selection based on the Akaike's Information Criterion (AIC) of the generalized linear mixed models predicting the survival after two years as a function of canopy openness (Ca), initial height (Hi) and fencing (Fen) in France and in Sweden. Np represents the number of parameters included in the model. The $|\Delta_{AIC}|$ is the absolute value of the difference between the AIC of the model and of the selected model, shown in bold for each country

Parameters	Np	AIC	$ \Delta_{AIC} $
<i>Sweden</i>			
Ca + Hi + Fen + Ca*Hi + Ca*Fen + Hi*Fen + Ca*Hi*Fen	7	789	7
Ca + Hi + Fen + Ca*Hi + Ca*Fen + Hi*Fen	6	787	5
Ca + Hi + Fen + Ca*Fen + Hi*Fen	5	785	3
Ca + Hi + Fen + Hi*Fen	4	784	2
Ca + Hi + Fen	3	782	0
<i>France</i>			
Ca + Hi + Fen + Ca*Hi + Ca*Fen + Hi*Fen + Ca*Hi*Fen	7	2433	1
Ca + Hi + Fen + Ca*Hi + Ca*Fen + Hi*Fen	6	2433	1
Ca + Hi + Fen + Ca*Fen + Hi*Fen	5	2433	1
Ca + Hi + Fen + Ca*Fen	4	2434	0

Table 6.6: Selection based on the Akaike's Information Criterion (AIC) of the generalized linear mixed models predicting browsing likelihood as a function of the occurrence of previous browsing (PreB), canopy openness (Ca), initial height (Hi), understory cover index (UCI) and understory height index (UHI) in France and in Sweden. Np represents the number of parameters included in the model. The $|\Delta_{AIC}|$ is the absolute value of the difference between AIC of the model and of the selected model, shown in bold for each country.

Parameters	Np	AIC	$ \Delta_{AIC} $
<i>Sweden</i>			
Ca + Hi + PreB + Ca*Hi + Ca*PreB + Hi*PreB + Ca*Hi*PreB	7	974	11
Ca + Hi + PreB + Ca*Hi + Ca*PreB + Hi*PreB	6	972	9
Ca + Hi + PreB + Ca*Hi + Ca*PreB	5	970	8
Ca + Hi + PreB + Ca*PreB	4	969	7
Ca + Hi + PreB	3	969	7
Ca + Hi + PreB	5	964	2
Ca + Hi + PreB	4	971	9
Ca + Hi + PreB	4	962	0
<i>France</i>			
Ca + Hi + PreB + Ca*Hi + Ca*PreB + Hi*PreB + Ca*Hi*PreB	7	953	80
Ca + Hi + PreB + Ca*Hi + Ca*PreB + Hi*PreB	6	951	78
Ca + Hi + PreB + Ca*PreB + Hi*PreB	5	949	76
Ca + Hi + PreB + Hi*PreB	4	948	74
Ca + Hi + PreB + Hi*PreB + UCI + UHI	6	874	1
Ca + Hi + PreB + Hi*PreB + UCI	5	873	0
Ca + Hi + PreB + Hi*PreB + UHI	5	877	3

Table 6.7: Selection based on the Akaike's Information Criterion (AIC) of the linear mixed models predicting seedling growth rate as a function of canopy openness (Ca), initial height (Hi), browsing (Br), understory cover index (UCI) and understory height index (UHI) in France and in Sweden. Np represents the number of parameters included in the model. The $|\Delta_{AIC}|$ is the absolute value of the difference between AIC of the model and of the selected model, shown in bold for each country.

Parameters	Np	AIC	$ \Delta_{AIC} $
<i>Sweden</i>			
Ca + Hi + Br + Ca*Hi + Ca*Br + Hi*Br + Ca*Hi*Br	7	16128	1
Ca + Hi + Br + Ca*Hi + Ca*Br + Hi*Br	6	16129	0
Ca + Hi + Br + Ca*Hi + Hi*Br	5	16130	0
Ca + Hi + Br + Ca*Hi	4	16129	0
Ca + Hi + Br + Ca*Hi + UHI + UCI	6	16131	2
Ca + Hi + Br + Ca*Hi + UHI	5	16131	2
Ca + Hi + Br + Ca*Hi + UCI	5	16128	0
<i>France</i>			
Ca + Hi + Br + Ca*Hi + Ca*Br + Hi*Br + Ca*Hi*Br	7	17334	1909
Ca + Hi + Br + Ca*Hi + Ca*Br + Hi*Br	6	17335	1910
Ca + Hi + Br + Ca*Hi + Hi*Br	5	17336	1911
Ca + Hi + Br + Ca*Hi + Hi*Br + UCI + UHI	7	15425	0
Ca + Hi + Br + Ca*Hi + Hi*Br + UCI	6	15486	60
Ca + Hi + Br + Ca*Hi + Hi*Br + UHI	6	15428	2

6.8.3 Computation of the site-specific impact of cervids on growth and survival

We estimated the magnitude of the “deer effect” on oak growth and survival at each study site in Sweden by adding a site \times fencing interaction to the most parsimonious growth and survival models (Appendix 6.8.2) (we simultaneously removed site from the random effects). From these models, we predicted the growth rate and the survival likelihood for each site - fencing combination, with the following values for two the other fixed effects: initial height of 40cm, and a canopy openness of 30% (appropriate conditions for oak regeneration). We chose an initial height of 40cm to minimize the uncertainty of the prediction, as the distribution of this variable reaches a peak at around 40cm (Appendix 6.8.5, Fig. 6.8). From these predictions, we computed indices that reflected the impact of deer on growth (IG_k) and survival (IS_k) at each site k .

$$IG_k = \log\left(\frac{GR_k(\text{unfenced})}{GR_k(\text{fenced})}\right) \quad (6.8)$$

$$IS_k = \log\left(\frac{SP_k(\text{unfenced})}{SP_k(\text{fenced})}\right) \quad (6.9)$$

where $GR_k(\text{fenced})$ and $SP_k(\text{fenced})$ are respectively the growth rate and survival likelihood predicted by the models described above in fenced plots at site k . We used the log-ratio to study the treatment effect (Hedges *et al.*, 1999) since its value is easily understandable (e.g. a negative value indicates a negative effect of the presence of deer on growth or survival).

6.8.4 Results of the selected mixed models

Table 6.8: Results of the most parsimonious linear mixed models predicting the growth rate as a function of canopy openness, initial height and fencing in France and in Sweden. Nested random effects (Site/Block/ID) were included to account for the structure of the experimental design. P-values were obtained with a post-analysis of deviance (Wald χ^2 , type II). Significant fixed effects are in bold ($\alpha = 0.05$).

	Estimate	SE	t	p
<i>Sweden</i>				
Intercept	6.692	1.059	6.322	
Canopy openness	1.537	1.137	1.352	0.02
Initial height	2.491	0.427	5.828	< 0.01
Fencing (Unfenced)	-5.589	0.745	-7.502	< 0.01
Canopy x Initial height	4.041	0.666	6.07	< 0.01
Canopy x Fencing	-2.395	1.15	-2.082	< 0.01
Initial height x Fencing	-0.763	0.588	-1.297	0.69
Canopy x Initial height x Fencing	-4.254	0.869	-4.896	< 0.01
<i>France</i>				
Intercept	13.662	1.027	13.305	
Canopy openness	0.989	0.264	3.745	0.11
Initial height	14.712	0.736	19.999	< 0.01
Fencing (Unfenced)	-1.578	0.809	-1.95	0.48
Canopy x Initial height	1.469	0.4	3.671	< 0.01
Canopy x Fencing	-2.414	1.307	-1.848	0.06

Table 6.9: Results of the most parsimonious generalized linear mixed models (Binomial error distribution with a 'logit' link function) predicting survival after two years as a function of initial height, canopy openness and fencing in France and in Sweden. Nested random effects (Site/Block) were included to account for the structure of the experimental design. Significant fixed effects are in bold ($\alpha = 0.05$).

	Estimate	SE	Z	p
<i>Sweden</i>				
Intercept	1.862	0.291	6.404	< 0.01
Canopy openness	0.499	0.236	2.113	0.03
Initial height	0.743	0.139	5.351	< 0.01
Fencing (unfenced)	-0.309	0.191	-1.618	0.11
<i>France</i>				
Intercept	0.411	0.424	0.969	0.33
Canopy openness	0.291	0.079	3.684	< 0.01
Initial height	-1.766	0.115	-15.307	< 0.01
Fencing (unfenced)	0.885	0.284	3.117	< 0.01
Canopy x Fencing	-0.314	0.111	-2.837	< 0.01

Table 6.10: Results of the most parsimonious generalized linear mixed models (Binomial error distribution with a ‘logit’ link function) predicting browsing likelihood as a function of the occurrence of previous browsing, initial height, canopy openness, and understory cover index (UCI) in France and in Sweden. Nested random effects (Site/Block/Year) were included to account for the structure of the experimental design. Significant fixed effects are in bold ($\alpha = 0.05$).

	Estimate	SE	Z	p
<i>Sweden</i>				
Intercept	-1.041	0.29	-3.593	< 0.01
Initial height	0.464	0.081	5.707	< 0.01
Canopy openness	0.787	0.219	3.59	< 0.01
Previous browsing (Yes)	1.474	0.183	8.039	< 0.01
Understory cover Index	-0.954	0.258	-3.692	< 0.01
<i>France</i>				
Intercept	-0.195	0.562	-0.348	0.73
Previous browsing (Yes)	-0.561	0.432	-1.298	0.19
Initial height	1.903	0.526	3.616	< 0.01
Canopy openness	-0.135	0.108	-1.248	0.21
Understory Height Index	-0.303	0.164	-1.848	0.06
Previous browsing x Initial height	-1.73	0.667	-2.593	< 0.01

Table 6.11: Results of the most parsimonious linear mixed models predicting seedling growth rate as a function of canopy openness, initial height, browsing, understory height (UHI) and cover (UCI) indices in France and in Sweden. Nested random effects (Site/Block/ID) were included to account for the structure of the experimental design. P-values were obtained with a post-analysis of deviance (Wald χ^2 , type II). Significant fixed effects are in bold ($\alpha = 0.05$).

	Estimate	SE	t	p
<i>Sweden</i>				
Intercept	3.785	1.419	2.668	
Canopy openness	-1.593	0.988	-1.612	0.5
Initial height	2.162	0.309	7.003	< 0.01
Browsing (Yes)	-4.821	0.903	-5.337	< 0.01
Canopy x Initial height	1.576	0.422	3.738	< 0.01
<i>France</i>				
Intercept	13.928	0.587	23.745	
Canopy openness	0.988	0.276	3.58	0.86
Initial height	13.347	0.713	18.709	< 0.01
Browsing (Yes)	-10.57	1.036	-10.207	< 0.01
UCI	0.829	0.398	2.085	0.04
UHI	2.049	0.251	8.155	< 0.01
Canopy x Initial height	1.87	0.394	4.744	< 0.01
Initial height x Browsing	-13.674	1.697	-8.059	< 0.01

6.8.5 Height and canopy openness distribution

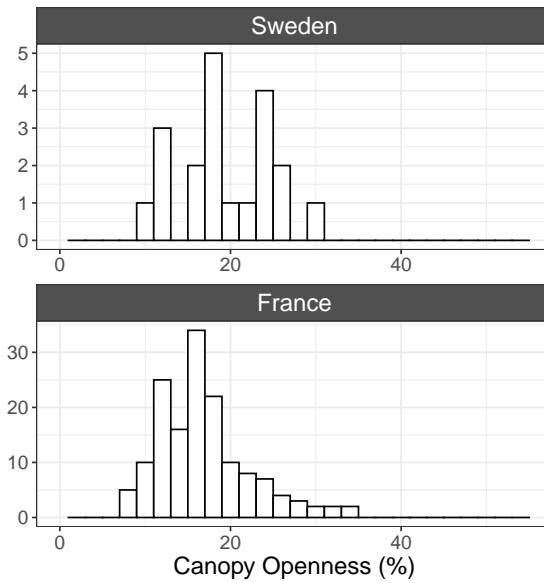


Figure 6.7: Distribution of the canopy openness values in Sweden and in France.

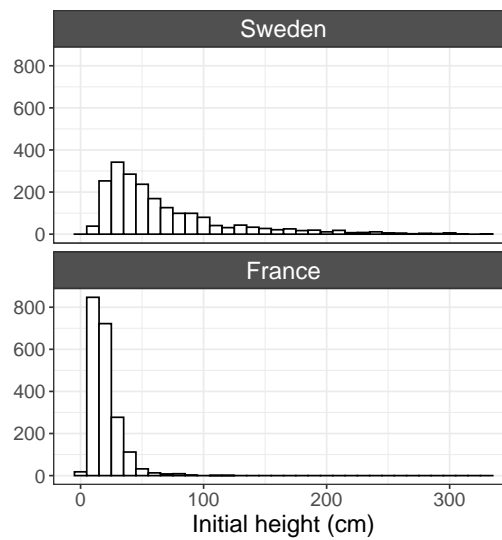


Figure 6.8: Distribution of the initial seedling height values in Sweden and in France.

6.8.6 Relationship between the impact of cervids on growth, and deer and moose density indices

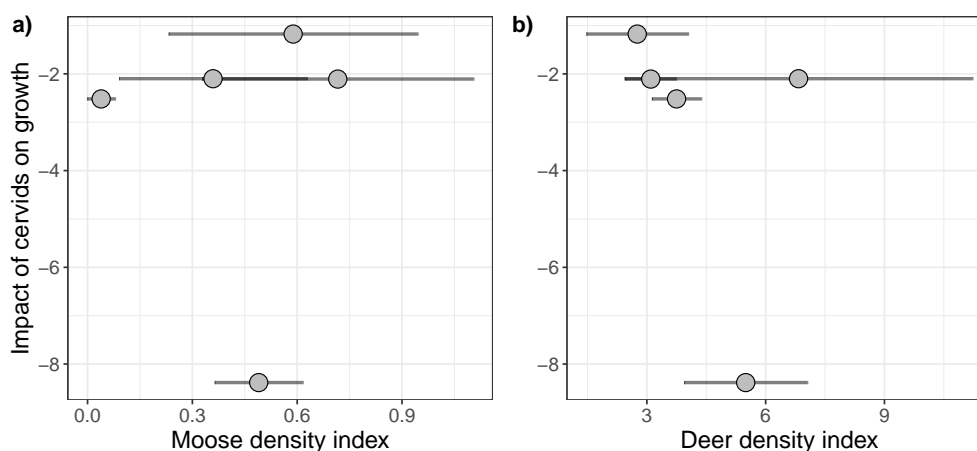


Figure 6.9: Variations of the impact of cervids on growth with a) moose and b) deer density indices ($animal.km^{-2}$) in Sweden. A negative value of the impact of cervids on growth indicates that the presence of cervids decrease seedlings growth. Horizontal error bars show the standard error of the density indices.

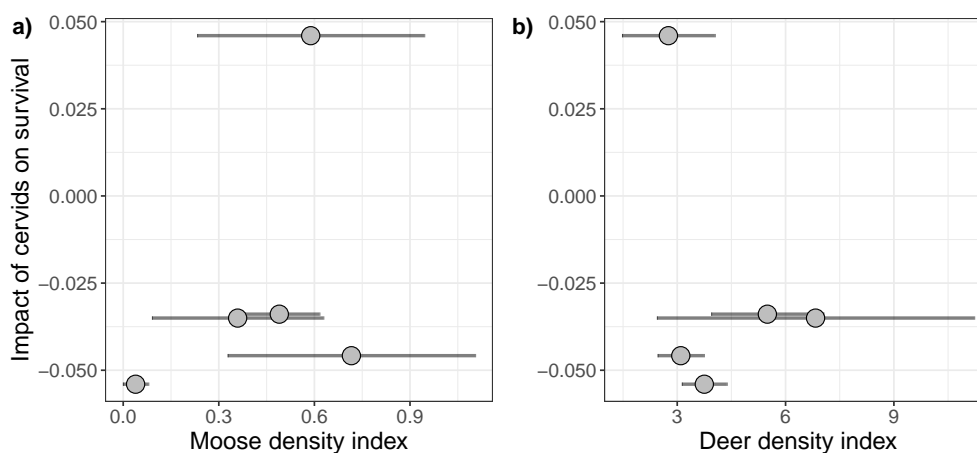


Figure 6.10: Variations of the impact of cervids on survival with a) moose and b) deer density indices ($animal.km^{-2}$) in Sweden. A negative value of the impact of cervids on survival indicates that the presence of cervids decrease seedlings survival. Horizontal error bars represents the standard error of the density indices.

6.8.7 Height and cover of the main understory species

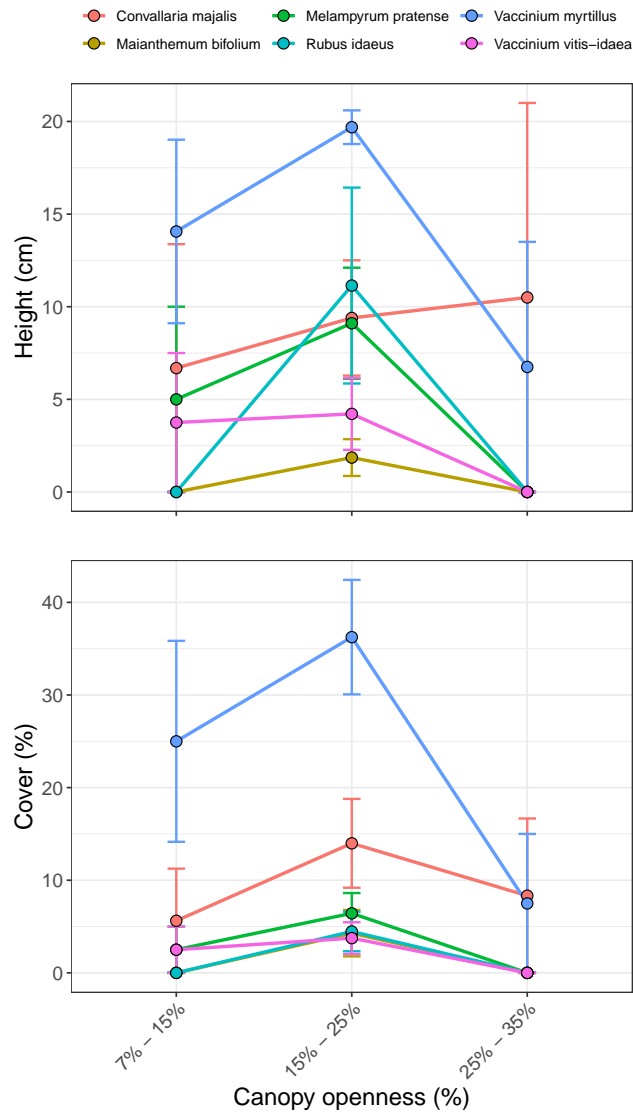


Figure 6.11: mean height and cover (\pm standard error) of the 6 more important understory species in the Swedish sites the last year of the experiment, as a function of canopy openness.

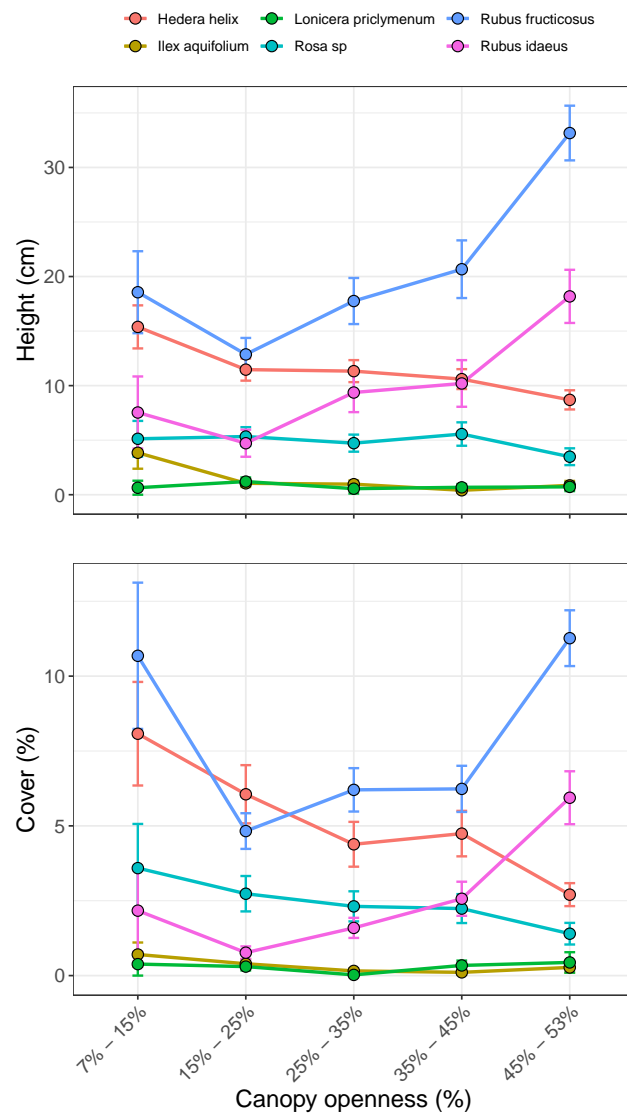


Figure 6.12: mean height and cover (\pm standard error) of the 6 more important understory species in the French sites the last year of the experiment, as a function of canopy openness.

CHAPTER

7

THE INFLUENCE OF DEER BROWSING ON OAK
REGENERATION IS CONDITIONED BY THE SHRUB
LAYER - INSIGHTS FROM A MODELING APPROACH

7.1 Preamble

The *in silico* study presented in this chapter is the result of a two-step process: the conception and implementation of the first version of a theoretical model of herbivory in CAPSIS regeneration library (Dufour-Kowalski *et al.*, 2012), and simulations with the RRESHAR model to test different research questions. To present these two steps with a comparable level of details, I chose to write this chapter as a stylistic hybrid between methodological report and scientific article. The introduction contextualizes the questions and hypotheses that led to the development of the model. Section 7.3 presents the model implementation and the data analyses leading to the equations used to parametrize the model. Section 7.4 presents the simulations that were conducted to address the hypotheses presented in the introduction. This chapter ends with a general conclusion and a discussion of the perspectives for further improvements of the model (section 7.5).

7.2 Introduction

The process of forest regeneration begins with the creation of a canopy gap which increases light availability for seedlings (Watt, 1947). Gap creation initiates a vertical race between the different compartments of the understory (Yamamoto, 2000): plants that manage to dominate the understory have access to most of the below-canopy light while smaller individuals are trapped in the lowest height classes due to insufficient light availability (Walters *et al.*, 2020). The ability of a given tree species to regenerate following a gap creation is therefore highly conditioned by the saplings' capacity to "win" this race and reach the overstorey before their competitors (Johnson *et al.*, 2019). Within the understory, saplings of a given species face two categories of light competitors: other saplings and interfering vegetation, mainly dense forbs (*e.g.* *Chenopodium sp*, *Epilobium sp*), shrubs (*e.g.* *Rubus fruticosus* and *R. idaeus*) and ferns (Balandier *et al.*, 2006). In contrast to competition for light with other saplings, the effect of the interfering vegetation is limited in time and affects only small saplings. Nevertheless, the interfering vegetation can intercept more light than the other competing saplings due to its higher investment in leaf biomass (Ülo Niinemets, 2010).

Deer browsing has been shown to exert a constraint on sapling height growth that adds to the effect of competition (Annighöfer *et al.*, 2015) and thus, has the potential to change winners to losers (and vice versa) in the vertical race among the understory components (Hegland & Rydgren, 2015). When light-demanding saplings have been overtopped by interfering vegetation, deer can mediate light competition to the benefit of the saplings by consuming the interfering vegetation first (Boulanger *et al.*, 2018; Jensen *et al.*, 2012; Ward *et al.*, 2018); this decreases the importance of light competition in the race (Laurent *et al.*,

2017). Inversely, once saplings have overtopped the interfering vegetation, they are more subject to browsing (Jensen *et al.*, 2012) and inter-sapling competition increases (Jensen & Löf, 2017). Deer browsing has also been shown to mediate patterns of inter-sapling competition to the benefit of the least palatable species (Bernard *et al.*, 2017; Tremblay & Ouimet, 2013). The overall effect of deer browsing on the height growth of a given tree species is therefore the sum of a negative direct effect (*i.e.* direct browsing) and of indirect effects that can be positive (consumption of competitive understory species) or negative (consumption of facilitative species). The magnitude of these direct and indirect effects is therefore likely to depend on the abundance, palatability and competitiveness (*i.e.* facilitative or competitive effect on the focal species) of the admixed understory species. This means that these specific understory characteristics probably contribute to the degree to which deer browsing influences the regeneration of a given species. Understanding the conditions that minimize the negative impact of deer browsing could therefore improve understory management practices in forest stands exposed to high browsing pressure (Stokely & Betts, 2020). Vriendt *et al.* (2020) illustrated this assumption nicely in their recent study; they evidenced that spruce plantations exposed to cervids regenerated better when admixed competitive species were retained in the stand as alternative forage.

Pedunculate oak (*Quercus robur* L., hereafter "oak") is an emblematic species of European temperate forests: it is valued for both economic reasons and the high level of biodiversity supported by oak-dominated forests (Mölder *et al.*, 2019a). Deer browsing and interspecific competition are two of the main factors constraining oak regeneration (Annighöfer *et al.*, 2015). In central Europe, oak frequently co-occur with beech (*Fagus sylvatica*) and hornbeam (*Carpinus betulus*), two species known to be more shade tolerant and to grow faster than oak at the sapling stage (Ligot *et al.*, 2013; Couwenberghe *et al.*, 2013). However, the two species differ in their relative palatability: hornbeam is more frequently browsed than oak while beech tends to be avoided (Boulanger *et al.*, 2009; Tixier *et al.*, 1997b). A shrub layer dominated by bramble also frequently colonize the understory of oak forests. This shrub species is highly competitive for light (Balandier *et al.*, 2013) but it is also known to be frequently browsed by deer, especially in winter (Barrere *et al.*, 2020; Storms *et al.*, 2008). While direct browsing constrains the oak saplings' growth, deer consumption of bramble, beech and hornbeam should enhance oak growth by decreasing competition for light, thus making the overall effect of deer browsing highly uncertain. In this context, we aimed to investigate how the characteristics of the understory (*i.e.* abundance, palatability and competitiveness) determine the degree to which deer browsing influences oak regeneration, and to describe the subsequent implications for understory management. We investigated the following hypotheses:

Hypothesis 1: Because hornbeam and beech are respectively more and less palatable than

oak (Boulanger *et al.*, 2009; Tixier *et al.*, 1997b), we expected the number of recruited oak saplings to be higher when the accompanying species was hornbeam rather than beech.

Hypothesis 2: Due to bramble’s high competitiveness for light (Balandier *et al.*, 2013), we assumed that bramble consumption by deer would be the “most positive” indirect effect of deer browsing on oak regeneration. Therefore, when oak was accompanied by both other saplings and bramble, we expected the effect of the overall browsing pressure on the number of recruited oak saplings to be positive when the deer consumed more bramble than saplings, and vice versa.

Hypothesis 3: In theory, clearing away admixed species that are more palatable than the focal species should have a strong negative effect by increasing browsing pressure on the focal species (Vriendt *et al.*, 2020). Therefore, we expected that, under high browsing pressure, removing the understory through clearing operations would shorten the regeneration time only when oak was accompanied by beech (less palatable), but not by hornbeam (more palatable).

7.3 Including deer browsing in the CAPSIS regeneration library

7.3.1 CAPSIS

CAPSIS is a computer tool providing a software architecture to run and display the results of several forestry models (Dufour-Kowalski *et al.*, 2012). In this study, I implemented the theoretical model of deer browsing in a CAPSIS library (*i.e.* the “regeneration” library), and conducted simulations with a model implemented on CAPSIS relying on this library (*i.e.* RRESHAR). To introduce the work I conducted, I will first describe the architecture and basic functions in CAPSIS.

CAPSIS has five structural compartments: the kernel, libraries, modules, pilots and extensions (Fig. 7.1). The **kernel** is a code common to all the models and contains fundamental classes (*e.g.* spatial or temporal data) and functions (projection and execution of simulations). The **libraries** contain specific objects (*e.g.* trees, stands) and functions (*e.g.* algorithms for light interception), which can be used by any model implemented on CAPSIS. The **modules** contain the forestry models (each model is implemented in a specific module). These modules do not interact with each other. They may re-use specific functions and objects in the kernel or from the libraries, or have their own functioning (most models mix both possibilities). The **extensions** are small independent pieces of software that can be

“plugged” into CAPSIS and used by different models (a specific silvicultural practice such as thinning is a typical example of an extension). Lastly, the **pilots** are the user interfaces, with two main options: a “user-friendly” graphical interface for simple simulations, and scripts to run more complex simulation plans.

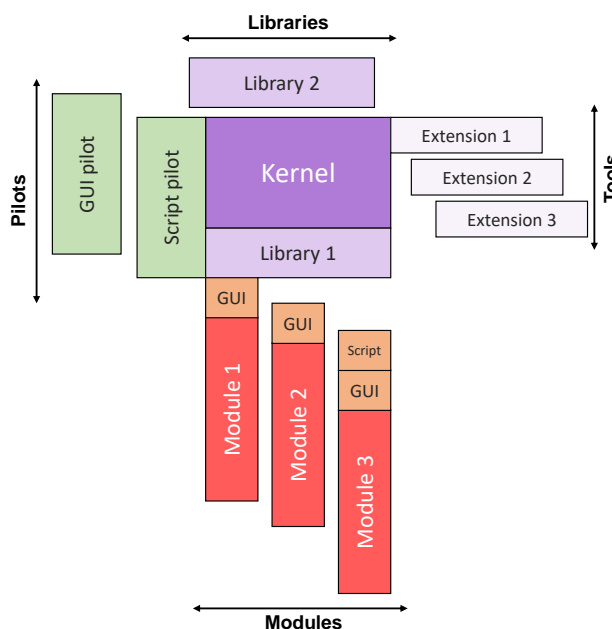


Figure 7.1: The open-software architecture of CAPSIS, redrawn from [Dufour-Kowalski et al. \(2012\)](#)

RRESHAR is a model that relies on two libraries: the “regeneration” library, which contains some of the vegetation objects included in the model; and the “Samsara light” library, which contains functions for light interception. This library connection is crucial; if RRESHAR had not been connected to any libraries, the browsing extension I built would necessarily have been specific to RRESHAR only. Since most of the vegetation objects come from the “regeneration” library, the browsing extension can be implemented in the same library. I chose this solution so that the browsing extension could be included in any other model relying on the “regeneration” library. First, let us clarify the basic structure and functions of the “regeneration” library and of RRESHAR before going through the browsing extension and its implementation.

7.3.2 Structure and functions of the “regeneration” library and of RRESHAR

RRESHAR (Balandier, Gaudio, Donès, INRAE, 2008) is the acronym for Regeneration and Resource Sharing: this model simulates the regeneration of forest stands and the exchange

of resources among the different vegetation compartments. This brief definition raises two questions: which vegetation compartments are included in the model, and which resources are being exchanged? RRESHAR relies on the regeneration library for both of these aspects. In this section, I will attempt to shed light on the structure of RRESHAR by describing the vegetation compartments modeled, the resources exchanged among these vegetation compartments and by highlighting the contribution of the regeneration library to RRESHAR functioning.

7.3.2.1 Vegetation classes

RRESHAR simplifies the representation of forest vegetation by distinguishing three “vegetation objects” depending on two criteria: the biological type and the growth stage. Shrubs and herbaceous species are grouped into one class of objects called “vegetation layers”, while trees are modeled at two distinct growth stages: the sapling stage and the adult stage. Saplings and vegetation layers come from the “regeneration” library, while the coding for adult trees is specific to RRESHAR. Fig. 7.2 shows a 3D representation of a RRESHAR scene where these three classes of object are present. This scene consists of a grid of “cells” whose dimensions are specified by the user. Adult trees (black sticks topped with a yellow spherical crown on Fig. 7.2) have exact spatial coordinates and are characterized by their diameter and height, and by the dimension and the porosity of their crown. Saplings (vertical yellow sticks on Fig. 7.2) also have spatial coordinates; they are characterized by their diameter and height. Vegetation layers (grey cuboids in Fig. 7.2) are porous layers at the cell level, characterized by their height and cover (percentage of the cell surface cover by the horizontal projection of the leaves).

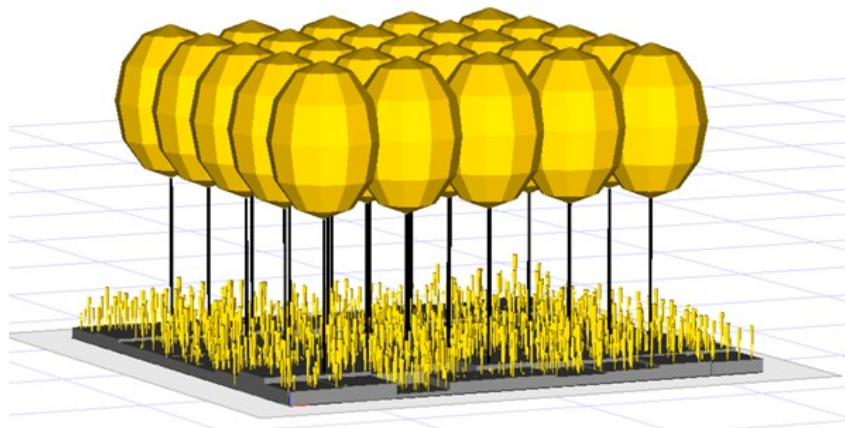


Figure 7.2: 3D representation of a RRESHAR scene. Adult trees are represented as black sticks with yellow oval crowns, saplings are represented as vertical yellow sticks, and vegetation layers are the grey cuboids below the saplings.+

7.3.2.2 Resource sharing

In RRESHAR, the three classes of vegetation objects exchange two types of resources that condition their growth: light and water; water competition is optional, however, and in this thesis, I focus on light competition only. Therefore, I will not describe the water exchanges here (but see the thesis by [Helluy \(2020\)](#) for a detailed and updated description of water exchanges in RRESHAR). The function of light interception by adult trees is computed from the Samsara light library, developed by Benoit Courbaud (INRAE) and Gauthier Ligot (ULG Gembloux). Below is a brief synthesis of how Samsara works (but see the paper by [Courbaud et al. \(2003\)](#) for a more detailed description, or [Ligot et al. \(2014\)](#) for a more recent example of the use of this library). The light-interception model simulates diffuse radiation and the light rays following the sun's path that reach the crown of adult trees (Fig. 7.3). Light interception by the canopy is a function of the shape and porosity of the crowns, and is computed at a daily scale and at the cell level following a Beer-Lambert law:

$$I_1 = I_0 * e^{-k*V} \quad (7.1)$$

Where I_1 is the radiation transmitted to the understory, I_0 is the incident radiation above the canopy, k is the species coefficient of extinction and V is a variable related to the porosity of the physical environment crossed, and to the vertical distance crossed by the light.

Light exchanges among the compartments of the understory are simulated in the “regeneration” library. In the understory, light rays can intercept different vegetation objects (“sapling” and “vegetation layer” classes) from the highest to the lowest layers (Fig. 7.3); the amount of energy intercepted by each object is estimated following the Beer-Lambert law. For instance, the light that is transmitted through the i^{th} highest understory vegetation object is computed as:

$$I_{i+1} = I_i * e^{-k*V} \quad (7.2)$$

Where I_{i+1} is the light available below the object I , I_i is the light available above the object, k is the extinction coefficient of object i , and V corresponds to vegetation layer cover or sapling diameter, depending on the nature of the object.

7.3.2.3 How the model works

Three input files are necessary to run a simulation in RRESHAR:

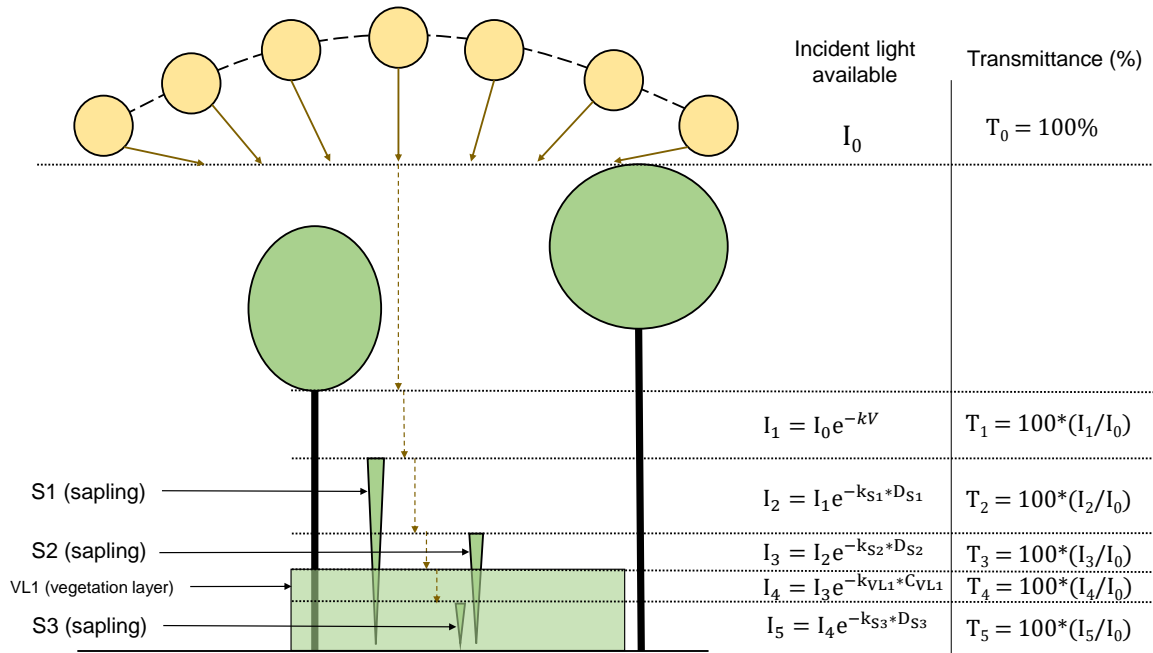


Figure 7.3: Illustration of the process of light interception by the different vegetation classes in RRESHAR. The reverse triangles and the rectangle respectively represent objects in the “sapling” and “vegetation layer” classes. k_i , D_i and C_i are respectively the extinction coefficient, the diameter (for saplings) and the cover percentage (for vegetation layers) of object i .

- *The inventory file* contains information on the modeled scene (dimension, number of cells), the adult trees (species, age, height, diameter at breast height, coordinates of all individuals and extinction coefficient for each species), the saplings (species, age, height, diameter and coordinates of all individuals) and the vegetation layers (cell, species, height and cover percentage). This file may also contain soil data for water exchanges, which I will not describe here.
- *The light file* contains hourly data for diffuse and direct radiation during one growing season. This file, read by the SamsaraLight library, makes it possible to illuminate the modeled scene and to calculate the light intercepted by the adult trees.
- *The climate file* contains data on temperature and precipitation at a daily scale, for all the duration of the simulations. This file is used to calculate water exchanges and is therefore irrelevant for the simulations that I conducted during my thesis since I did not take water exchanges into account.

RRESHAR works at a yearly time step, for a duration specified by the user. The first year (called year 0), the model creates the initial scene described in the inventory file. Each year, the model starts by completing an annual radiative budget with functions from the Samsara light library designed to compute transmittance below the canopy in each cell (Fig. 7.4). Based on the below-canopy transmittance computed by SamsaraLight, RRESHAR uses

functions from the “regeneration” library to compute the amount of light intercepted by the saplings and vegetation layers; RRESHAR also estimates their growth.

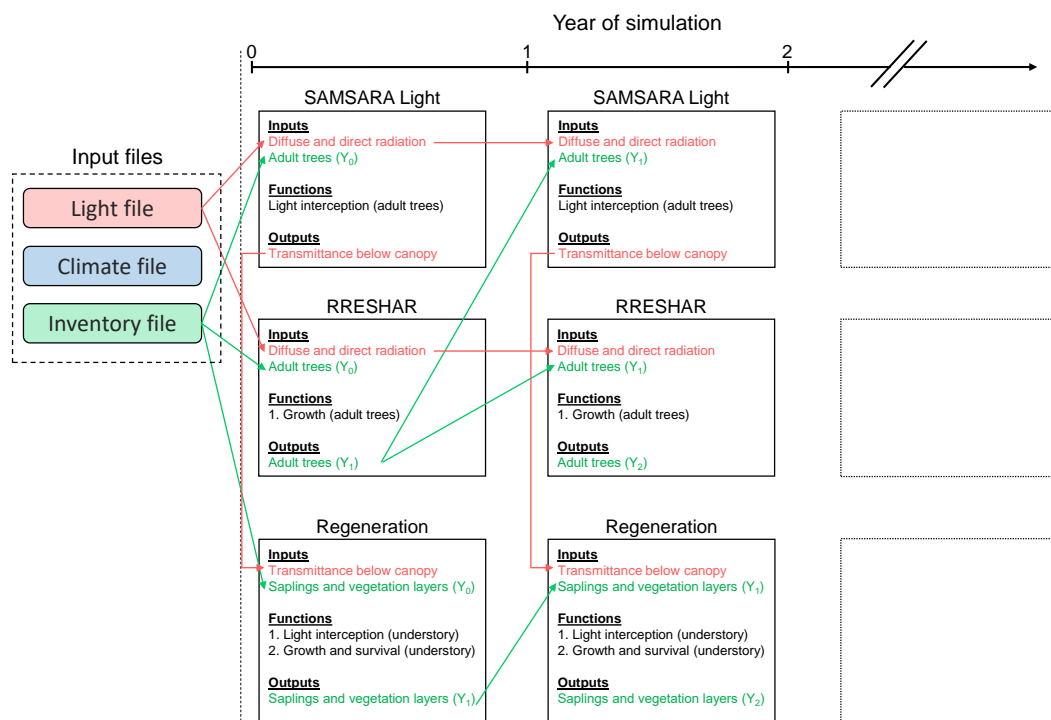


Figure 7.4: Simplified representation of the structure and functions of RRESHAR. For a description of RRESHAR including water exchanges, see chapter 5, Fig. 1 in [Helluy \(2020\)](#)

Vegetation layers have species-specific equations for annual height and cover growth, while saplings have species-specific equations for survival probability, height and diameter growth. The explanatory variables included in these different equations are transmittance and the initial characteristics of the vegetation object (height or cover for vegetation layers, height or diameter for saplings).

Thanks to the representation of different types of understory vegetation, and to the functions representing the exchange of resources among these vegetation types, the “regeneration” library is perfectly adapted to studying the first stages of the regeneration process. However, the “regeneration” library lacked two elements to run simulations to test the hypotheses presented in section 7.2. First, the species studied during my thesis work (bramble in the vegetation layer; and oak, beech and hornbeam as saplings) were not included in the library. Though RRESHAR was originally calibrated with data on sessile oak–Scots pine mixed stands in the Orleans Forest, it was designed to be generic and adapted to any type of stand, climate, understory vegetation and soil conditions. Therefore, I first added the species pertinent to my thesis to the “regeneration” library by including equations from different sources (e.g. field data and the literature). Secondly, the process of herbivory had not

yet been included so I built a theoretical model that takes herbivory into account and implemented this new theoretical model in CAPSIS (here again, included in the “regeneration” library). In the following sections, I will present these two steps, which represent by far the largest part of the work associated with this chapter of my thesis.

7.3.3 Inclusion of the biological models in the “regeneration” library

In this section, I describe the parameters and equations that I used to introduce bramble as a vegetation layer and oak, beech and hornbeam as saplings in the “regeneration” library. In both classes, I used two types of data: I analyzed data collected in the field and models reported in the literature.

7.3.3.1 Adding bramble to the “regeneration” library

Adding any vegetation layer class to the regeneration library requires the following equations:

- *Height increment*: an equation predicting height after the growing season, as a function of height before the growing season, and of transmittance.
- *Cover increment*: an equation predicting cover after the growing season, as a function of cover before the growing season, and of transmittance (if relevant).
- *Light interception parameters*: an equation predicting Leaf Area Index (LAI) as a function of cover, and an extinction coefficient.
- *Maximum height and cover*: either as fixed values, or equations predicting the maximum height and cover as a function of transmittance

a. Height and cover incrementation

I computed height and cover increments with data from the EFFORT protocol, piloted by the French Office for Biodiversity (Saïd *et al.*, 2019) and extensively presented in section 6.3. This protocol encompasses three forest sites in northeastern France – Arc-en-Barrois, Trois Fontaines and La Petite Pierre – where 19 pairs of fenced-unfenced plots were set up (see section 6.3 for a complete description of the experimental design). Because bramble was much scarcer in La Petite Pierre, I chose to focus on Arc-en-Barrois and Trois Fontaines, which respectively host nine and four pairs of fenced-unfenced plots. Once a year in early spring, from 2017 to 2020 in Arc-en-Barrois, and from 2016 to 2019 in Trois-Fontaines, the

cover class (5 classes: 0.01-5%, 5-25%, 25-50%, 50-75% and 75-100%) of bramble per vegetation layer (3 vegetation layers: below 50cm, 50-130cm, and 130-300cm) in eight square subplots of 1 m² per treatment subplot was estimated (Fig. 6.1). Because cover classes are not suited to computing annual increment, I used the median values to convert the classes into percentages (e.g. if a species is in the 25-50 % cover class, its percentage cover will be 37.5%). Following the methodology of Fischer (2015), I then combined the cover values of the different vegetation layers to obtain a total bramble cover value C_k for each subplot k :

$$C_k = 1 - \prod_{i=1}^{n_{layer}} (1 - c_{i,k}) \quad (7.3)$$

Where $c_{i,k}$ is the bramble cover in layer i and subplot k .

I used a similar approach to estimate bramble height in each subplot. I converted each vegetation layer into its median height (e.g. 25cm for the 0-50cm vegetation layer) and then computed mean bramble height H_k in subplot k as the mean of the median heights weighted by the median bramble cover in each vegetation layer:

$$H_k = \frac{\sum_{i=1}^{n_{layer}} (c_{i,k} * h_i)}{\sum_{i=1}^{n_{layer}} c_{i,k}} \quad (7.4)$$

Where h_i is the median height of vegetation layer i .

Computing annual increment from these data was likely to result in a high number of null values (in all cases where the bramble layer did not grow enough to reach the upper vegetation layer or cover class). To overcome this, I chose to compute the annual height (iH) and cover (iC) increment as the mean annual increment in each subplot during the full monitoring period.

$$\begin{cases} iH = \frac{H_{2020} - H_{Y_0}}{2020 - Y_0} \\ iC = \frac{C_{2020} - C_{Y_0}}{2020 - Y_0} \end{cases} \quad (7.5)$$

Where Y_0 is the first year of the experiment (2017 for Arc-en-Barrois and 2016 for Trois-Fontaines). I fitted several linear models to predict bramble height as a function of initial bramble height (H_{Y_0}) and transmittance (T), and obtained the best fit ($R^2 = 47.2\%$) with the following model:

$$H = H_{Y_0} + iH = 1.12 * H_0 + 0.57 * T + 1.11 \quad (7.6)$$

Similarly, I fitted several linear models to predict bramble cover as a function of initial bramble cover (C_{Y_0}) and transmittance (T), and obtained the best fit ($R^2 = 39.8\%$) with the fol-

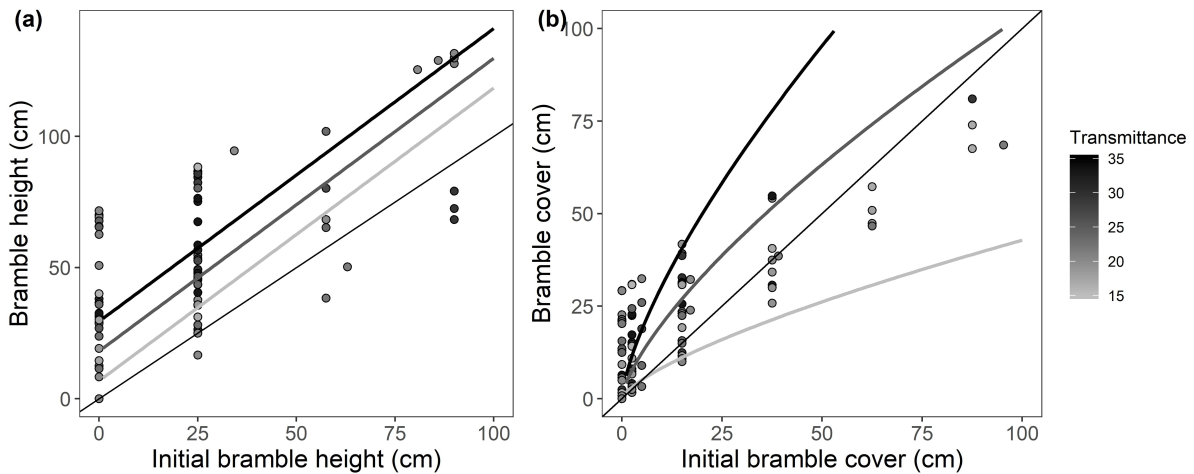


Figure 7.5: (a) Relation between bramble height before and after the growing season, and transmittance. (b) Relation between bramble cover before and after the growing season, and transmittance. Lines represent model predictions.

lowing model:

$$C = C_{Y_0} + iC = C_{Y_0}^{0.71} * T^{0.80} * e^{-1.36} \quad (7.7)$$

In both models, I only included the data collected in fenced plots in order to simulate bramble growth without browsing pressure.

b. Light interception

To obtain the bramble extinction coefficient and the equation predicting bramble LAI as a function of its cover (C , expressed as a percentage), I used the publication of [Balandier et al. \(2013\)](#). The bramble extinction coefficient in their paper was calculated with a Beer Lambert law from bramble LAI ($I/I_0 = e^{-k*LAI}$), and is equal to 0.074. LAI can be calculated with the following equation:

$$LAI = (0.327 * \log(C))^2 \quad (7.8)$$

c. Maximum height and cover

I chose to set bramble maximum cover to 100%, without taking transmittance into account. However, since other studies have found that the maximum height of similar species is related to transmittance – e.g. blackberry (*Rubus Idaeus*) in [Gaudio et al. \(2008\)](#) – I chose to include a relation between maximum bramble height and transmittance. To parametrize this relation, I used field data collected by Morgane Gillard (an intern under the supervision of P. Balandier) in 2010.

The protocol is described in section "Experiment 2" in [Balandier et al. \(2013\)](#). The study was conducted from April to June 2010, at ten sites located in the Massif Central mountain range (France). Since I wanted to implement bramble under an overstorey of oak, I restricted my analysis to the four sites that had an oak overstorey. At each site, two to four transects were set up along a gradient of canopy openness, and along each transect, between four and eight measurement points were selected. At each measurement point, average and maximum bramble height was measured, and transmittance was recorded as the ratio of the PAR measured under the tree canopy to the incident PAR measured with a point sensor in an open field located close to the site.

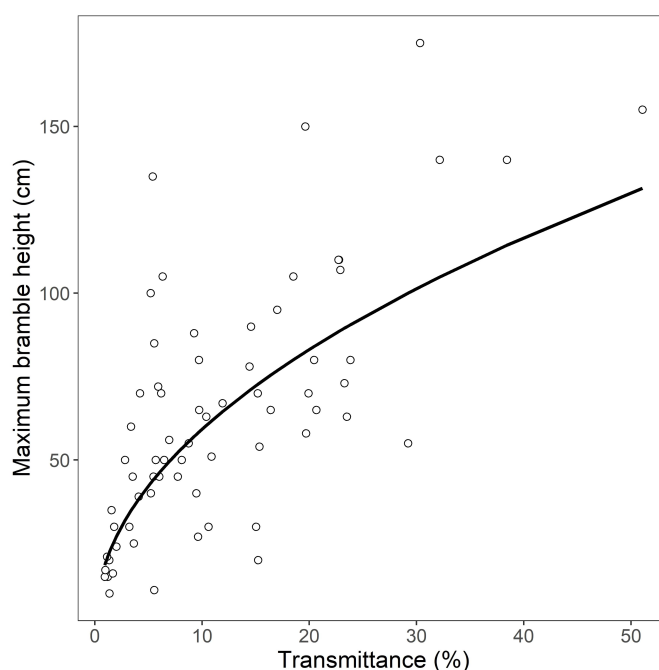


Figure 7.6: Relationship between maximum bramble height and transmittance. The solid line represents the model's prediction.

I fitted different models to explain maximum bramble height, and found the best fit ($R^2 = 53.3\%$) with the following:

$$H_{max} = T^{0.489} * e^{2.96} \quad (7.9)$$

7.3.3.2 Adding oak, beech and hornbeam saplings to the "regeneration" library

Adding a new sapling class to the "regeneration" library requires the following equations:

- *Height increment*: an equation that predicts height after the growing season, as a function of height before the growing season, and transmittance (if relevant).

- *Diameter increment*: an equation that predicts diameter after the growing season, as a function of diameter before the growing season, and transmittance (if relevant).
- *Survival probability*: an equation predicting survival probability as a function of height before the growing season.
- *Light interception parameter*: an extinction coefficient calculated from the one existing for adult trees.

a. Height and diameter incrementation

The height increment (iH) (in $\text{cm}\cdot\text{year}^{-1}$) of oak and beech saplings was modeled as a function of transmittance (T) and initial height (H_0) in a study conducted over five years in the Belgian Ardennes (Ligot *et al.*, 2013) with the following equation:

$$iH = \frac{a * \sqrt{H_0}}{1 + e^{1-\frac{T}{b}}} \quad (7.10)$$

Values for parameters a and b for oak and beech are presented in table 7.1. Because equations for hornbeam height increment are scarce in the literature, I chose to use the same parameters as for beech, since the growth rates of the two species are comparable (P. Balandier, pers. com.).

Table 7.1: Parameter estimates of the model presented in eq. 7.10. Data from Ligot *et al.* (2013).

	a	b
Oak	2.059	6.058
Beech	2.431	3.964

In their study, Ligot *et al.* (2013) also measured sapling diameter 5cm above ground level. Though diameter increment was not modeled like height increment, the authors did establish an allometric relation between diameter (D) and height (H) for both oak and beech (G. Ligot, unpublished data):

$$D = \alpha + \beta * H \quad (7.11)$$

From this equation, it is possible to model diameter increment (iD , expressed in $\text{mm}\cdot\text{year}^{-1}$) as a function of iH :

$$iD = \beta * iH \quad (7.12)$$

With $\beta_{Oak} = 0.079$ and $\beta_{Beech} = 0.093$. Here again, for hornbeam, I chose to use the same parameter as for beech.

b. Survival probability

In the regeneration library, each individual sapling has a survival probability $p_{Survival}$ that is necessarily computed with an equation of the following structure:

$$p_{Survival} = \frac{e^{a*H_0+b}}{1 + e^{a*H_0+b}} \quad (7.13)$$

Where H_0 is sapling height before the growing season, and a and b are species-specific parameters.

To compute these parameters, I again used data from the EFFORT project, more specifically the protocol for individual oak sapling monitoring in the study sites of Arc-en-Barrois and Trois Fontaines (see section 6.3 for a complete description of the protocol). I used a generalized linear model with a binomial error distribution and a 'logit' link function to model survival (binary response variable, 1 = alive after the growing season, 0=dead) as a function of the initial height for each individual sapling each year. Due to the occurrence of repeated measurements for the same individuals (one measurement per year), I included sapling ID as a random effect. From this model, I obtained the following equation:

$$p_{Survival} = \frac{e^{0.067*H_0+1.14}}{1 + e^{0.067*H_0+1.14}} \quad (7.14)$$

Since I did not have similar data for beech and hornbeam, I implemented the same equation for all three species.

c. Light interception parameter

The process of light interception for saplings in the regeneration library is an adaptation of the process of light interception by adult trees in the Samsara Light library. Because no study to date has measured an extinction coefficient at the sapling growth stage, I used the thesis by [Gobin \(2015\)](#) who calculated an extinction coefficient of $k = 0.4$ following a Beer Lambert law from oak adult tree LAI ($I/I_0 = e^{-k*LAI}$). Since I had no similar data on beech and hornbeam, I implemented this coefficient for all three species of saplings.

7.3.4 Theoretical model for a browsing extension

7.3.4.1 Modeled system

To conceptualize the theoretical model, I started with the description of the studied environment, divided into three compartments, as is common: the active environment, the studied system and the passive environment ([Lamanda et al., 2012](#)). The studied system

corresponds to the elements modeled; the active environment includes elements from other systems that influence the studied system; and the passive environment is the output variable. The environment that I built for my theoretical model is the result of a trade-off among four questions:

- Can this system answer the research questions that I seek to investigate?
- Does this system accurately represent reality?
- From a practical point of view, is it possible to implement this system in the "regeneration" library?
- Do I have access to data to parametrize this model?

I included five plant classes in the studied system: adult oak trees; oak, beech and hornbeam saplings; and bramble. In field conditions, forest stands containing beech, oak and hornbeam saplings in the understory are likely to host adult trees of these same three species. However, in this study, the adult trees were merely a way to control for canopy openness and their growth was not relevant to the research questions. Therefore, I chose to include only the oak canopy – already implemented in RRESHAR – rather than to spend additional time searching for equations in the literature to parametrize the growth of adult beech and hornbeam trees. I included three elements in the active environment: deer browsing on saplings, deer browsing on shrubs and clearing. Since shrubs have a very different structure from saplings (both in the model and from a biological point of view), the consequences of shrub browsing on oak regeneration are likely to differ from the consequences of sapling browsing. Modeling the browsing pressure on saplings and on shrubs separately enabled me to identify the respective effects of these two pressures, and should therefore improve our understanding of the overall consequences of deer browsing on understory vegetation. Lastly, the passive environment is a variable that should reflect regeneration success. Since this study deals with the effect of deer browsing on oak regeneration, the target objective was for the saplings to grow above the maximum height accessible to deer. To parametrize browsing pressure, I included field data on cervid preferences (see section 7.3.4.3 for details), mostly measured on saplings smaller than 130 cm, which corresponds approximately to the maximum height reachable by roe deer (Nichols *et al.*, 2015). Therefore, I chose the density of oak saplings above 130 cm after 15 years as an output variable. The environment as a whole is shown in Fig. 7.7.

7.3.4.2 Implementing vegetation layer browsing

Deer browsing may influence both height growth and cover growth of vegetation layers. The simplest approach for modeling this browsing pressure is to include coefficients that

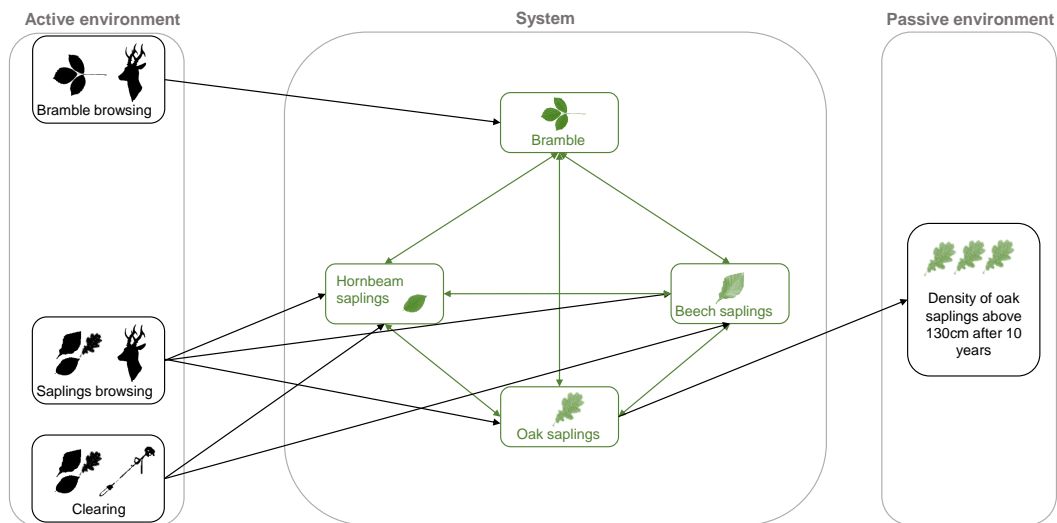


Figure 7.7: Diagram of the studied environment. The elements of the system and their relations are represented in green. To simplify the diagram, adult trees were not included since they do not interact directly with the active environment.

reflect the “impact” of deer browsing in the height growth and cover equation of the vegetation layers. To compute these coefficients for bramble, I used the same dataset as I did to calculate the bramble growth equation, but this time with data from both fenced and unfenced plots. I added a “fencing” effect to the height growth and cover model, resulting in the following equations:

$$\begin{cases} C = C_0^{0.71} * T^{0.80} * e^{-1.36-K_C} \\ H = 1.12 * H_0 + 0.57 * T + 1.11 - K_H \end{cases} \quad (7.15)$$

Where K_C and K_H respectively represents the yearly decrease in cover and height due to deer presence. By comparing bramble growth in fenced and unfenced plots, I found that in the field experiment $K_C(field) = 0.30$ and $K_H(field) = 4.27cm$. In order to test the hypotheses raised in section X, browsing pressure on bramble must be a continuous (or at least a semi-quantitative) variable. To this end, I introduced three variables with values specified by the user: the fixed values of (i) $K_C(unfenced)$ (ii) $K_H(unfenced)$, and (iii) vegetation layer browsing intensity (VBI hereafter), a continuous variable that multiplies these two coefficients so that:

$$\begin{cases} K_C = K_C(field) * VBI \\ K_H = K_H(field) * VBI \end{cases} \quad (7.16)$$

VBI has the advantage of being intuitive: values of 0, 1 and 2 respectively indicates that the browsing pressure exerted on bramble is null, equivalent to or double the pressure observed in unfenced plots. Since I wanted the browsing functions to be technically useable for all vegetation layer species included in the "regeneration" library, I implemented this function so that for any vegetation layer species j :

$$\begin{cases} C_j = f_{C_j}(C_{0j}, T) * e^{-K_C(field)_j * VBI} \\ H_j = f_{H_j}(H_{0j}, T) - K_H(field)_j * VBI \end{cases} \quad (7.17)$$

Where f_{C_j} and f_{H_j} are species-specific equations respectively predicting cover and height growth of vegetation layer species j . VBI, $K_C(field)_j$ and $K_H(field)_j$ must be specified by the user in a new input file created for the browsing extension: the herbivory file.

7.3.4.3 Implementing sapling browsing

Among the equations associated with the class "sapling" in the "regeneration" library (height and diameter growth, survival probability, light interception), two are likely to be affected by deer browsing: height growth and survival probability. However, since survival already depends on height, I chose to only implement an effect of browsing on height growth. The hypotheses raised in section 7.2 also deal with the differential palatability of the three sapling species: it was therefore crucial to include interspecific differences in the susceptibility to browsing. To that end, I chose to introduce a probabilistic approach: each year and in each cell, only a subset of the saplings present are browsed, and the probability for each sapling to be browsed depends on the species. Like bramble browsing, sapling browsing must also be a continuous, or at least semi-quantitative, variable. I chose to use a biomass approach in this case: the user specifies an annual biomass of saplings consumed (BSC hereafter) per unit area (all species confounded). I first needed to add a calculation for sapling biomass to the "regeneration" library. I used the publication by [Annighöfer et al. \(2016\)](#), which includes species-specific aboveground biomass (AGB) equations as a function of the diameter (D) and height (H) of the sapling:

$$AGB = \beta_1(D^2 * H)^{\beta_2} \quad (7.18)$$

Where β_1 and β_2 are species-specific coefficients. Table 7.2. presents the value of these coefficients for the three sapling species studied.

Once I had implemented the biomass calculation, the next step was to translate a reduction in height growth into biomass removal. For all three species, I assumed that browsing-induced height reduction corresponded to bite size (*i.e.* length of the shoot removed by the deer, BS hereafter). I set this variable at 5cm of the apical shoot based on roe deer rumen

Table 7.2: Value of β_1 and β_2 coefficients for the three studied species (cf. eq. 7.18). Values are from [Annighöfer et al. \(2016\)](#)

	β_1	β_2
Oak	0.67311	0.85202
Beech	0.62342	0.87409
Hornbeam	0.35633	0.92508

content. This means that the height growth of a sapling browsed during year y is computed as:

$$H_{y+1} = f_H(H_Y, T) - BS \quad (7.19)$$

Where f_H is the function predicting sapling height as a function of transmittance and initial height. I assumed that sapling biomass was homogeneously allocated along the height of the sapling, so that the aboveground biomass consumed on a given sapling i ($AGBC_i$) is computed as:

$$AGBC_i = \frac{AGB_i * BS}{H_i} \quad (7.20)$$

Fig. 7.8 describes the algorithm associated with the process of sapling browsing at the cell level. I assumed that sapling biomass consumed per unit area was constant in each cell k ($BSC_k = BSC, \forall k$ in $[1; n_{cells}]$). To sum up: each sapling is associated with a probability of being browsed, and the model randomly “browses” the saplings one by one until the cumulated biomass consumed reaches the biomass consumed per unit area specified by the user.

I computed a browsing probability for each individual sapling using data from the fencing experiment in Arc-en-Barrois and Trois-Fontaines, where oak, beech and hornbeam are the most abundant tree species. More specifically, I used the exhaustive vegetation surveys from the unfenced plots only. Each year, in $1m^2$ vegetation subplots (Fig. 6.1), the cover class and height class of each tree species was noted, along with the occurrence of browsing (binary data: 1 = browsed and 0 = unbrowsed). Before fitting a model, I checked the number of occurrences of each species per height and cover class (Fig. 7.9).

Fig. 7.9 shows that, for all three species, there are very few cases for which height exceeds 130cm (which is likely due to the short time span of the study), and cover is greater than 25%. I therefore excluded these data and kept only the two lowest vegetation layers (0 – 50 cm and 50 – 130 cm) and cover classes (0.01 – 5% and 5 – 25%) for analysis. I fitted a generalized linear model with a binomial error distribution and a logit link function to model the occurrence of browsing as a function of species (a factor with three modalities: “oak”, “beech”, and “hornbeam”), height class (a factor with two modalities) and cover class (a

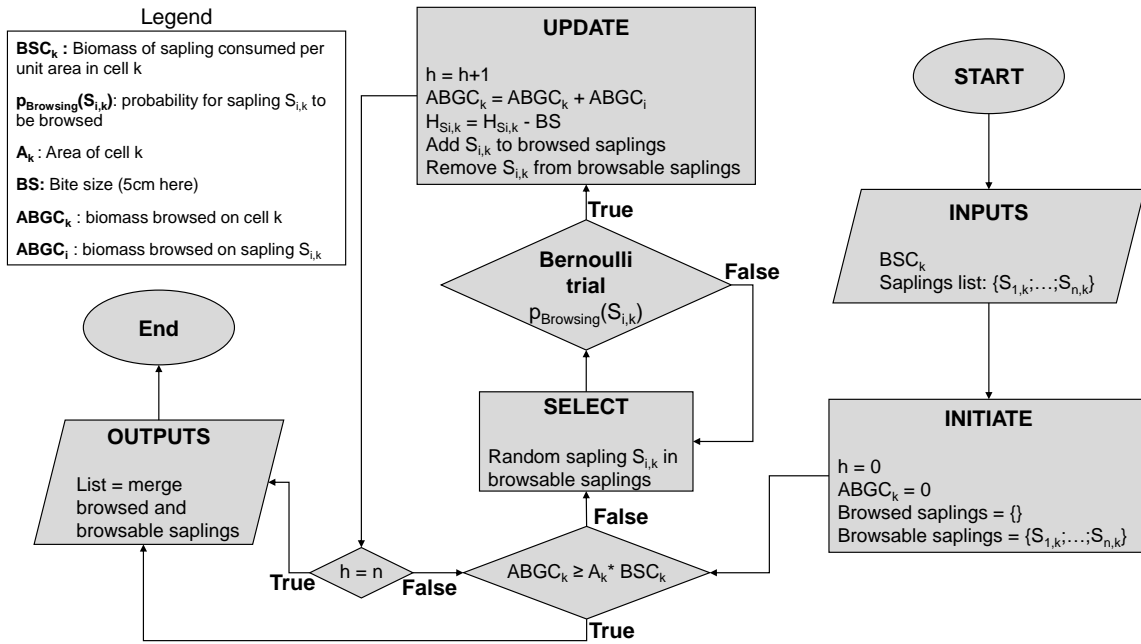


Figure 7.8: Flowchart of the algorithm implemented in the regeneration library to model sapling browsing at the cell level.

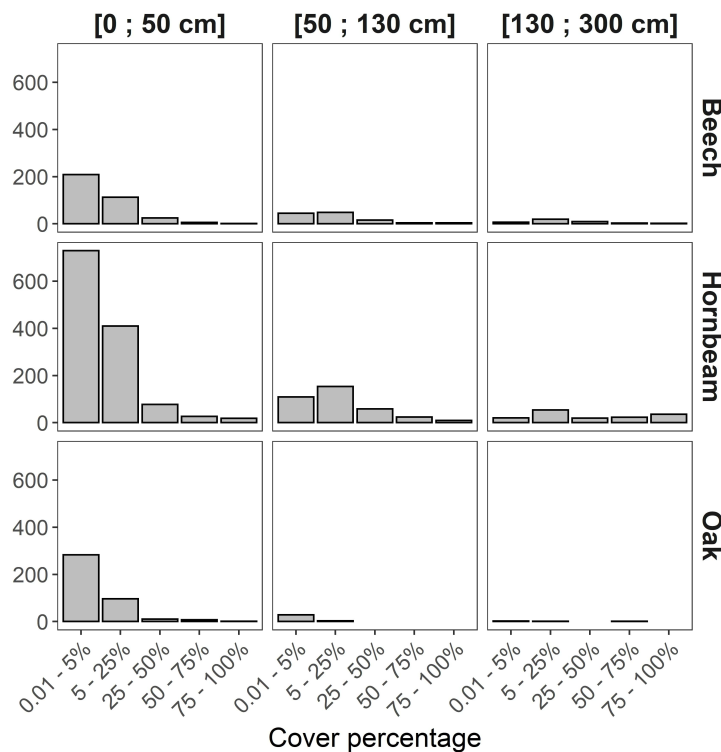


Figure 7.9: Number of occurrences of each sapling species per height class (columns) and per cover class (x-axis) in the exhaustive vegetation surveys conducted in the unfenced plots from 2016 to 2019 at Arc-en-Barrois and Trois Fontaines. The null cover data were excluded.

factor with two modalities). I first included all possible interactions and removed any non-significant terms one by one to select for the most parsimonious model, which contained only three fixed effects: species, height class and the interaction between these two factors. Fig. 7.10.a. shows the browsing probability predicted by this model:

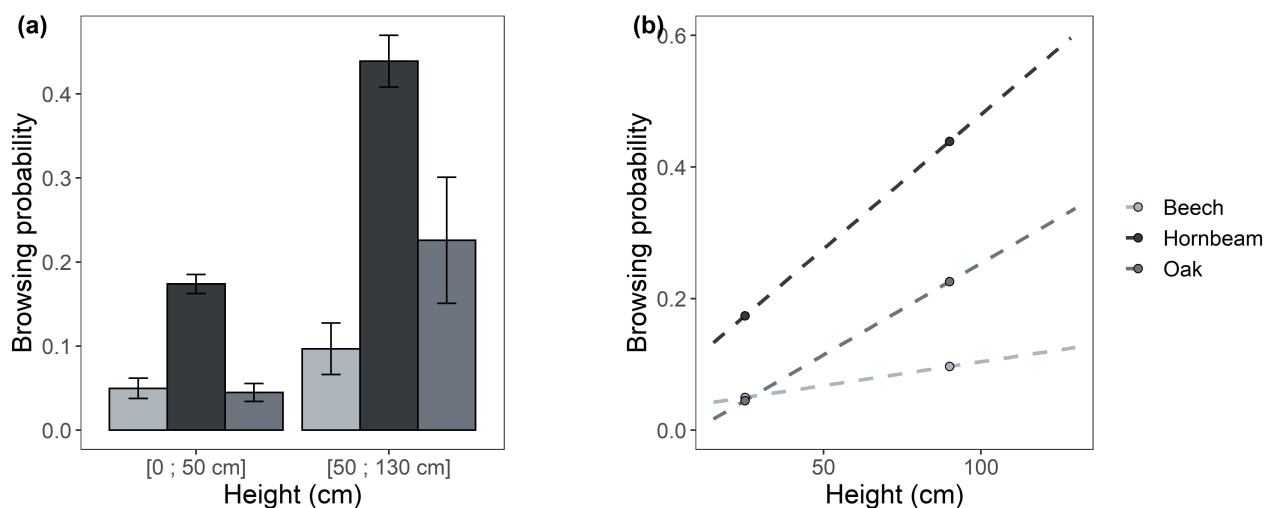


Figure 7.10: Browsing probability (\pm standard error) for each sapling species predicted by the generalized linear model, with height on a (a) discrete or (b) continuous scale.

Fig. 7.10.a confirms the existence of a gradient of palatability among these three species. However, the height-class approach has the disadvantage of over-simplifying reality: in field conditions, browsing probability tends to increase continuously with sapling height. To consider this, I converted height into a continuous variable using the median values (Fig. 7.10.b) so that the browsing probability ($p_{Browsing}$) for a sapling S_i is computed as:

$$p_{browsing}(S_i) = \alpha_{species(S_i)} * H_{S_i} + \beta_{species(S_i)} \quad (7.21)$$

The species-specific values of the α and β coefficients are presented in table 7.3.

Table 7.3: Value of α and β coefficients for the three studied species (cf. eq. 7.21).

	α	β
Oak	0.00278	-0.02474
Beech	0.00072	0.03158
Hornbeam	0.00408	0.07188

7.3.4.4 Implementing clearing operations

The aim of a clearing operation is to cut away the saplings and shrubs that could interfere with the regeneration of the target species. In practice, foresters never manage to remove all

the competing saplings, and they always cut down some target-species saplings. The clearing model that I implemented was designed to be compatible with the reality in the field. Therefore, to launch a clearing operation, the user must specify the following information in the herbivory file:

- The year when the clearing operation is to occur (column 1 in Fig. 7.11).
- The sapling species removed during the clearing operation (column 2 in Fig. 7.11).
- The minimum height above which saplings of the undesirable species are to be cleared (column 3 in Fig. 7.11).
- The proportion of saplings of the undesirable species to be cleared in the stand (column 4 in Fig. 7.11).

Fig. 7.11 presents an example from the section of the herbivory file where clearing operations are specified. In this simulation example, clearing will take place during the 5th, 7th and 9th years, 20% of the oak saplings above 20cm and 80% of all beech and hornbeam saplings above 20cm will be cleared.

```
# Sapling clearing
# date  saplingSpeciesName  clearingThresholdHeight_m  clearingPercentage]0,100]
5      QUERCUS_ROBUR  0.2  20
5      CARPINUS_BETULUS  0.2  80
5      FAGUS_SYLVATICA  0.2  80
7      QUERCUS_ROBUR  0.2  20
7      CARPINUS_BETULUS  0.2  80
7      FAGUS_SYLVATICA  0.2  80
9      QUERCUS_ROBUR  0.2  20
9      CARPINUS_BETULUS  0.2  80
9      FAGUS_SYLVATICA  0.2  80
```

Figure 7.11: Screenshot of an example from the herbivory file where the information on clearing operations is specified.

Once a sapling is cleared, its height is reduced to 20 cm while the diameter remains unchanged.

7.4 A first set of simulations

7.4.1 Building the initial scene

7.4.1.1 Silvicultural itinerary

In this study, I modeled the specific stages in a typical silvicultural itinerary in France designed to naturally regenerate oak stands (Fig. 7.12). Foresters initiate regeneration after a

large seeding crop (mast year) by harvesting mature trees representing from 25% to 50% of the stand basal area to open the canopy and provide sufficient light for seedlings (*i.e.* seeding cut). Some seed trees are maintained in the stands to ensure a minimal flow of seeds in case the regeneration fails. Once the regeneration growing beneath the canopy cover is well established (*i.e.* a sufficient number of saplings have grown above 3m high), the foresters remove the remaining adult trees (*i.e.* final cut) so that they can be replaced by the saplings growing beneath them. I modeled this itinerary from one year after the seeding cut (one-year-old seedlings are established) to the 16th year (Fig. 7.12). Between the seeding cut and the final cutting, some intermediate cuttings are commonly performed to progressively increase canopy openness, but I did not model these operations.

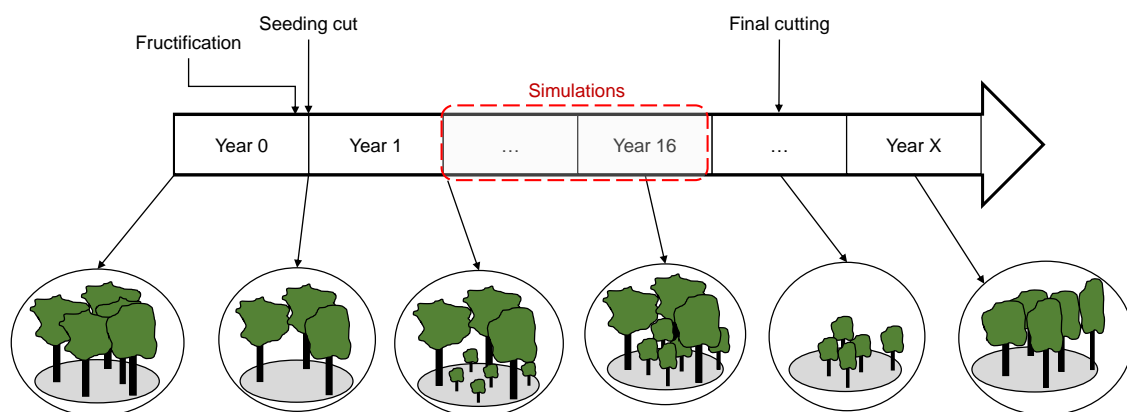


Figure 7.12: Simplified representation of the silvicultural itinerary studied, and of the stages that were modeled during this study.

7.4.1.2 Scene dimension

The main limitation when choosing the scene dimension is the computation time: the larger the scene, the longer the computation time. This is even more pertinent since I chose to work on objects of the sapling class instead of more timesaving cohorts. I conducted simulations in $900m^2$ scenes that consisted of 36 (6x6) square cells of $25m^2$ each (Fig. 7.2). With these dimensions, it took between 1h25 and 4h30 (depending mainly on the initial sapling density and the browsing pressure applied) to launch a thousand simulations on a Latitude 5490 Dell computer (i7 processor, 16GB RAM) (*i.e.* between 5 and 16 seconds per

simulation).

7.4.1.3 Position of the adult trees

In this study, the only function of adult trees was to intercept light. To investigate my research questions, I needed to contrast different levels of canopy openness even though the output variable (*i.e.* the density of oak saplings above 130cm after 15 years) was computed at the scene level. This meant that the transmittance conditions needed to be as homogenous as possible within a scene. To that end, I initiated each scene with an even distribution of adult trees of the same age (40 years), diameter at breast height (14cm) and height (17m). To contrast different levels of canopy openness among scenes, I changed the tree density but always kept the equal distribution of the adult trees (see fig. 7.2 for an illustration).

7.4.1.4 Initial sapling distribution

In the inventory file, the user must specify the age, species, height and diameter of each modeled sapling. Since the simulations start one year after the seeding cut: all the saplings present are one-year-old. Species composition is an explanatory variable needed to investigate some hypotheses presented in section 7.2. To determine the height and diameter of each modeled sapling, I used a height-diameter joint distribution of all one-year-old oak saplings monitored in the fencing experiment in Arc-en-barrois and Trois Fontaines (Fig. 7.13) to build a contingency table containing a probability for each height-diameter combination.

From this contingency table, I built an algorithm (Fig. 7.14) to create a list of height-diameter combinations. I used the same table for all three species, which is acceptable since oak saplings have a comparable height-diameter distribution to beech and hornbeam at the one-year-old stage (*pers. obs.*).

7.4.1.5 Initial bramble distribution

In the inventory file, the user must specify bramble height and cover in each cell to initialize the plant's distribution. I used the same probabilistic approach as for sapling distribution. I built a contingency table for bramble height (H_{Y_0} in eq. 7.6) and cover (C_{Y_0} in eq. 7.7) joint probability distribution during the first year of the fencing experiment. I set the probability of null cover or height to 0 to make sure that bramble was present in each cell. I used an algorithm similar as the one described in Fig. 7.14, where n is the number of cells, and where saplings are replaced by vegetation layers.

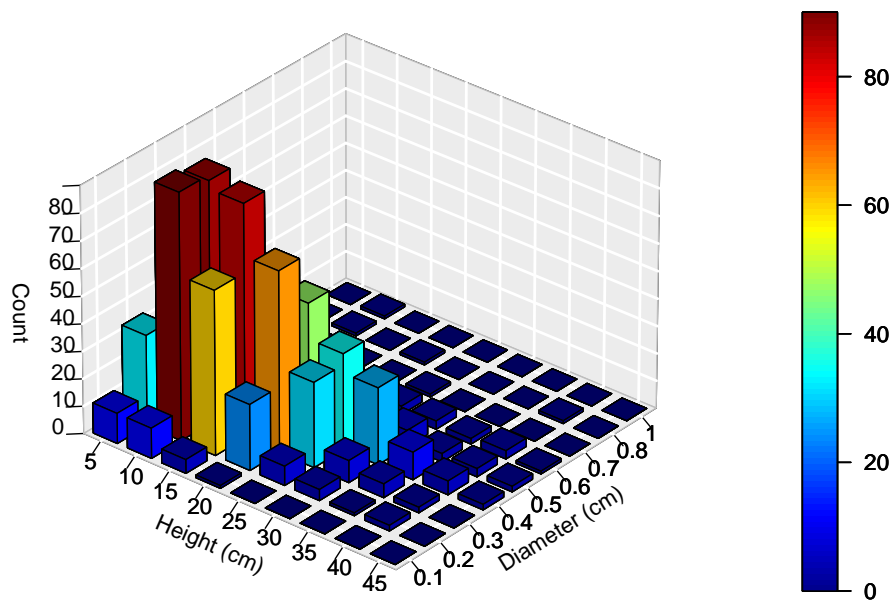


Figure 7.13: Height and diameter distribution of one-year-old oak saplings during the first year of the fencing experiment in Arc-en-Barrois and Trois Fontaines.

7.4.2 Simulation plan and data analysis

Table 7.4: Abbreviations of the different variables mentioned in the simulation plan

Abbreviation	Variable	Unit
Oak_{130}	Density of oak above 130cm in height after 15 years	sapling.ha ⁻¹
CS	Companion species of oak (beech and/or hornbeam)	
BSC	Biomass of sapling consumed	kg.ha ⁻¹ .year ⁻¹
pO	Initial % of oak relative to the companion species	%
VBI	Vegetation layer browsing intensity	
ISD	Initial sapling density	sapling.m ⁻²
T	Transmittance	%
$T_{500/ha}$	Time required to reach 500 oak above 130cm per ha	Year
ClSc	Clearing scenario	

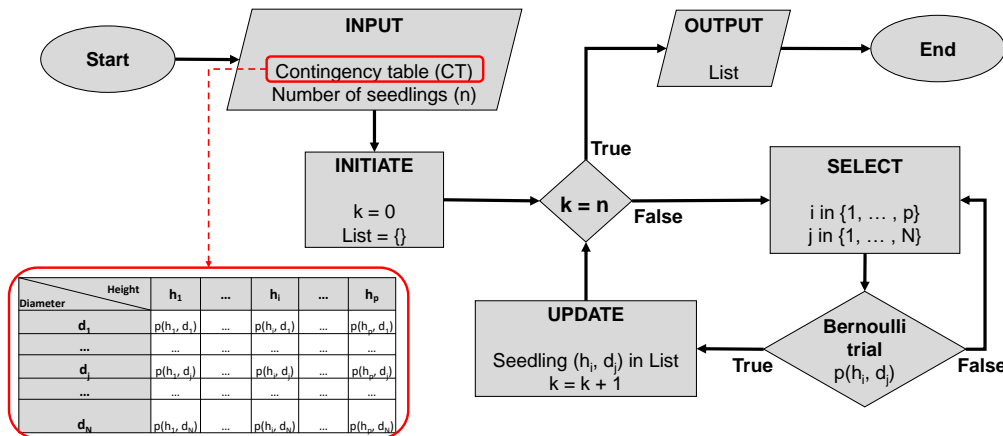


Figure 7.14: Flowchart of the algorithm used to obtain a list of n height-diameter combinations using a contingency table

7.4.2.1 Effect of species and relative density of admixed saplings on oak regeneration

Simulation plan

To investigate this first hypothesis, I crossed two companion species (*CS* hereafter) modalities (beech and hornbeam), three *BSC* values (0, 3 and 6 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) and 21 values of initial oak percentage (*pO* hereafter, 0%, 5%, [...], 100%), leading to a total of 126 possible factor combinations. Transmittance ($T = 35\%$), initial sapling density ($ISD = 5 \text{ sapling}\cdot\text{m}^{-2}$) and vegetation layer browsing intensity ($VBI = 1$) were maintained constant during the simulations. Due to the existence of potential stochastic effects related to the probabilistic approach used to model sapling browsing and to the random distribution of saplings throughout the scene, I replicated each of these 126 factor combinations ten times, for a total of 1260 simulations.

Data analysis

I modelled the relation between Oak_{130} and *pO* with a quadratic relation where each parameter depends on the *CS* and on the *BSC*:

$$\log(Oak_{130}) = a_{CS,BSC} + b_{CS,BSC} * \log\left(\frac{pO}{1-pO}\right) + c_{CS,BSC} * \log\left(\frac{pO}{1-pO}\right)^2 \quad (7.22)$$

I log transformed Oak_{130} to keep its value strictly positive. Because *pO* is a proportion variable ranging strictly between 0 and 1, I used the logit transformation to convert it into a continuous variable. I tested the effect of *BSC* and *CS* on each parameter of the equation

with an ANOVA test comparing the model described above to three naive models where the effect of the two factors was removed on parameters a, b and c respectively.

7.4.2.2 Effect of the browsing pressure on oak regeneration under a gradient of shrub palatability

Simulation plan:

I crossed three theoretical relations between *BSC* and *VBI* (Fig. 7.15), 3 species composition modalities (SC hereafter: 50% oak - 50% beech, 50% oak - 50% hornbeam and 50% oak - 25% beech - 25% hornbeam), 21 *BSC* values (0, 0.5, 1, [...], 9.5 and 10 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) and 20 values of initial sapling density (0.5, 1, [...], 9.5 and 10 $\text{saplings}\cdot\text{m}^{-2}$). Transmittance ($T = 35\%$) was kept constant during the simulations. Due to the high number of factor combinations ($n = 3780$), I did not replicate the simulations.

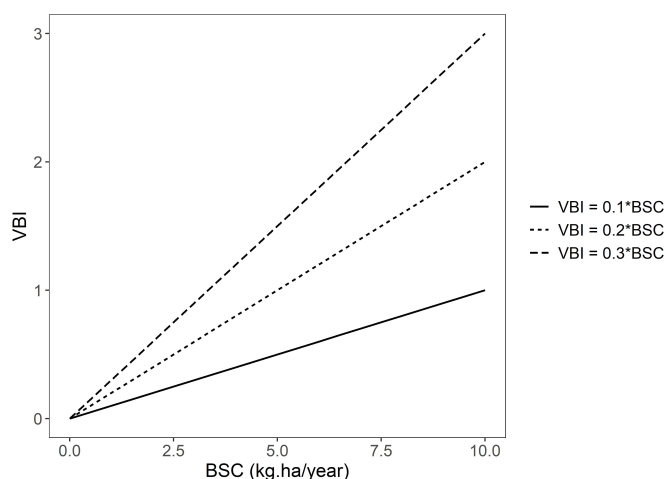


Figure 7.15: Theoretical relations between *VBI* and *BSC* tested for hypothesis 2. The higher the slope, the higher shrub palatability relative to saplings

Data analysis

For each theoretical relation between *BSC* and *VBI*, I tested both the influence of *BSC* and of initial sapling density on Oak_{130} with an analysis of deviance (ANODEV). Oak_{130} was log-transformed prior to analysis to fit the assumptions of a Gaussian error distribution.

7.4.2.3 Effect of the browsing pressure and of the companion species on the efficiency of clearing operations

Simulation plan

To investigate this third hypothesis, I crossed two *CS* modalities (beech and hornbeam), 11 *BSC* values (0, 1, 2, [...], 10 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) and five clearing scenarios (*ClSc* hereafter, D0,

D2, D3, D4 and D5). D0 indicates no clearing, D2 one clearing every 2 years, D3 one clearing every 3 years, and so on. These scenarios were chosen to be "management compatible" with no operations until the 5th year, and a maximum clearing frequency of every two years thereafter. At each clearing operation: 80% of companion saplings, 20% of oak saplings, and the bramble layer are cleared (*i.e.* height reduced to 20cm but no changes in cover or diameter). To represent overall browsing pressure (on shrubs + saplings), *VBI* was calculated as a function of *BSC* with the intermediate scenario presented in Fig. 7.15 (*i.e.* $VBI = 0.2 * BSC$). Transmittance ($T = 35\%$), oak proportion ($pO = 50\%$), and initial sapling density ($ISD = 5$ sapling.m⁻²) were maintained constant during all simulations. I replicated each of the 110 factor combinations 10 times, which gives a total of 1100 simulations.

Data analysis

For each *CS* modality, I calculated the time necessary to reach a density of *Oak*₁₃₀ equal to 500 saplings.ha⁻¹ (t_{500} hereafter) as a function of the browsing pressure and the clearing scenario, according to the following non-linear model:

$$t_{500} = c_{CISc} + \frac{d_{CISc} - c_{CISc}}{1 + e^{b_{CISc} * (BSC - e_{CISc})}} \quad (7.23)$$

This model fits a logistic curve to the relation between t_{500} and *BSC* where d is the upper asymptote, c is the lower asymptote, e is the value of *BSC* when $t_{500} = d$ and b is the slope around the inflexion point. For both *CS* modalities, I tested the effect of the clearing scenario on each of these four parameters by comparing the model described in eq. 7.23 to naive models where each parameter is independent of the clearing scenario.

7.4.3 Results and discussion

7.4.3.1 Effect of species and the relative density of admixed saplings on oak regeneration

In the quadratic model predicting the density of recruited oak (*Oak*₁₃₀) as a function of oak proportion (pO) (eq. 7.22), parameters a (ANOVA, $F_5 = 1174$, $p < 0.01$), b (ANOVA, $F_5 = 411$, $p < 0.01$) and c (ANOVA, $F_5 = 43$, $p < 0.01$) were all significantly influenced by the biomass of saplings consumed (*BSC*) and by the companion species (*CS*). More specifically, *Oak*₁₃₀ decreases with *BSC* at high pO values while *CS* only influences *Oak*₁₃₀ at high browsing pressures ($BSC = 6$ kg/ha/year) (Fig. 7.16). This means that as expected, the companion species influences oak regeneration when browsing is taken into account.

In this model, beech and hornbeam exhibit similar growth rates (Fig. 7.17) and only differ in palatability (Fig. 7.10). This result supports the well-documented theory that the influ-

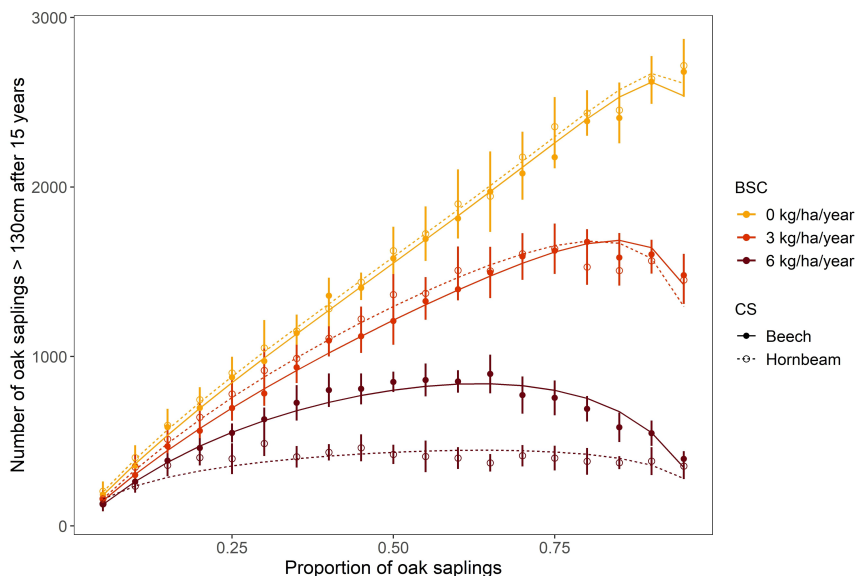


Figure 7.16: Oak_{130} (mean \pm standard deviation) as a function of the initial oak proportion (pO), of the biomass of sapling consumed (BSC) and of oak companion species (CS). Solid lines represent the fit of the model described in eq. 7.22

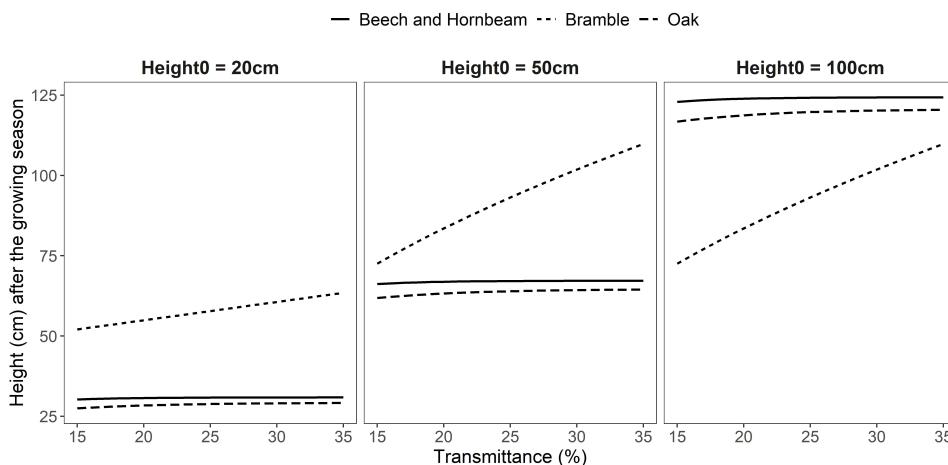


Figure 7.17: Height growth of bramble, oak, beech and hornbeam simulated for different initial heights and transmittance from the equations used to parametrize the model.

ence of deer browsing on a given species does not depend solely on the palatability of the neighboring species (Bee *et al.*, 2009). However, we found that oak regenerates better when accompanied by beech rather than by hornbeam, and this contradicts our initial hypothesis, since beech is less palatable than either hornbeam or oak. Indeed, the ‘attractant decoy’ hypothesis predicts that a plant species exposed to herbivory benefits from being surrounded by more palatable neighbors at the feeding-patch level since it diverts the herbivory pressure towards the neighbors (Hjältén *et al.*, 1993). A possible explanation for the observed pattern is that, since beech saplings are less subject to browsing than hornbeam, they out-

grow and over-shade the bramble more rapidly, thereby hindering bramble height growth. Fig. 7.18 shows that, for a comparable browsing pressure and oak proportion, the density of admixed saplings above 130cm in height is always greater when beech is the admixed species rather than hornbeam, which supports this assumption.

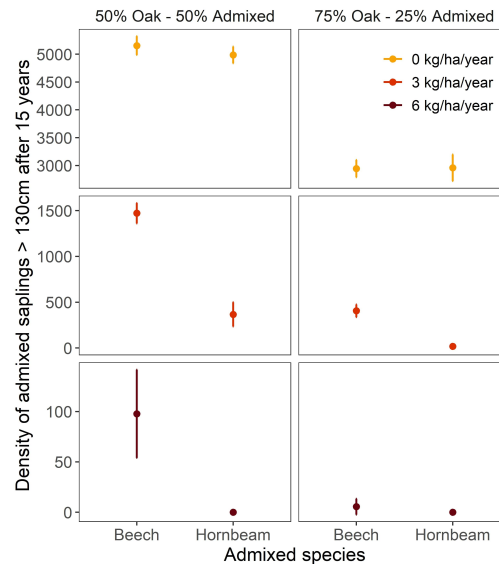


Figure 7.18: Density of beech and hornbeam saplings > 130cm after 15 years (mean \pm standard deviation) as a function of initial oak proportion (pO), biomass of saplings consumed (BSC) and oak companion species (CS).

Indeed, though bramble grows much more rapidly than saplings in this model, its maximum height is conditioned by transmittance (Fig. 7.18). Therefore, each sapling outgrowing the bramble layer reduces both the transmittance above the bramble and bramble maximum height. This could mean that, in the presence of bramble, beech and hornbeam saplings have a general facilitative effect on oak saplings – *i.e.* the indirect reduction in bramble growth benefits oak sapling growth more than direct sapling competition reduces it. The assumption of a facilitative effect is also consistent with our observation of an optimal initial oak proportion which tends to decrease with browsing – *e.g.* around 85% of oak when $BSC = 3$ kg/ha/year and around 65% when $BSC = 6$ kg/ha/year (see Fig. 7.16). Indeed, since both beech and hornbeam have higher growth rates than oak, bramble is more likely to be outgrown in the presence of these two competitive species than in the context of a monospecific oak sapling cohort. To verify the assumption that bramble results in admixed saplings having a facilitative effect on oak regeneration, the same simulations were conducted without bramble in the understory (results presented in Fig. 7.19).

These simulations show that, without bramble, (i) the optimal oak proportion is always 100% and (ii) oak regenerates better with hornbeam than with beech, consistently with our initial hypothesis (Fig. 7.19). These findings support the assumption that admixed saplings have a facilitative effect on oak regeneration in the presence of bramble and a competitive

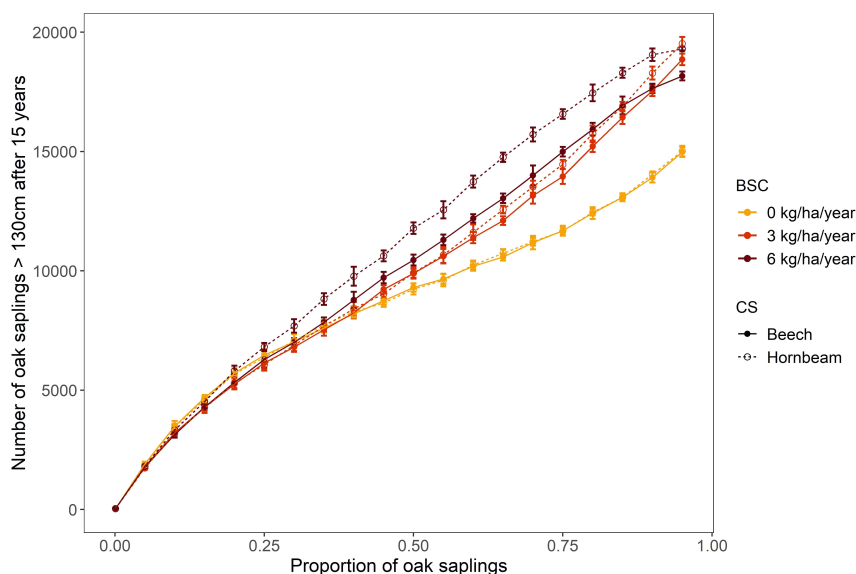


Figure 7.19: Oak_{130} (mean \pm standard deviation) as a function of initial oak proportion (pO), biomass of saplings consumed (BSC) and oak companion species (CS) when bramble is not included in the understory.

effect in the absence of bramble. Whether this facilitative effect exists in field conditions may be subject to debate. The simulations were conducted with an initial density of five saplings. m^{-2} , which is consistent with the densities we observed in field conditions (ranging roughly from 0 to 10 saplings. m^{-2}). However, other field studies have documented significant among-sapling competition effects at higher densities – e.g. 12 saplings. m^{-2} on average in [Jensen & Löf \(2017\)](#), or from 0 to 45 saplings. m^{-2} in [Collet *et al.* \(2017\)](#) – even in the presence of a shrub layer ([Jensen & Löf, 2017](#)). Nevertheless, my simulations confirm that the nature of the effect (*i.e.* competitive or facilitative) exerted by admixed understory species on the focal species contributes to explaining the degree to which deer browsing influences regeneration. When the admixed species is competitive, browsing can have a global positive effect on regeneration (Fig. 7.19). Indeed, some field studies have documented a neutral ([Ward *et al.*, 2018](#)) or even positive ([Vriendt *et al.*, 2020](#)) effect of deer browsing via the consumption of competitive admixed species. Conversely, when the admixed species are facilitative, browsing necessarily reduces focal species growth. More interestingly, I also found an interaction with the palatability of the admixed saplings. Oak regenerated better i) in the presence of a more palatable species (*i.e.* hornbeam) when the admixed saplings exerted a competitive effect (Fig. 7.19), and ii) with a less palatable species (*i.e.* beech) when the admixed saplings exerted a facilitative effect (Fig. 7.16).

7.4.3.2 Effect of browsing pressure on oak regeneration with a gradient of shrub palatability

For each theoretical relation between the biomass of sapling consumed (BSC) and the vegetation layer browsing intensity (VBI), all of the interactions between BSC , initial oak density and species composition had a significant effect on the density of recruited oaks (Oak_{130}) (ANODEV, $p < 0.01$ for all interactions).

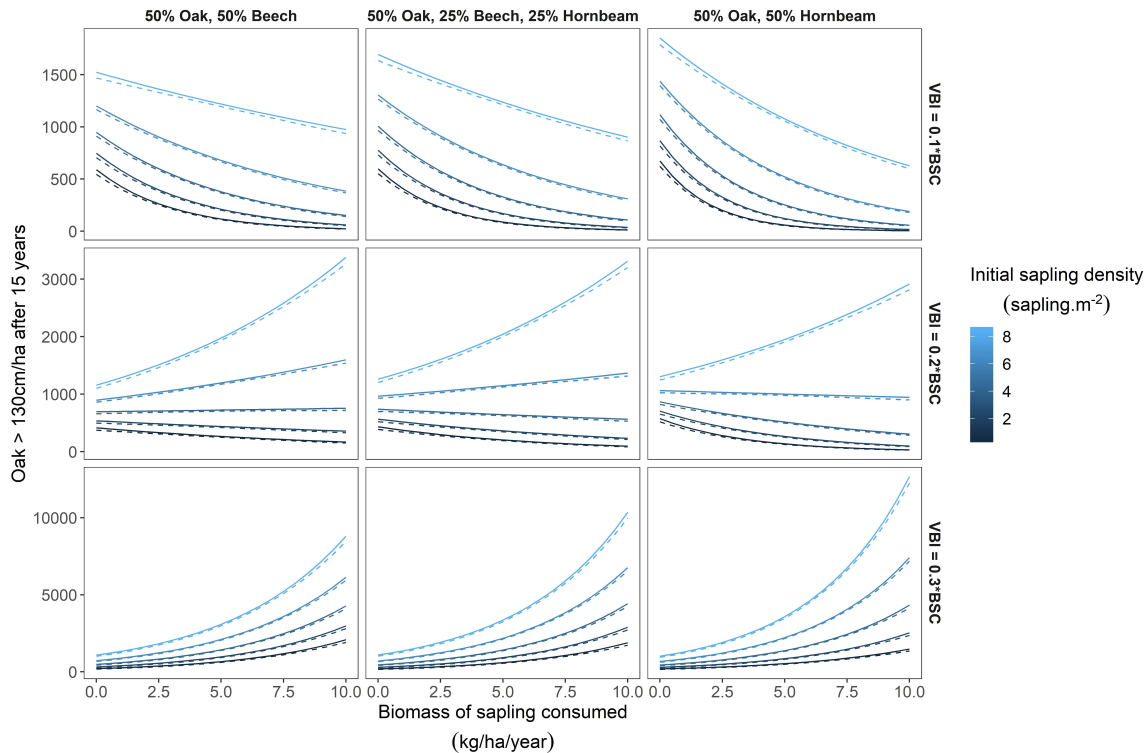


Figure 7.20: Oak_{130} as a function of BSC , species composition, and initial oak density for different theoretical relationships between VBI and BSC . Solid lines represent the prediction of the model described in section 7.4.2.2 (dashed lines represent the standard error). Note that the scale of the y-axis changes with the theoretical relation between VBI and BSC .

In Fig. 7.20, the palatability of the admixed saplings differs among columns (increasing admixed sapling palatability from left to right), while the palatability of shrubs relative to saplings varies in each line (increasing shrub palatability from top to bottom). Compared to the effect of sapling species composition, shrub palatability had a strong influence on the effect of the overall browsing pressure on oak regeneration. When deer were assumed to consume relatively small amounts of bramble for a given quantity of saplings ($VBI = 0.1 * BSC$), Oak_{130} tended to decrease with browsing pressure (Fig. 7.20). Conversely, Oak_{130} increased with overall browsing pressure when deer were assumed to consume higher amounts of bramble ($VBI = 0.2 * BSC$ and $VBI = 0.3 * BSC$), especially at high sapling densities. This observation is consistent with our initial hypothesis, and with the premise that the degree to which deer consume bramble relative to saplings is likely to determine the overall influ-

ence of deer browsing on oak regeneration.

These relationships between shrub and sapling browsing are only theoretical, but their strong influence on the result of the simulations raises the question as to which of these scenarios is the most realistic in field conditions. Browsing has been shown to be directly related to forage availability (Borowski *et al.*, 2021): deer are likely to mostly consume saplings in sapling-dominated patches and to mostly consume shrubs in shrub-dominated patches. The relative availability of bramble and saplings can vary with different environmental factors such as light or water availability (Gaudio *et al.*, 2008). For instance, high transmittance has been shown to promote the development of a high, dense shrub thicket that acts as a bottleneck, preventing saplings reaching higher height classes (Walters *et al.*, 2020). We could therefore expect that high browsing pressure would mostly benefit oak in open areas, where deer significantly hinder the development of the bramble layer instead of consuming young saplings. Another critical factor determining the relative consumption of shrubs and saplings is regeneration stage. Indeed, shrubs have been shown to protect the saplings growing below from browsing, but once the saplings have outgrown the shrub layer, browsing pressure is mostly directed toward them (Jensen *et al.*, 2012; Perea *et al.*, 2020).

7.4.3.3 Effect of the browsing pressure and of the companion species on the efficiency of clearing operations

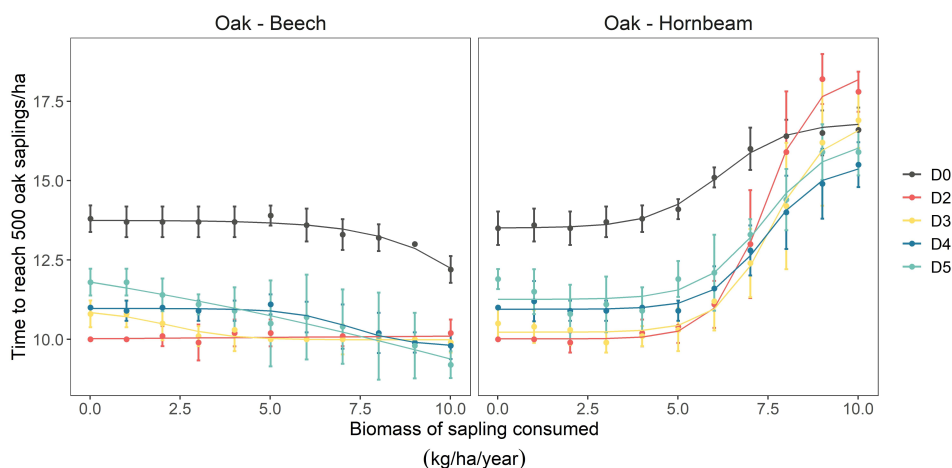


Figure 7.21: t_{500} (mean \pm standard deviation) as a function of BSC and clearing scenario. Solid lines represent the prediction of the model described in eq. 7.23.

In the logistic models predicting t_{500} as a function of BSC , the lower asymptote (*i.e.* t_{500} when browsing pressure is null) is significantly influenced by the clearing scenario when oak is accompanied by hornbeam (ANOVA, $F_4 = 25$, $p < 0.01$) or by beech (ANOVA, $F_4 = 3$, $p = 0.04$). For both CS, t_{500} has the highest value when no clearing is applied (D0) while

there is little difference among the other clearing scenarios (Fig. 7.21). Dense shrub layers have been reported to cause a bottleneck for sapling recruitment by intercepting most of the incident light (Walters *et al.*, 2020). Clearing aims to release the saplings from this bottleneck, and several studies recommend this operation for oak regeneration in stands with highly competitive companion species (Kohler *et al.*, 2020; Lüpke, 1998). The simulations conducted in this study show that clearing efficiently improves oak regeneration in the absence of browsing, but that a higher clearing frequency does not necessarily improve clearing efficiency. This is likely due to the fact that, in the absence of browsing, once oak saplings “escape” from the bottleneck thanks to clearing, brambles cannot outgrow them, thus making additional clearing operations unnecessary.

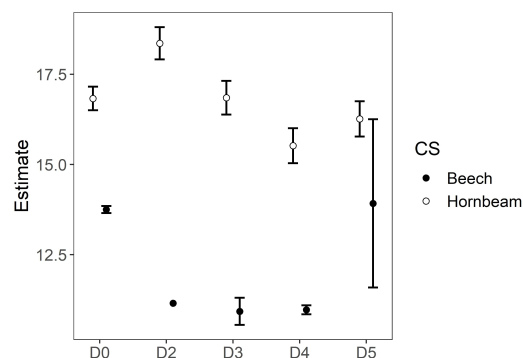


Figure 7.22: Predicted estimates (mean \pm standard deviation) of the four parameters in the logistic model described in eq. 7.23.

Clearing scenario significantly influences the upper asymptote (*i.e.* the value of t_{500} at high browsing pressure) when oak is accompanied either by hornbeam (ANOVA, $F_4 = 7$, $p < 0.01$) or by beech (ANOVA, $F_4 = 4$, $p < 0.01$), but with a different hierarchy depending on the companion species. When oak is accompanied by hornbeam, the best clearing scenarios are D4 and D5 (*i.e.* low clearing frequency) ($t_{500} = 15$ years at asymptote) while scenario D0 (no clearing) is equivalent to D3 (*i.e.* intermediate frequency) (t_{500} at around 16.5 years at asymptote) and better than D2 (*i.e.* high frequency) ($t_{500} = 18$ years at asymptote). Conversely, when oak is accompanied by beech, t_{500} is lower overall than with hornbeam, and scenario D0 has by far the highest upper-asymptote value (around 14 years, versus 10 years for D2, D3 and D4) (Fig. 7.21 and 7.22). These simulations therefore suggest that at high browsing pressures, clearing is always beneficial when oak is accompanied by a less palatable species (*i.e.* beech), but not when it is accompanied by a more palatable species (*i.e.* hornbeam), as is consistent with our initial hypothesis. Field studies have shown that the reduced competition following clearing could be negated by an increase in the browsing pressure exerted on the target species (Vriendt *et al.*, 2020; Miller *et al.*, 2009). Our simulations complete these field observations by suggesting that such compensations are likely to occur only when the admixed species are more palatable than the target species.

7.5 Perspectives and conclusion

7.5.1 Perspectives for further improvements of the model

To build this browsing extension, I made several strong assumptions about cervid behavior and plant responses to browsing. Some of these assumptions have significant ecological consequences that must be kept in mind further improve the model.

7.5.1.1 Between-patch selection

In this study, I assumed homogeneous browsing pressure throughout the modeled scene – *i.e.* the same *VBI* and *BSC* was applied in every cell in the scene. In reality, there can be important spatial variations in browsing pressure within a forest stand. More particularly, cervids tend to browse more intensively in patches where the abundance and quality of the vegetation is higher (Bee *et al.*, 2009; Bergqvist *et al.*, 2018), under canopy gaps (Barrere *et al.*, 2021; Kuijper *et al.*, 2010) or in patches that are the furthest from forest roads (Mathisen *et al.*, 2018). Several studies have also documented spatial auto-correlations: cervids tend to come back to previously browsed patches (Brough *et al.*, 2017; Cromsigt & Kuijper, 2011). From a strictly technical point of view, introducing spatial variations in the magnitude of the browsing pressure would simply require, for each of the N modeled cells, computing a coefficient k that reflects the relative palatability of cell k so that $\sum_{k=1}^N k = N$. In each cell k , vegetation-layer browsing intensity (VBI_k) and biomass of saplings consumed (BSC_k) would then simply be computed as the product of the value specified by the user (*VBI* and *BSC* of the scene) and of the k coefficient.

7.5.1.2 Within-patch selection

I assumed that the consumption of saplings and shrubs was independent in order to assess the respective effects of sapling browsing and shrub browsing on oak regeneration. However, these two components are far from independent in reality. Notably, it has been shown that shrubs may protect the saplings growing beneath them from browsing (Jensen *et al.*, 2012). This interaction could be implemented by adding the height difference between saplings and shrubs to the browsing probability equations.

7.5.1.3 Plant responses to browsing

Deer browsing modifies tree species composition through interspecific variations in palatability and browsing tolerance (Hegland & Rydgren, 2015). In the browsing extension, I took into account inter-specific differences in palatability, but I assumed that, for all saplings,

browsing tolerance remained the same. However, several studies have acknowledged the existence of strong inter-specific differences in the ability of saplings to recover from browsing in terms of height growth and survival (Bee *et al.*, 2007; Krueger *et al.*, 2009). In addition, some browse-tolerant species have developed adaptations that give them a competitive advantage over browse-intolerant species. For instance, hornbeam saplings have been shown to form dense thickets after repeated browsing, thus preventing other sapling species from growing (Cromsigt & Kuijper, 2011). Lastly, at the intra-specific level, the negative influence of browsing on height growth can also be influenced by resource availability (Wise & Abrahamson, 2005; Baraza *et al.*, 2010) or by sapling ontogenic stage (Elger *et al.*, 2009). Since most of these factors (species, light, initial height) are modeled in CAPSIS, their influence on a plant's response to browsing could easily be implemented. Experimental studies with simulated browsing in field or controlled conditions should be able to provide the data necessary to parametrize these relationships, thus greatly improving the model.

7.5.2 General conclusion

This chapter gives an overview of the challenges raised when deer browsing is included in forest dynamic models, and of the relevance of such an approach to research questions that cannot be elucidated through experimental or observational approaches. The work presented in the methodological section of this chapter led to the creation of a promising modeling tool that can be re-used and easily improved. Although, in its current state, the model remains imperfect, several interesting patterns have already emerged. The simulations show that the bramble-dominated shrub layer conditions the influence of deer browsing on oak regeneration, which is positive when browsing is focused on the shrub layer, and negative when it is focused on saplings. We also show that the palatability of the competitive species (both shrubs and saplings) plays a crucial role in oak regeneration dynamics. At high browsing pressures, and when oak is accompanied by more palatable admixed species such as hornbeam, clearing may not improve oak regeneration if it concomitantly increases the browsing pressure exerted on oak.

CHAPTER

8

DISCUSSION AND PERSPECTIVES

8.1 Overview of the results

Recent overviews on the drivers of oak natural regeneration have identified that increasing deer densities interfere with the regeneration process (Annighöfer *et al.*, 2015; Kohler *et al.*, 2020). As deer populations are continually increasing in European forests, a better understanding of the mechanisms governing the influence of cervids on oak regeneration seems crucial. The objectives of this thesis were (i) to unravel and quantify the mechanisms underlying the constraints exerted by cervids on oak regeneration through the consumption of acorns, oak saplings and admixed understory species, and (ii) to identify how specific forest management operations (*i.e.* fencing, felling and clearing) could limit or enhance these constraints. To that end, I conducted different studies focusing on two regeneration stages – *i.e.* germination (chapter 3), and sapling establishment and growth (*i.e.* chapters 4 to 7) – at different organizational levels – *i.e.* animal (chapter 3), individual plant (chapters 4 and 5), and plant population (chapters 6 and 7).

8.1.1 Seed predation by deer: a significant constraint for oak regeneration?

The consumption of acorns by cervids may hinder the process of oak regeneration by inducing post-dispersal seed losses that reduce the number of seeds that eventually germinates (Leiva & Fernández-Alés, 2003). The first study in this thesis showed that, in a context of high fructification, while acorn availability theoretically decreases from autumn to winter due to predation, the proportion of acorns consumed remained steady for both red and roe deer. Under the assumption that the proportion in the diet reflects the quantity of acorns consumed, this implies that the proportion of available acorns consumed by deer decreases with acorn availability at high availabilities (Fig. 8.1.a). This is analogous to a type II or type III functional response (Holling, 1973), and supports the resource depletion hypothesis (Moreira *et al.*, 2017). The resource depletion hypothesis is one of the main hypotheses explaining the evolutionary causes of mast seeding; it predicts that high fructifications during infrequent mast years saturate seed-predator diets, thereby enabling a sufficient amount of seeds to escape predation (Janzen, 1971; Ims, 1990; Waller, 1993). The efficiency of this strategy relies on the assumption that increasing seed availability saturates seed consumption (Moreira *et al.*, 2017), which is supported by our findings on acorn predation by deer. Overall, this first study highlights the significant contribution of red and roe deer to acorn predation (over 50% and 30% of red and roe deer diets respectively in mast years), but it also suggests that the proportion of acorns escaping predation by red and roe deer should increase in high fructification years (Fig. 8.1.b), thereby enabling a significant proportion of the acorns to survive and germinate.

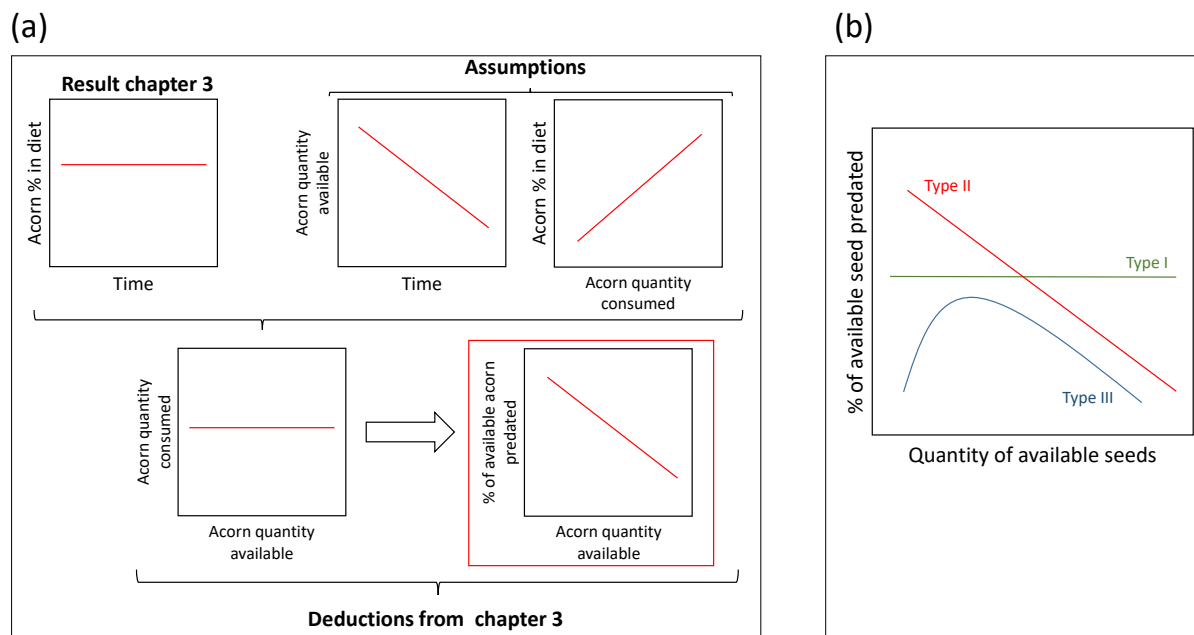


Figure 8.1: Relation between the proportion of available seed consumed and seed availability (a) deduced from the results presented in chapter 3 in the case of acorn predation by red and roe deer and (b) for different types of functional response to seed predators (Moreira *et al.*, 2017). Functional responses types II and III support the resource depletion hypothesis as an evolutionary cause of mast seeding.

8.1.2 Consequences of direct browsing on sapling establishment and growth

8.1.2.1 Direct browsing and oak survival: a context-specific constraint

The influence of a simulated winter browsing event on the survival of one-year-old oak saplings was monitored in the studies presented in chapters 4 and 5 for two different contexts – *i.e.* in controlled conditions where resources (water, nutrient and light) were not limited (chapter 4), and in field conditions (chapter 5). The two contexts yielded contrasting results. Oak sapling mortality was negligible and unrelated to browsing in controlled conditions, which is consistent with other studies where survival rates for oak saplings following browsing were high (Drexhage & Colin, 2003; Götmark *et al.*, 2014). Conversely, in field conditions, browsing caused the mortality rate to double. This is likely explained by two factors acting in synergy: resource availability and sapling age. Indeed, the young saplings in the study had already suffered from high drought-induced mortality, and the simulated browsing could have acted as an additional stress, further reducing survival. Moreover, the ability of saplings to tolerate browsing is known to increase with age since older saplings have more accumulated resources and larger organs for resource acquisition (Boege & Marquis, 2005). The high mortality rate we observed is all the more remarkable as only the api-

cal shoot was removed during the simulated browsing event: in real conditions, browsing can occur on several shoots of the same sapling (Götmark *et al.*, 2014; Mathisen *et al.*, 2017). This raises the question of the consequences of more severe browsing events on oak sapling mortality.

In the fencing experiment presented in chapter 6, oak saplings exposed to free-ranging cervids are compared to saplings protected from deer. This study provided an opportunity to gain better insights into the influence of actual deer browsing on oak mortality, though it must be kept in mind that potential differences in mortality could also be related to other ungulate-related effects. In our Swedish experiment, oak sapling mortality was low and remained unaffected by fencing even for small saplings (*i.e.* < 50 cm). Conversely, oak sapling mortality was much higher in the unfenced plots in the French experiment, but this was probably due to the activity of wild boar. Indeed, wild boar turn over the soil and litter to search for belowground sources of food (a process called rooting) and in so doing, they uproot young seedlings (Bueno *et al.*, 2009; Burrascano *et al.*, 2015). We observed damage related to rooting in most of the unfenced plots at the French sites, all of which host high wild boar populations. Though this thesis focused on the influence of cervids, the use of fences that also exclude other ungulate species highlights the constraint exerted by wild boar on oak regeneration (Sütő *et al.*, 2019).

Overall, our results indicate that even a single browsing event has the potential to increase oak sapling mortality, but that this effect seems to be context-dependent. In particular, we suggest that events such as droughts that induce resource scarcity could cause browsing to become a significant mortality factor, especially for young saplings.

8.1.2.2 Poor leaf trait plasticity as an explanation for the negative effect of browsing on growth?

The studies presented in chapters 6, 4 and 5 all show that a single deer browsing event was sufficient to significantly reduce oak sapling height growth, in both controlled (chapter 4) and field conditions (chapters 5 and 6), regardless of light availability or sapling height (chapter 6). Therefore, the results of this thesis reinforce the idea that browsing has a significant negative effect on oak sapling growth (Harmer, 2001; Drexhage & Colin, 2003; Leonardsson *et al.*, 2015; Petersson *et al.*, 2020), regardless of the conditions in which the oak saplings are growing. By analyzing leaf functional traits following browsing, we investigated how this disturbance modify oak sapling investment in leaf traits related to fast growth (chapter 4). Due to the well-documented trade-off between fast carbon acquisition and anti-herbivore defense (Coley, 1988; Herms & Mattson, 1992; Züst & Agrawal, 2017),

the consequences of deer browsing on sapling growth are expected to depend on sapling resource allocation strategies. Saplings that do not modify their carbon allocation or that invest in anti-herbivore defenses are expected to exhibit experience reduced growth in response to browsing (Fig. 8.2). Conversely, saplings that respond to browsing by allocating more resources to fast carbon acquisition can compensate (or even overcompensate) for the tissues lost to herbivores (Wise & Abrahamson, 2005). A drawback of this strategy is that it can increase the probability of subsequent browsing (Mathisen *et al.*, 2017). The study presented in chapter 4 showed that 1.5-year-old saplings had a weak trait-response to browsing, which helps explain why browsing had a negative effect on oak sapling height growth. Interestingly, 2.5-year-old oak saplings exhibited more plasticity in resource allocation; they reallocated toward faster carbon acquisition; this suggests that the older saplings had higher browsing tolerance. This finding is consistent with the assumption that older saplings tend to be less impacted by browsing (Barton, 2013; Elger *et al.*, 2009).

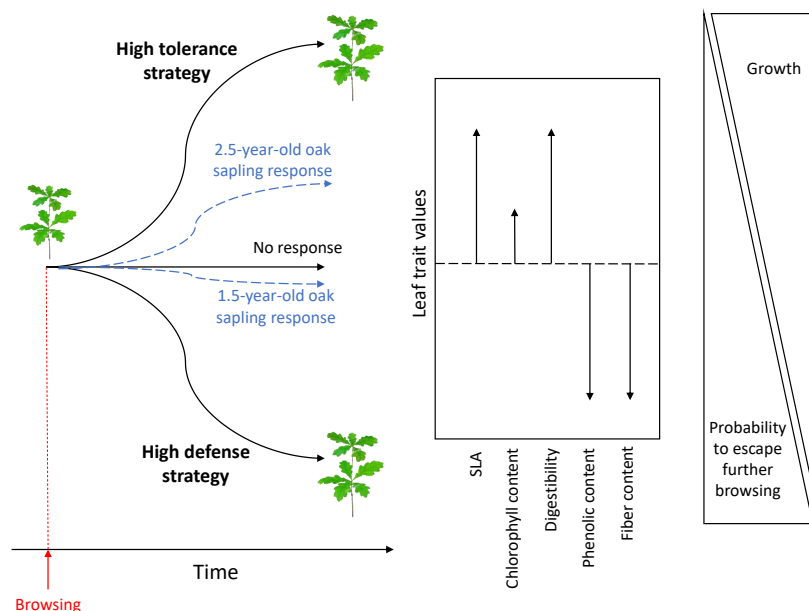


Figure 8.2: Summary of the results presented in chapter 4. Gradient of resource allocation strategy in response to browsing and leaf-trait values associated with each strategy. Blue arrows represent oak sapling responses based on the observed trait values.

8.1.3 The role of deer in the mediation of plant-plant competition

In section 1.5.3 of the first chapter, I introduced a theoretical framework predicting the magnitude and direction of the effect of deer browsing on oak sapling growth in a context of species mixture (equivalent abundance between oak and admixed species) as a function of the effect of the understory on oak (facilitative or competitive), and of the understory

palatability relative to oak (Fig 8.3.a). In this framework, deer browsing can be more or less constraining for oak regeneration depending on the competitiveness and palatability of the admixed understory species accompanying the oak. Chapter 7 tested this assumption by focusing on the three main sources of understory competition at the study sites included in the EFFORT protocol: beech and hornbeam, two tree species that differ in their relative palatability compared to oak (Boulanger *et al.*, 2009), and bramble, a highly competitive shrub species (Balandier *et al.*, 2013). The simulations conducted during this *in silico* study evidenced two patterns that tend to support the theoretical framework.

First, the model showed that in a three-species system (oak + bramble and either beech or hornbeam), both beech and hornbeam had a facilitative effect on oak since they rapidly outgrew the shrub layer and since the between-species sapling competition was negligible compared to the shrub competition. Simulations showed that, in this context deer browsing had an overall negative effect but that the magnitude of the effect was lower when oak was accompanied by beech (less palatable) than by hornbeam (more palatable). Given that, in the model, beech and hornbeam only differ in terms of their palatability (similar growth rate, competitiveness), this finding is perfectly in line with the predictions of the theoretical framework (Fig. 8.3.b). Secondly, a simulated increase in bramble palatability turned the overall effect of deer browsing from negative to positive. This also supports the theoretical framework with the assumption that bramble is highly competitive for oak, which was the case in the model (Fig. 8.3.b).

Interestingly, this theoretical framework also provides elements to help interpret the results observed in chapter 6. By comparing the average growth rate of oak sapling populations growing in fenced and unfenced plots, this study investigated the overall effect of deer presence *in situ*, and revealed two contrasted results depending on the country: deer presence decreased oak sapling growth rate in Sweden, but had no effect in France. The Swedish experiment was conducted in monospecific oak stands: the main understory companion species were herbs and shrubs known to be more competitive than facilitative (Jensen & Löf, 2017). Under the theoretical framework, the observed negative effect implies that this accompanying understory was less palatable than oak, and that indirect effects were negligible compared to the direct effect of oak browsing. Conversely, the absence of a fencing effect in France can, in theory, result from two mechanisms. (i) The overall browsing pressure may have been too low to influence the oak sapling growth rate at the population level; or (ii) the competitive understory may have been both competitive and more palatable than oak, leading to a trade-off between a negative direct effect and a positive indirect effect (scenario presented in Fig. 8.3.a). Considering the strong correlation between sapling height and browsing probability (Götmark *et al.*, 2014; Nichols *et al.*, 2015), the fact that most of the saplings monitored in the French experiment belonged to the lowest height classes (Fig.

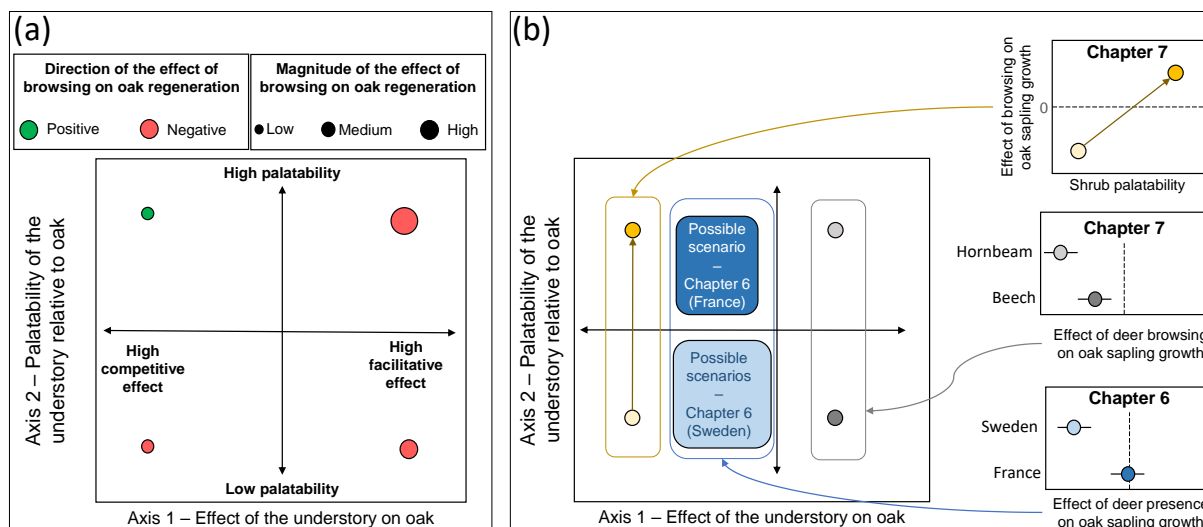


Figure 8.3: (a) theoretical framework presented in section and predicting the direction and magnitude of the effect of deer browsing on oak regeneration as a function of the effect of the understory on oak (competitive or facilitative), and of its palatability relative to oak. (b) Position of results obtained in chapters 6 and 7 along this theoretical framework.

6.8) tends to support the hypothesis that overall browsing pressure was insufficient to have an effect. Nevertheless, the understory at the French sites was dominated by bramble and hornbeam, two species known to compete with oak, but which are also highly palatable to deer, thus making the second hypothesis plausible as well.

8.1.4 How do forest management operations modify the studied interactions?

This thesis investigated how red and roe deer could influence the efficiency of three specific forest management operations commonly conducted to regenerate oak stands (Box 1.1 for the definition of each term): (i) the cutting removal of adult trees, (ii) clearing to control the competitive vegetation, and (iii) fencing.

Harvesting the adult trees to increase light availability for the understory is crucial to initiating the process of oak regeneration. However, increasing canopy openness can also potentially influence the effect of deer browsing on oak growth and survival by modifying oak-sapling browsing probability (Kuijper *et al.*, 2009; Moser *et al.*, 2008), and the saplings' response to browsing (Wise & Abrahamson, 2005; Baraza *et al.*, 2010). Chapter 6 presents

the study investigating these two indirect effects. We show that canopy openness correlated positively with oak-sapling browsing probability (in Sweden), but did not influence oak sapling response to browsing (France and Sweden). Consequently, increasing canopy openness (from 10% to 30%) only improved oak sapling average height growth at the population level when it was combined with fencing. This result confirms that harvesting is necessary for oak stand regeneration, but that, in forests where browsing damage constrains forest dynamics, harvesting should be complemented with protective measures (*e.g.*, fencing) to ensure oak sapling growth.

Clearing operations control the understory competition, and as such are particularly useful in oak regeneration (Lüpke, 1998) since competition is one of the main factors constraining this process (Annighöfer *et al.*, 2015; Kohler *et al.*, 2020). However, clearing operations may also increase the browsing pressure exerted on oak saplings by removing alternative forage for deer (Miller *et al.*, 2009; Vriendt *et al.*, 2020). Based on the theoretical framework discussed in the previous section (Fig. 8.3), deer browsing should fill the same function as clearing in the presence of palatable competitive species, making this operation less necessary. The simulations conducted in chapter 7 confirmed that, when oak is accompanied by palatable competitive species (*i.e.* hornbeam and bramble), clearing improves oak regeneration in the absence of browsing, but not at high browsing levels. Similarly, a recent field study conducted in North-American temperate forests found that moose browsing on understory species competing with spruce in plantations had the potential to efficiently replace clearing operations, thereby supporting our theoretical prediction (Vriendt *et al.*, 2020).

Our results suggest that, as browsing pressure increases, the frequency and intensity of clearing operations should be reduced and that they should primarily target poorly palatable species like beech and avoid highly palatable species like hornbeam. However, it must be kept in mind that our results are based on computer simulations relying on several strong assumptions (see section 7.5), though studies conducted on other tree species tend to support our findings (Miller *et al.*, 2009; Vriendt *et al.*, 2020). Empirical support in the context of oak regeneration is needed to verify the validity of our simulations.

Box 8.1. Summary of L f et al. (2021)

During my three-month mission in Sweden, I had the opportunity to collaborate on a study led by Magnus L f (I built hypotheses with ML, conducted the statistical analyses and contributed to the publication along with the other co-authors). This study was published in 2021 in the *European Journal of Forest Research*.

Context – Oak regeneration failures are frequently observed in Scandinavia, and both ungulate browsing and seed predation have been identified as significant constraints. Several regeneration techniques are used as alternatives to natural regeneration (i.e. planting, direct seeding, fencing, acorn protection devices) to help counteract these constraints, but they come with a significant financial cost for forest managers. In this context, the study aimed to evaluate this trade-off by testing the effect of different regeneration techniques on certain metrics related to regeneration success (height growth, sapling establishment and survival), and by evaluating the respective financial cost of the different regeneration techniques.

Methods – The study was conducted over five years in oak stands located on the island of Visings  (Sweden). We monitored the establishment, survival, growth and browsing rates of oak seedlings and saplings in a randomized block experiment crossing four regeneration techniques (natural regeneration, planting, and direct seeding with or without acorn protection devices) with two fencing modalities (fenced and unfenced). The fences protected the oak from roe deer and hares.

Results – After five years, both planted and naturally regenerated oak saplings were taller inside the fences, while fencing did not influence the height of the oak saplings established from direct seeding. Fencing improved the establishment rate when direct seeding was combined with acorn protection devices but it had no effect on the survival of planted oak saplings nor on the recruitment of naturally regenerated seedlings. The oak saplings in the unfenced plots had higher browsing rates (i.e. over 50%) than in any other treatment combination. The costs associated with each treatment combination is presented in the table below.

	Regeneration technique			
	Planting	Direct seeding without protection	Direct seeding with protection	Natural regeneration
Unfenced	2946	823	2296	0
Fenced	7586	5463	6936	4640

Conclusions – Five years after the initiation of the regeneration phase, and under current in these circumstances – *i.e.* site with a sparse shelterwood of old oaks – this study concluded that:

- (i) Fencing does not influence direct seeding during the first five years since the seedlings are too small to be heavily impacted by browsing. However, fencing is highly recommended for natural regeneration, and required for planting.
- (ii) Natural regeneration is the most cost-efficient regeneration method, resulting in the highest seedling density and taller saplings than with direct seeding, at the lowest cost.
- (iii) Planting is the best regeneration technique to rapidly obtain tall oak saplings, but it is also the most expensive.

The study I collaborated on in Sweden (see Box 8.1, or appendix A for the complete paper) highlights the importance of the financial aspect in the balance between deer populations and forestry. The cost comparison for the different regeneration techniques showed that planting promotes rapid oak regeneration, but comes with a significant financial cost, and needs to be combined with fencing to be efficient, while the use of natural regeneration is less costly, but increases the duration of the process. Interestingly, this study also illustrated that the negative consequences of deer browsing mostly occur once oak saplings have reached a certain height. Indeed, fencing did not influence the height of the seedlings that had germinated from direct seeding (height < 25cm) and it had only a weak effect on naturally regenerated saplings (25 cm < height < 50cm), while it did have a strong effect on planted saplings after five years of growth (height > 50cm). I confirmed this trend in my thesis through other studies showing that browsing probability increases with sapling height both at the population (chapters 6 and 7) and individual (chapter 4) levels. While fences to protect seedlings from browsing are often erected at the same time as the seeding cut, the results of this thesis suggest that fences (or other means of protection) could be implemented later, therefore over shorter time periods, to save maintenance costs without significantly affecting efficiency. From a practical point of view, this would mean erecting fences when the tallest saplings have reached a height of around 50cm and maintaining them until the saplings grow beyond the maximum height reachable by deer – *i.e.* 130cm, or 200cm if red deer are present (Nichols *et al.*, 2015). Nevertheless, this suggestion is based on a simple cost comparison and a full cost-benefit analysis covering the process of oak regeneration in its entirety should be conducted, as in other studies (Boulanger & Rakotoarison, 2013; Rey, 2019).

8.1.5 Unraveling deer foraging decisions at different spatial scales

The computer simulations described in chapter 7 showed that the overall influence of deer browsing on oak sapling growth was highly conditioned by the relative consumption of oak and the admixed understory species, and highlight the importance of deer foraging decisions for oak regeneration. The mechanisms governing the foraging decisions of large herbivores like red and roe deer have been shown to occur at different spatial scales – *i.e.* within the species spatial distribution (regional level), within the animal home range (landscape level), between feeding stations (feeding patch level) and within a feeding station (feeding station level) (Fig. 8.4) (Senft *et al.*, 1987). At each spatial scale, the optimal foraging theory predicts that deer make their foraging decisions to maximize their net energy and nutrient intake (Schoener, 1971; Stephens & Krebs, 1986). Any factor influencing these metrics at a given spatial scale is therefore likely to influence deer foraging decisions. This thesis focuses on the process of oak regeneration, and therefore primarily investigates cervid-vegetation interactions from the plant point of view. Nevertheless, several results obtained in the different studies I conducted also enlighten the mechanisms underlying deer foraging decisions (*i.e.* the interaction from the animal point of view). To summarize these results, I chose to present them in Senft *et al.*'s framework, grouping each result by spatial scale (Fig. 8.4) (Senft *et al.*, 1987).

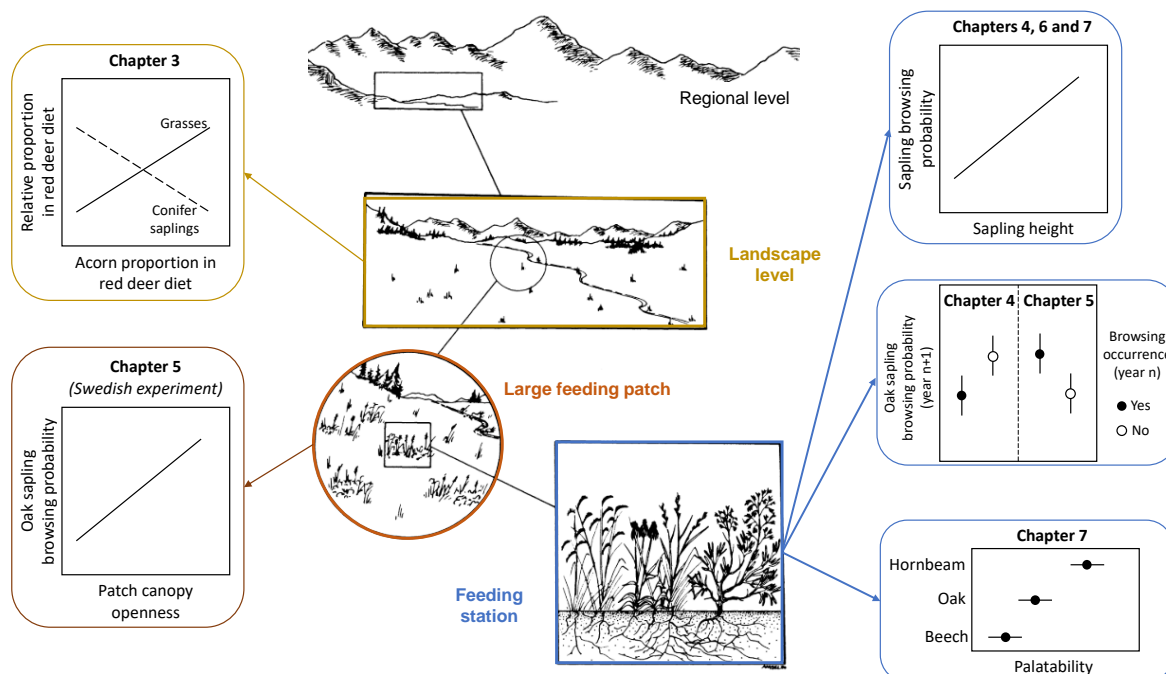


Figure 8.4: Ecological spatial hierarchy encountered by large herbivores when foraging as described by Senft *et al.* (1987), and applications to the deer-forest system investigated in this thesis.

8.1.5.1 Landscape level

The study presented in chapter 3 is based on the composition of red and roe deer rumen sampled in animals shot within the whole forest of LPP, and thus therefore provides information on deer feeding choices at the landscape level. One of the objectives of this the study was to investigate potential dietary shifts induced by the consumption of acorns. The consumption of acorns can be seen as a perfect illustration of the trade-off between nutrient and energy intake (Edouard *et al.*, 2010): this resource has a high energy content, but a very low nutrient content (Kirkpatrick & Pekins, 2003). Consequently, animals consuming high proportions of acorns may exhibit a negative nitrogen balance (Harlow *et al.*, 1975), unless they are able to balance their diet with complementary food items with a particularly high nutrient content (Simpson & Raubenheimer, 2011; Felton *et al.*, 2016b). Our results evidenced that, in autumn and winter, high acorn availability induced a dietary shift for red deer: in order to balance their diet, the animals replaced conifer shoots with grasses as the proportion of acorns they consumed increased. Under the assumption that the proportion in the diet reflects the quantity consumed, this finding implies that during mast years, the browsing pressure exerted by red deer on the understory vegetation is diverted from conifers to grass. Whether this dietary shift results in positive or negative outcomes for oak sapling growth depends on various parameters (i.e. red deer density, tolerance to browsing and competitiveness of the conifer saplings relative to grass) and therefore remains highly uncertain.

8.1.5.2 Large feeding patch level

At the large feeding patch level (Fig. 8.4), deer should preferentially select feeding stations containing a high quantity and quality of vegetation, since these two metrics are directly related to their nutrient and energy intake (Schoener, 1971). Because light availability increases both the quality (Giertych *et al.*, 2015) and quantity (Willms *et al.*, 2017) of the understory vegetation, canopy openness is a potential driver of food selection at the patch level. However, studies investigating the relationship between canopy openness and browsing pressure exerted show conflicting results (Moser *et al.*, 2008; Kuijper *et al.*, 2009). The Swedish fencing experiment described in chapter 6 found that feeding-station canopy-openness increased the probability of browsing for oak saplings (Fig. 8.4). As such, this finding confirms that canopy openness constitute a factor driving deer foraging decisions at the feeding patch level. This result also implies that in a context of high deer densities, oak regeneration switch from a bottom-up (insufficient light availability) to a top-down (herbivory) control when canopy openness increases.

8.1.5.3 Feeding station level

Within a feeding station, one of the main criteria driving a deer's decision to browse a particular item of vegetation is its quality (nutrient content, digestibility). Because woody species differ in quality for herbivores, plant species is an important criterion to determine the probability for a given vegetation item to be browsed (Bee *et al.*, 2007; Boulanger *et al.*, 2009). In chapter 7, with data from the EFFORT protocol (presented in section 6.3), I evidenced a gradient of palatability between oak and two of its major woody competitors: hornbeam and beech, which were found to be respectively more and less palatable than oak.

In recent years, several studies have suggested that browsing history could also constitute a factor driving foraging within a feeding station, due to the higher quality of previously browsed saplings (Makhabu & Skarpe, 2006; Moore *et al.*, 2000; Mathisen *et al.*, 2017). The studies I conducted for this thesis yielded contrasting results on this issue: the Swedish experiment (chapter 6) confirmed that previous browsing increased subsequent browsing probability, while chapter 4 evidenced the opposite trend in controlled conditions. Unlike chapter 6, chapter 4 included a winter shoot trait analysis to evaluate potential differences in quality between browsed and unbrowsed saplings. When the feeding trials were conducted, browsed and unbrowsed saplings had a comparable quality, but unbrowsed saplings were much taller. This result highlights the second criterion known to influence deer foraging decisions at the feeding station level: plant morphology. Indeed, plant morphology may influence the animal's net intake rate via the feeding rate (biomass ingested per time unit) or via the energy spent for consumption (Charles-Dominique *et al.*, 2020). Most cervids preferentially browse near their shoulder height – *i.e.* 75cm for roe deer – which limits energy expenditure while foraging (Duncan *et al.*, 1998b; Nichols *et al.*, 2015). As such, several studies found that as long as the sapling apical shoot is within the herbivore's reach, height positively influences the probability for a given sapling to be browsed (Götmark *et al.*, 2014; Nichols *et al.*, 2015). The preference of tame roe deer for unbrowsed saplings tends to support this, along with the positive effect of height on browsing probability found in chapters 6 and 7.

8.2 Perspectives

Thorstein Veblen, a renowned American economist, once said that “*the outcome of any research can only be to make two questions grow where only one grew before*”. This thesis work enlightened some aspects of the interactions between red and roe deer and forest vegetation during the process of oak regeneration, but also raised many additional questions. In this section, I will address only a fraction of the perspectives opened up by the research presented here, hoping that some will materialize into concrete research projects in the years

to come.

8.2.1 Intraspecific trait response to deer browsing: perspectives for an interspecific generalization

Chapter 4 investigated the functional traits driving the process of feeding loops – i.e. the theory that plants previously damaged by herbivores are more subject to subsequent herbivory. One of the main assumptions put forward in the literature to explain this process is that saplings respond to browsing by investing in compensatory growth, resulting in higher values of fast carbon acquisition traits at the expense of anti-herbivore defense traits (DuToit *et al.*, 1990; Moore *et al.*, 2000; Makhabu & Skarpe, 2006; Mathisen *et al.*, 2017). Although the precept of compensatory growth is well established for herbaceous species (McNaughton, 1983; Staalduinen & Anten, 2005; Fornoni, 2011), such a response has rarely been observed in woody species (Danell & Huss-Danell, 1985; Edenius *et al.*, 1993). In woody plants, more commonly observed responses to browsing include a higher investment in anti-herbivore defense mechanisms (Iason, 2005; Bee *et al.*, 2007), or alternatively, increased biomass allocation to roots to protect carbon resources from aboveground herbivores (Strauss & Agrawal, 1999; Moreira *et al.*, 2012). Nevertheless, during the second year of the experiment described in chapter 4, we observed that browsed oak saplings had higher values for leaf traits correlated to fast resource acquisition (*i.e.* digestibility, chlorophyll content, specific leaf area) and lower anti-herbivore defense traits (*i.e.* phenol and fiber content) than did unbrowsed saplings, which corroborates the assumption of a browsing-induced investment in compensatory growth. Considering that such response has rarely been observed in other temperate tree species (though Danell & Huss-Danell (1985) found a similar response in birch saplings), these findings raise the question of the factors determining the induced response of a given tree species to browsing.

The trade-off between browsing tolerance and the defense against herbivory has been well studied at the interspecific level: constitutive differences among plant species reflect a gradient of strategies from slow-growing, highly-defended species (*i.e.* defense strategy) to fast growing, poorly-defended species (*i.e.* tolerance strategy) (Coley, 1988; Herms & Mattson, 1992; Züst & Agrawal, 2017). However, whether the position of a given tree species along this interspecific defense-tolerance continuum gives an indication of its induced response to herbivory has rarely been investigated in the literature (Fornoni, 2011). The fact that both birch and oak tolerate browsing relatively well compared to other temperate tree species (Hees *et al.*, 1996) supports the assumption that the induced response to browsing (investment in compensatory growth for these two species) is consistent with their position along the interspecific defense-tolerance continuum (tolerance for these two species). This as-

sumption could be verified for a large number of temperate tree species through an experiment comparing the leaf traits of browsed and unbrowsed saplings to compare their induced response to browsing in terms of defense versus tolerance.

8.2.2 Challenges for representing deer browsing in forest dynamics models

Modeling approaches synthesize our understanding of the processes governing forest dynamics, and as such, represent powerful tools to enlighten how disturbances like deer browsing will affect forest ecosystems in the years to come. Until the end of the 20th century, modeling approaches neglected the role of disturbances in forest dynamics (Seidl *et al.*, 2011). The first models including browsing by large mammals appeared relatively late (Jorritsma *et al.*, 1999; Kienast *et al.*, 1999) compared to forest fires (Martell *et al.*, 1987), insect outbreaks (Sutherst & Maywald, 1985), windstorms (Frelich & Lorimer, 1991) and droughts (Running & Coughlan, 1988), among the various biotic and abiotic disturbances. One of the reasons for this is that, except for bark stripping and antler fraying, which affect adult trees (Vospertnik, 2006), ungulates mostly influence forest dynamics during the beginning of the regeneration stage (Gill, 1992), while the vast majority of forest models in the 20th century did not include trees less than 2m in height. This historic neglect of the regeneration stage has two causes: i) a relatively poor understanding of the factors governing the processes during this stage (the growth of seedlings and young saplings cannot be predicted by classic yield tables), and ii) a lack of sufficient processing capacity needed to model thousands of young individuals, unlikely to reach adulthood (Bugmann, 2001). Although these two constraints have become less limiting due to improvements in computer processing power and to a better understanding of the regeneration phase, the number of forest models including ungulate browsing remains relatively low. In chapter 7, we aimed to do more than simply test specific research questions; we also integrated the process of deer browsing into a forest dynamics model. This raises the question of how to position our newly integrated model in relation to other forest-dynamics models taking deer browsing into account. I therefore chose to focus on the process of deer browsing both from the animal point of view (*i.e.* deer foraging decisions) and from the plant point of view (*i.e.* plant response to browsing).

8.2.2.1 Representing deer foraging decisions in forest dynamics models

Browsing pressure exerted on forest stands has been shown to vary over four different spatial scales (*i.e.* region, landscape, feeding patch and feeding station), and this spatial variability needs to be taken into account when modeling the influence of deer browsing on forest dy-

namics (Senft *et al.*, 1987). At the regional level, the main factor known to influence browsing pressure is deer density (Ramirez *et al.*, 2018). In the two studies that have attempted to include deer browsing in a forest dynamics model at the regional level, Kienast *et al.* (1999) assumed a constant browsing pressure over the study area, while Lesser *et al.* (2019) computed deer density indices from hunting logs. Considering how difficult it is to obtain reliable density data over large spatial scales (Pfeffer *et al.*, 2018) and to link deer densities to browsing damage (Pfeffer *et al.*, 2021), Lesser *et al.* (2019) approach is probably the best available, especially since hunting statistics are correlated to browsing damage (Boulanger *et al.*, 2018). At the landscape level, modeling studies have focused on the role of forage availability as a main driver of the browsing pressure (Champagne *et al.*, 2018), by modeling a higher browsing pressure in the feeding patches hosting a high abundance of preferred plant species (Riggs *et al.*, 2015; Jager *et al.*, 2017). Because linear structures such as forest roads are also known to drive foraging decisions at the landscape level (Mathisen *et al.*, 2017), Riggs *et al.* (2015) included the effect of physical barriers such as livestock fences, in addition to forage quality. However, to our knowledge, no study to date has included other important additional factors such as water proximity, the presence of alternative habitats or slope. At the feeding-patch level, browsing pressure has been modeled as a function of forage quality (Jorritsma *et al.*, 1999; Kramer *et al.*, 2003) and/or quantity (Seagle & yuen Liang, 2001).

Still, the factors driving spatial variations in browsing pressure at the regional, landscape and feeding-patch levels represent the knowledge that we have of these processes quite well overall. On the other hand, at the feeding-station level, the current models risk oversimplifying reality. We included spatial variations in browsing pressure at the feeding-station level in the model presented in chapter 7, thus helping resolve this problem. Note that, at the feeding-patch level, including spatial variations in browsing pressure at the feeding patch level is considered for further improvements of the model (see between-cell variations in section 7.5). At the feeding-station level, most existing modeling studies do include a species-specific browsing likelihood but our study presented in chapter 7 is the first to include sapling height, despite the well-documented positive relation between sapling height and browsing probability (Nichols *et al.* (2015) and reinforced by chapters 4, 6 and 7). Our study is also the first to include components of the understory other than saplings (*i.e.* shrubs), despite their proven crucial importance in regeneration dynamics. Though our representation of deer foraging decisions between shrubs and saplings remains imperfect (we separated shrub browsing and sapling browsing), our work lays a basis for modeling the role of deer browsing in mediating the competition between shrubs and saplings, of crucial importance in regeneration dynamics (Jensen *et al.*, 2012; Walters *et al.*, 2020).

8.2.2.2 Representing plant responses to browsing

The widest gap between what we know from the literature and what is implemented in current forest dynamics models taking deer browsing into account probably concerns our knowledge of plant responses to browsing. Indeed, deer browsing influences sapling growth and mortality differently depending both on plant characteristics – *e.g.* species (Baraza *et al.*, 2010), age (Elger *et al.*, 2009; Hóðar *et al.*, 2008), height (Barrere *et al.*, 2021) – and on the intensity (Frank *et al.*, 2019), and timing (Woolery & Jacobs, 2014) of the browsing event. Jager *et al.* (2017) did include species-specific thresholds of biomass removed that triggers a growth reduction while Kienast *et al.* (1999) included species-specific equations linking the number of shoots removed and the reduction in height. However, apart from these two approaches, the other studies modeling the influence of deer browsing on forest regeneration simply include the same browsing-induced growth or modification in survival rate for all saplings, regardless of browsing intensity and timing, or plant species, age or height (Jorritsma *et al.*, 1999; Seagle & yuen Liang, 2001).

From this point of view, our study is comparable to most of the other studies, since we assumed the same reduction in height for all saplings browsed (chapter 7). However, this is the priority issue that we plan to improve in the model. An experiment comparing the height-growth response of beech, oak and hornbeam saplings to simulated browsing is being considered, and would enable us to include species-specific responses to browsing in the model. Ideally, such an experiment should include saplings of different ages to investigate the effect of ontogenic stage on sapling response to browsing as well.

8.2.3 Are the findings of this thesis still valid under a changing climate?

8.2.3.1 Climate-related changes in oak mast seeding patterns, and consequences for acorn predation by deer

Recent studies have shown that the occurrence of oak mast seeding events are driven by both a deterministic component related to resource storage and allocation to reproduction, and a stochastic component related to pollination efficiency (Scherner *et al.*, 2018; Bogdziewicz *et al.*, 2019). The stochastic component is sensitive to climatic conditions: drier and warmer spring conditions promote acorn production via an increase in pollination efficiency (Caignard *et al.*, 2017; Scherner *et al.*, 2018), while late spring frosts constrain fruit production (Bogdziewicz *et al.*, 2018b). Therefore, patterns of oak mast seeding are likely to be sensitive to future changes in climatic conditions (IPCC, 2014), though the influence

of climate change on the magnitude and frequency of mast seeding events remains highly uncertain. Studies attempting to predict future patterns of oak mast seeding are scarce, and have not shown any consistent trends in the magnitude and frequency of these events with climate change (see chapter 3 in [Schermer \(2019\)](#)).

Because oak mast seeding is resource limited, high fructification is necessarily followed by several years of low fructification. As a result, climate-related changes in mast seeding patterns could follow two scenarios: more frequent mast years of lower magnitude (scenario A), or less frequent mast years of higher magnitude (scenario B). These changes in mast seeding magnitude and frequency could have a strong influence on the constraint exerted by deer on oak regeneration through seed predation. Indeed, the first study in this thesis (chapter 3) suggests that high acorn availability saturates the red and roe deer diet ([Barrere et al., 2020](#)), which implies that the proportion of acorns escaping deer predation increases with fructification magnitude ([Moreira et al., 2017](#)). More frequent mast years of a lower magnitude (scenario A) should therefore result in increased predation rates, while more infrequent mast years of a higher magnitude (scenario B) should result in lower predation rates during mast years. The results presented in chapter 3 therefore suggest that seed predation by deer should be more constraining for oak regeneration under scenario A (*i.e.* increased frequency, lower magnitude) than scenario B (*i.e.* decreased frequency, higher magnitude).

8.2.3.2 Drought: a factor interacting with the effect of deer browsing ?

A significant drought-induced seedling mortality event in summer 2019 compromised the study presented in chapter 5 and illustrated how climate-related hazards can compromise experimental studies conducted in field conditions. The high mortality rate that occurred following water scarcity was not surprising since, unlike sessile oak, pedunculate oak is particularly intolerant to drought ([Früchtenicht et al., 2018](#); [Hees et al., 1996](#)). Surprisingly, the simulated herbivory further increased the mortality rate: deer browsing is not known to be a significant mortality factor for young oaks ([Drexhage & Colin, 2003](#); [Götmark et al., 2014](#)). The contradiction between this observation and the literature raises the question of a potential interaction between herbivory and drought: could water limitations decrease young oak tolerance to herbivory? Based on the limiting resource model (LRM), which provides a theoretical framework linking resource availability and tolerance to herbivory, the limitation of a given resource should decrease herbivory tolerance only if herbivory directly or indirectly reduces this resource in the plant ([Wise & Abrahamson, 2005](#)). However, studies testing this theoretical prediction on water limitations are scarce. [Lama et al. \(2019\)](#) showed that simulated herbivory in controlled conditions modified the water content of tropical *Jatropha curcas* (L.) seedlings, which would imply the existence of a herbivory-drought interaction

under the LRM framework (Wise & Abrahamson, 2005). However, the only similar study conducted with temperate seedlings showed that the effect of experimental variations in herbivory and drought stress on *Chamaecyparis thyoides* (L.) seedling growth did not interact (Steven & Gaddis, 2017). The existence of an interaction between the effects of drought and herbivory on oak sapling growth could be tested with a relatively simple *ex situ* experiment: different treatments of simulated herbivory (e.g. three levels: (i) no herbivory, (ii) removal of the apical shoot, and (iii) removal of apical shoot + all lateral shoots) could be crossed with different water availability treatments applied to young oak saplings growing in controlled conditions. Comparing initial and one-year oak sapling height growth and aboveground and belowground biomass should be sufficient to conclude on the existence of an interaction between the effects of these two factors on oak sapling growth. Studying this interaction seems all the more necessary since droughts are likely to become more and more frequent in the years to come with climate change (IPCC, 2014).

8.3 General conclusion

The objectives of this thesis were to quantify and unravel the mechanisms underlying the constraint exerted by cervids on oak regeneration through the consumption of acorns and the browsing of oak saplings and admixed understory species, and (ii) to identify how specific forest management operations (*i.e.* fencing, felling, and clearing) could limit or increase this constraint. To fulfill these objectives, I used complementary methodologies (observational, experimental *in situ* and *ex situ* and *in silico*) conducted at various organizational levels. At the animal level, I showed that acorns represent a significant proportion of red and roe deer diets, but that high acorn availability saturates the diet: the proportion of seeds escaping deer predation should therefore increase during mast years (chapter 3). At the plant level, I showed that young oak saplings have weak but significant plasticity in response to browsing, increasing with age toward faster carbon acquisition and lower levels of anti-herbivore defense (chapter 4). At the oak population level, I evidenced that both canopy openness (chapter 6) and sapling height (chapters 4, 6, 7 and Löf *et al.* (2021)) increase the negative influence of red and roe deer on growth and survival. Lastly, chapter 7 explains that the constraint exerted by deer browsing on oak sapling growth could decrease with the competitiveness and palatability of the admixed understory vegetation.

In addition to these theoretical results, my thesis work also resulted in the development of a research support tool through the inclusion of deer browsing in the "regeneration" library of the CAPSIS modeling platform. The implemented model remains imperfect, and the version described in this manuscript is only a first step, which will be improved in the months (years?) to come, but the foundation of a publicly-accessible theoretical model has

been laid. Hopefully, this model will be reused in future research projects and will further improve our understanding of deer influences on forest dynamics.

I started this manuscript by highlighting how human activities can disrupt the balance among interacting trophic species. Our results confirm that, following the human-induced increase in deer population in northern hemisphere forests, the damage caused by these species can constrain the process of forest regeneration through seed predation and browsing. Nevertheless, the modeling study also showed that adapting understory vegetation management to cervid populations by reducing clearing frequency and promoting palatable admixed species could considerably reduce the constraint exerted by these species on oak regeneration. This finding illustrates that, although the imbalance between large herbivores and forest regeneration has an anthropogenic origin, humans can also help restore a balance through appropriate forest management.

CHAPTER

9

RÉSUMÉ DE LA THÈSE EN FRANÇAIS

9.1 Introduction

Le développement des activités humaines est désormais identifié comme le principal vecteur de changements environnementaux. L'une des conséquences de ces changements globaux est la perturbation de l'équilibre trophique entre les espèces, avec des répercussions en cascades pour les écosystèmes. L'équilibre entre les écosystèmes forestiers et les populations de grands herbivores dans l'hémisphère Nord fournit un exemple particulièrement éclairant de ce phénomène. D'une part, il a été montré que l'augmentation des températures combinée à des précipitations plus faibles accentue la mortalité des arbres adultes, leur sensibilité aux pathogènes, et s'associe à une hausse de la fréquence de certaines perturbations (feux de forêt, sécheresse). D'autre part, les populations de grands herbivores voient leur abondance et distribution spatiale augmenter fortement depuis le début du 20^{ème} siècle, ce qui s'explique notamment par des changements d'usages des terres ayant permis une expansion de leur habitat, ainsi que par des politiques de gestion de la faune (réintroduction, quotas de chasse, préservation d'habitat) conduites dans le but de restaurer ces populations qui avaient atteint un niveau très bas fin du 19^e siècle.

Les cervidés influencent le processus de renouvellement forestier par le biais de deux mécanismes principaux : la consommation des graines dispersées qui empêche la germination, et la consommation des pousses des jeunes arbres qui réduit leur croissance, et leur taux de survie. Si les cervidés sont essentiels au fonctionnement des écosystèmes forestiers (dispersion des graines, fertilisation du sol, influence sur la structure de la végétation de sous-bois), le niveau actuel des populations compromet le renouvellement des peuplements dans de nombreuses forêts et donc les objectifs de production fixés par les forestiers. La chasse permet aujourd'hui une régulation partielle des populations, mais des facteurs économiques et sociaux empêchent une baisse des populations à un niveau compatible avec les objectifs sylvicoles – e.g. importance de la densité de population pour la rentabilité et l'attractivité d'un territoire de chasse, valeur patrimoniale des cervidés. La protection des jeunes arbres par des protections individuelles, des répulsifs chimiques ou naturels ou par des clôtures permettent de limiter l'influence négative exercée par les cervidés, mais ces mesures s'accompagnent aussi de coûts économiques importants.

De nombreuses études ont montré que l'influence des cervidés sur le renouvellement forestier n'était pas uniquement liée à la densité des populations, mais aussi à des facteurs environnementaux tels que la disponibilité en ressources végétales, ou l'ouverture de la canopée. Des études conduites en Amérique du Nord ont par exemple montré que la plantation d'espèces peu appétentes pour les herbivores, ou le maintien de végétation de sous-bois non valorisable d'un point de vue sylvicole mais servant de source d'alimentation alternative permettait de réduire les dégâts engendrés par les herbivores. L'identification et la ma-

nipulation de ces facteurs environnementaux offre ainsi la perspective d'une gestion plus écologique et économique des interactions entre forêt et cervidés, mais nécessite au préalable une fine compréhension des interactions faune-flore pendant le processus de renouvellement forestier. Les efforts de recherche sur cette thématique doivent en particulier se concentrer sur les essences forestières les plus impactées par les grands herbivores, et pour lesquelles les enjeux économiques et écologiques sont les plus élevés.

Les chênes pédonculés (*Quercus robur*) et sessiles (*Q. Petraea*) sont deux essences emblématiques des forêts tempérées européennes. Le chêne fait partie des espèces les plus importantes en Europe à la fois d'un point de vue économique (forte valeur commerciale du bois), et écologique (source d'habitat, et de ressource pour de nombreuses espèces animales et végétales). Ces deux essences sont présentes dans la quasi-totalité du continent suite à une expansion particulièrement dynamique après la dernière ère glaciaire. Paradoxalement, malgré cette dynamique positive, de nombreuses études font état d'une difficulté du chêne à régénérer sous sa propre canopée depuis le début du 20ème siècle. De nombreuses hypothèses ont été formulées pour expliquer ce phénomène, la principale étant que les changements globaux ont entraîné une modification de l'importance de certains des facteurs contraignant la régénération du chêne, la dynamique actuelle des populations de cervidés faisant partie des facteurs identifiées. Dans ce contexte, les objectifs de cette thèse sont de :

- Quantifier et décrire les mécanismes sous-jacent de la contrainte exercée par les cervidés sur la régénération à travers la prédation des graines, et la consommation des pousses de chêne et de la végétation accompagnatrice
- Identifier dans quelle mesure certaines opérations sylvicoles (coupe, dégagement et pose d'enclos) influencent cette contrainte.

9.2 Influence du masting du chêne sur le comportement alimentaire du cerf et du chevreuil.

Le chêne, comme de nombreuses autres espèces d'arbres tempérés, se reproduit par la stratégie de masting, qui se caractérise par de fortes variations interannuelles dans la production de glands synchronisées à l'échelle de la population. Des années de forte fructification sont ainsi suivies de plusieurs années consécutives où la production de glands est très faible. L'une des interprétations évolutives de cette stratégie est que cela permet une saturation du régime alimentaire des prédateurs de graines les années de forte fructification, permettant ainsi à une partie des graines produites d'échapper à la prédation. Si les glands ont été identifiés comme une ressource fréquemment consommée par les cervidés, la

relation entre fructification et consommation est mal connue. Par ailleurs, les glands sont considérés comme nutritionnellement déséquilibrés : très riche en contenu énergétique mais pauvres en protéines. Une forte consommation de glands peut ainsi conduire à un bouleversement du régime alimentaire, ce qui aurait pour conséquence une modification des autres ressources végétales consommées pour rectifier l'équilibre nutritionnel, et donc une modification de la pression d'herbivorie exercée sur la végétation.

L'objectif de cette première étude était d'évaluer (i) la relation entre la fructification du chêne et la consommation de glands, et (ii) les conséquences de la consommation de glands pour la consommation d'autres ressources végétales. Pour remplir ces objectifs, j'ai analysé un jeu de données existant incluant la composition de panses de cerf et de chevreuil abattus dans la Réserve Nationale de Chasse et de Faune Sauvage de La Petite Pierre (48.5°N, 7.0°E) entre 1986 et 2017. En parallèle, la fructification du chêne est suivie sur le site depuis 2010 par comptage au sol.

Cette étude a permis de mettre 3 principaux résultats en évidence. Tout d'abord, l'étude a permis de valider l'hypothèse que les glands sont une ressource privilégiée par les deux espèces de cervidé lorsqu'ils sont disponibles (respectivement plus de 50% et 30% du régime du cerf et du chevreuil les années de forte fructification). Deuxièmement, l'étude des variations intra-annuelles a permis de mettre en évidence que les années de fortes fructifications seulement, la proportion de gland consommée restait constante au cours de l'hiver alors que la disponibilité diminuait, ce qui suggère une saturation du régime alimentaire lors des pics de fructification. Cette saturation impliquerait que la proportion de graines échappant à la prédation par les cervidés diminuera lors des années de forte fructification. Enfin, un bouleversement du régime alimentaire a pu être mis en évidence pour le cerf : au fur et à mesure que la proportion de gland dans le régime augmente, le cerf réduit sa consommation de pousses de ligneux et augmente sa consommation de graminées, plus riches en azote. Ce résultat suggère ainsi une légère diminution des dégâts sylvicoles les années de fortes fructifications.

9.3 Réponse des jeunes chênes à l'abrutissement, et conséquence pour l'attractivité du plant

Plusieurs études conduites en forêts tempérées observent que les jeunes arbres abrutis par des cervidés ont une plus forte probabilité d'être de nouveau consommés l'année suivante. Ce phénomène, baptisé boucle alimentaire, a pour conséquence le maintien de cohortes d'individus à une hauteur accessible aux cervidés, diminuant ainsi la valeur sylvicole du peuplement en régénération. Ce phénomène est interprété comme la conséquence d'une

croissance compensatoire suite à l'abroustissement, dans la mesure où l'investissement des plantes dans une croissance rapide est associée à une plus forte digestibilité des tissus, et à une plus faible teneur en défenses anti-herbivore. Ainsi, les boucles alimentaires seraient propres aux espèces d'arbres adoptant une stratégie de tolérance à l'herbivorie, par opposition à la stratégie de défense consistant à augmenter la production de défenses chimiques ou physiques contre les herbivores suite à l'abroustissement. Cependant, cette hypothèse se fonde principalement sur les réponses observées chez les plantes herbacées, mais aucune étude n'a jusqu'ici cherché à lier la réponse à l'abroustissement en terme de traits à de futurs patrons d'herbivorie chez les ligneux.

Le chêne est caractérisé par une forte capacité de survie suite à l'abroustissement, ce qui est caractéristique d'une espèce adoptant une stratégie de tolérance à l'abroustissement. Le chêne fait ainsi figure de modèle approprié pour tester le lien entre réponse à l'abroustissement et future attractivité du plant. Dans les forêts tempérées, le chêne est principalement abrousti à la fin de l'hiver et au début du printemps. L'objectif de cette deuxième étude est de tester les conséquences de l'abroustissement hivernal sur (i) la morphologie du plant, et les traits foliaires de croissance et de défense, (ii) sur la composition chimique des rameaux de l'hiver suivant, et (iii) sur l'attractivité pour le chevreuil l'hiver suivant. Pour traiter ces différentes questions, j'ai mis en place un protocole expérimental *ex situ*. Différents traitements d'abroustissement hivernal simulé ont été appliqués à des plants de chêne à la pépinière de l'ONF située à Cadarache (43°42' N, 5°44' E). Les effets de ces traitements sur la morphologie, les traits foliaires et la composition chimique des rameaux ont été suivis pendant deux ans. Enfin, un test comportemental avec des chevreuils domestiqués a été mené l'hiver suivant l'application du traitement à l'installation expérimentale INRAE de Gardouch (43°22' N, 1°40' E) pour tester l'influence du traitement sur la préférence de l'animal.

L'abroustissement a significativement réduit la croissance en hauteur des plants mais n'a pas eu d'effet sur les traits foliaires la première année. L'hiver suivant l'application du traitement, les plants abroustis avaient des rameaux plus riches en fibres, mais avec une plus faible teneur en défense chimique (phénols). Il s'agit ainsi d'une des premières preuves empiriques que les réponses chimiques induites par l'abroustissement peuvent persister dans les pousses de l'année suivante. Durant les tests comportementaux, les chevreuils ont préférentiellement consommé les plants n'ayant pas subi le traitement d'abroustissement, ce qui tend à contredire l'applicabilité des boucles alimentaires au chêne. Ce résultat peut s'expliquer à la fois par des facteurs morphologiques (les plants abroustis étaient plus bas et le chevreuil privilégie les plants à la hauteur du garrot) et chimiques (le chevreuil digère très mal les fibres mais relativement bien les phénols contrairement à d'autres cervidés). Enfin, les mesures de traits la 2^e année de l'expérience ont mis en évidence un effet marqué de l'abroustissement qui a réduit la teneur en phénols et en fibres des feuilles, et entraîné une hausse de la di-

gestibilité et de la surface spécifique foliaire, deux traits liés à la croissance rapide. Ce résultat supporte l'idée que le chêne répond à l'abrouissement par une stratégie de tolérance visant à accélérer l'acquisition de ressources carbonées pour compenser la perte des tissus. La fait que cette plasticité ne s'observe que la 2^e année de l'expérience souligne l'importance du stade ontogénique dans la réponse du plant, et supporte l'hypothèse que la capacité des jeunes chênes à résister à l'herbivorie augmente avec l'âge.

9.4 Influence croisée de l'ouverture de la canopée et de l'exclusion des ongulés sauvages sur la régénération du chêne

La croissance des arbres en forêt est contrôlée par des processus bottom-up (acquisition des ressources) et top-down (herbivorie). En sylviculture, la coupe d'arbre adulte afin d'augmenter la disponibilité en lumière pour les semis est généralement nécessaire pour initier le processus de régénération forestière, en particulier pour des espèces ayant de forts besoins en lumière. Cependant, il a été documenté que cette augmentation des ressources lumineuses pouvait aussi avoir des conséquences négatives pour la régénération en accentuant les effets liés à l'herbivorie, par le biais de deux mécanismes. Tout d'abord, l'augmentation de la productivité primaire suite à une ouverture de la canopée augmente la quantité des ressources végétales disponibles, et de récentes études suggèrent que les cervidés se nourrissent préférentiellement sous des canopées plus ouvertes. Par ailleurs, une augmentation de la disponibilité en lumière est aussi susceptible d'influencer la tolérance des jeunes arbres à l'abrouissement, mais la magnitude et la direction de cet effet est fortement variable d'une espèce d'arbre à l'autre.

Le chêne est une espèce ayant de forts besoin en lumière, et une ouverture de la canopée est indispensable pour initier sa régénération. Cette espèce étant aussi fréquemment abroutie par les cervidés, l'existence d'interactions entre les effets de l'abrouissement et de l'ouverture de la canopée pourrait donc avoir des conséquences importantes pour la régénération de cette espèce. Dans ce contexte, cette étude a pour but d'évaluer la conséquence d'une ouverture de la canopée sur la contrainte exercée par les cervidés sur la croissance et la survie du chêne à l'échelle populationnelle. Afin d'étudier les mécanismes sous-jacent de cette interaction, nous avons aussi cherché à déterminer l'influence de l'ouverture de la canopée sur la probabilité d'abrouissement, et sur la réponse du chêne à l'abrouissement (échelle individuelle). Pour tester ces différentes questions, j'ai exploité deux protocoles expérimentaux *in situ* : le dispositif EFFORT en France pour lequel j'ai contribué à la récolte d'une année supplémentaire de donnée, et un protocole similaire en Suède auquel j'ai eu accès

suite à une mobilité de 3 mois effectuée dans le laboratoire à l'origine de ce protocole. Dans ces deux expériences, la croissance, la survie, et les marques d'abroustissement de jeunes semis de chênes ont été suivi pendant 2 à 3 saisons de croissance dans des paires d'enclos-exclos situés sous des conditions d'ouverture de canopée différentes.

Les résultats valident l'hypothèse d'une interaction entre les effets de l'ouverture de la canopée et de l'exclusion des ongulés sur la régénération du chêne. L'ouverture de la canopée augmente la survie (en France) et la croissance (en Suède) des semis de chêne mais en enclos uniquement, ce qui implique qu'en exclos, les bénéfices de l'augmentation de la lumière sont compensés par une accentuation de la contrainte exercée par les ongulés. Le fait que des variables différentes ont répondu entre la France (survie) et la Suède (croissance) vient probablement du stade de la régénération, et de la nature de la contrainte exercée par les ongulés. En effet, les semis étaient encore jeunes en France (principalement < 50cm) et principalement affectés par le retournement de sol du sanglier qui détruit les semis, tandis que les semis en Suède étaient en moyenne plus grands (jusqu'à 2m de haut), et plus affectés par l'abroustissement qui ralentit la croissance. Dans les deux pays, l'abroustissement réduit la croissance à l'échelle individuelle, et cette réduction de croissance est indépendante de l'ouverture de la canopée. En revanche, la probabilité d'abroustissement augmentait avec l'ouverture de la canopée en Suède. En conclusion, cette étude a mis en lumière qu'une ouverture du couvert arborée avait tendance à accentuer la contrainte exercée par les ongulés sur la régénération du chêne, via une plus forte fréquentation des ongulés sous des canopées ouvertes. La réussite de la régénération reflète ainsi un équilibre subtil entre augmentation de la disponibilité en ressources et limitation de l'herbivorie.

9.5 L'influence de l'abroustissement sur la régénération du chêne est conditionné par la végétation accompagnatrice

L'influence globale de l'abroustissement sur la croissance des jeunes arbres d'une espèce donnée est la résultante d'un effet direct (abroustissement sur l'espèce) généralement négatif, mais aussi d'effets indirects (consommation d'espèces accompagnatrices), qui peuvent être positifs si ces espèces exercent un effet compétitif. Par ailleurs, les cervidés étant des herbivores sélectifs, la consommation des différentes espèces du sous-bois va dépendre de leur abondance relative mais aussi de leur appétence. Ainsi, certaines caractéristiques de la végétation de sous-bois accompagnatrice (appétence, abondance, compétitivité) risquent d'avoir une influence marquée sur l'effet global de l'abroustissement sur l'essence à régénérer. Une connaissance fine de ces différentes interactions pourrait ainsi permettre

de gérer la végétation de sous-bois de manière à limiter l'impact négatif de l'abrutissement sur l'essence objectif.

La croissance des jeunes chênes est principalement contrainte par deux types de compétiteurs pour la lumière: les semis d'autres espèces ligneuses (le charme et le hêtre principalement), et une couche de végétation interférente, souvent dominée par la ronce. L'appétence et la compétitivité de ces espèces par rapport au chêne diffèrent. Dans ce contexte, l'objectif de cette étude était (i) de déterminer dans quelle mesure la composition du sous-bois influence l'effet global des cervidés sur la croissance du chêne, et (ii) d'identifier les scénarios de gestion de la végétation compétitrice (*i.e.* dégagement) les plus adaptés selon la pression d'herbivorie exercée. Ces questions de recherches sont difficilement testables par une approche expérimentale, j'ai donc choisi de mobiliser une approche par la modélisation.

La première étape de cette étude a donc été la construction et l'implémentation d'un modèle théorique d'herbivorie dans la bibliothèque régénération de la plateforme de modélisation CAPSIS. Cette bibliothèque permet de modéliser la croissance et l'interception de la lumière d'arbres adultes, et des semis et couches de végétations interférentes présents dans le sous-bois. Afin d'intégrer les espèces étudiées (chêne, charme, hêtre et ronce) dans la bibliothèque et de paramétrer le modèle d'herbivorie, j'ai mobilisé à la fois des données issues de la littérature, et des données issues du dispositif EFFORT. Enfin, en m'appuyant sur le modèle RRESHAR qui utilise la bibliothèque régénération, j'ai pu conduire des simulations afin d'adresser les différentes questions soulevées par cette étude.

Les simulations ont permis de montrer qu'en présence d'une forte pression d'abrutissement et en l'absence de ronce, la régénération du chêne était meilleure lorsqu'il était accompagné par le charme (plus appétant que le chêne) que par le hêtre (moins appétant). En présence de ronce, ce résultat s'inversait, ce qui pourrait s'expliquer par un effet devenu facilitateur du charme et du hêtre de par leur capacité à ombrager la ronce. En augmentant artificiellement l'appétence de la ronce par rapport aux semis de chêne, hêtre et charme, l'effet global de la pression d'abrutissement passait de négatif à positif, ce qui souligne l'effet hautement compétitif de la ronce par rapport aux semis. Enfin, les simulations indiquent qu'en présence d'une forte pression d'abrutissement, la conduite de dégagements permet d'améliorer la régénération du chêne lorsqu'il est accompagné par le hêtre (moins appétant), mais pas lorsqu'il est accompagné par le charme. Ce résultat souligne que ces opérations coûteuses permettent de réguler la compétition, mais sont aussi susceptible d'augmenter la pression d'abrutissement exercée sur l'essence objectif, en particulier lorsque les espèces accompagnatrices sont plus appétentes. En conclusion, ces résultats suggèrent qu'une gestion de la végétation de sous-bois favorisant le maintien d'espèces accompagnatrices appétentes pourrait permettre de réduire localement l'influence négative des cervidés sur la croissance

des semis de chêne. Bien que ces résultats restent théoriques dans la mesure où ils ont été obtenus à partir d'un modèle ayant fait de nombreuses hypothèses simplificatrices, les tendances dégagées mériteraient d'être testées sur le terrain pour vérifier leur validité.

9.6 Synthèse et perspectives

Cette thèse avait pour objectif de:

- Quantifier et décrire les mécanismes sous-jacents de la contrainte exercée par les cervidés sur la régénération à travers la prédation des graines, et la consommation des pousses de chêne et de la végétation accompagnatrice
- Identifier dans quelle mesure certaines opérations sylvicoles (coupe, dégagement et pose d'enclos) influencent cette contrainte.

Au stade de germination, nous avons montré que les cervidés représentaient bien un prédateur significatif des glands (plus de 50% du régime alimentaire du cerf les années de forte fructification). Cependant, nos résultats suggèrent qu'à travers une saturation du régime alimentaire de ces deux espèces, la proportion de graines échappant à la prédation devrait augmenter les années de forte fructification, diminuant ainsi la contrainte exercée par les cervidés sur ce stade de la régénération.

Durant la phase de croissance des semis, nous avons montré que même un unique épisode d'abrouissement sur la pousse apicale était suffisant pour entraîner une diminution de la croissance en hauteur, ce qui s'explique par une plasticité d'allocation des ressources relativement faible, et ne permettant pas d'induire de croissance compensatoire. Les résultats obtenus la 2^{me} année de l'expérience en pépinière suggèrent toutefois un investissement plus fort dans la croissance compensatoire chez les semis plus âgés. Nous avons aussi pu identifier deux facteurs susceptibles d'augmenter la probabilité qu'un semis soit abroui : la hauteur, et le niveau d'ouverture de la canopée – *i.e.* les cervidés consommant principalement les semis supérieurs à 50cm, et situés sous des canopées plus ouvertes. Ainsi, lorsque la végétation de sous-bois est soumise à une forte pression d'abrouissement, la coupe d'arbre adulte doit s'accompagner de la pose d'enclos, afin d'éviter que les bénéfices d'une augmentation de la ressource lumineuse pour le chêne soient compensés par une hausse de la pression d'abrouissement.

Enfin, le travail de modélisation montre que la compétitivité et l'appétence de la végétation de sous-bois étaient négativement corrélées à la contrainte exercée par les cervidés sur la

régénération. Ainsi, lorsqu'une forte pression d'abrouissement s'exerce sur la végétation de sous-bois, et à niveau de disponibilité égale entre végétation accompagnatrice et chêne, la densité de chêne recrutés est plus élevée en présence de végétation compétitrice (*e.g.* ronce), et d'essences appétentes (*e.g.* charme). Ainsi, en présence de fortes densités de cervidés, des opérations de dégagement moins fréquentes, et visant à maintenir des essences appétentes comme le charme pourraient permettre de limiter l'impact de l'abrouissement sur la régénération du chêne. Ces résultats proviennent toutefois de simulations effectués avec un modèle ayant fait un certain nombre d'hypothèses simplificatrices : des études sur le terrain sont ainsi indispensables pour vérifier leur validité.

En conclusion, les résultats de cette thèse tendent à supporter l'idée que le niveau actuel des populations de cervidés représente une contrainte significative pour le processus de régénération du chêne. Cependant, si le niveau actuel des populations résulte de facteurs anthropiques, les résultats de l'étude de modélisation illustrent le fait que l'homme détient également la clé pour restaurer un équilibre durable entre faune sauvage et renouvellement forestier, via des pratiques de gestion forestière réduisant la contrainte exercée par les cervidés sur le processus de renouvellement.

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APPENDIX

A

LÖF ET AL. 2021

This paper is the result of a collaboration with Magnus Ljöf during my stay in Sweden. My contribution to this work was to elaborate the hypotheses along with M. Ljöf, to conduct the statistical analyses and to read and comment the manuscript along with the other co-authors. It was published in 2021 in the *European Journal of Forest Research*, and is presented with the formatting of the journal.



The influence of fencing on seedling establishment during reforestation of oak stands: a comparison of artificial and natural regeneration techniques including costs

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Abstract

In temperate Europe, oak-dominated forests are widespread, supporting high biodiversity and providing important ecosystem services. Insufficient natural regeneration has, however, been a concern for over a century. The objective of this study was to gain insights into differences in regeneration success using artificial and natural regeneration techniques for reforestation of oak (*Quercus robur* L.) stands. We monitored seedlings following planting, direct seeding and natural regeneration over five years in a randomized block experiment in southern Sweden with fenced and non-fenced plots. Fencing had a strong positive effect on height growth, especially for planted seedlings that were taller than the other seedlings and more frequently browsed in non-fenced plots. In contrast, there was little effect of fencing on survival, establishment rate and recruitment rate of seedlings. Due to aboveground damage on seedlings from voles, protection of acorns did not improve establishment rate following direct seeding. Under current circumstances at the site with a sparse shelterwood of old oaks, we conclude that natural regeneration was the most cost-efficient regeneration method. It resulted in the most seedlings at the lowest cost. However, regeneration success was heavily influenced by interference from herbaceous vegetation. With a small additional investment in vegetation control, the results might have been improved for planting and direct seeding.

Keywords Competition · Deer · Herbivory · Pedunculate oak · Regeneration method · Silviculture

Introduction

Pedunculate and sessile oak (*Quercus robur* L. and *Q. petraea* (Matt.) Liebl.) are foundational species in European temperate forests where they support more biodiversity than most other tree species (Mölder et al. 2019; Sundberg et al. 2019). Oak forests also provide many ecosystem services

including quality timber, firewood, forage, recreation, aesthetic/cultural/historical values and watershed protection (Gil-Pelegrín et al. 2017). Additionally, oak forests, because of their high resilience to disturbance and environmental stress, offer a promising alternative for inclusion into management plans addressing increasingly common extreme weather events (Kohler et al. 2020). Sustainable management of oak-dominated forests and habitats is therefore an important issue connected to environmental and land management strategies.

Oak dominance is declining in many parts of the world (Dey et al. 2019), which is particularly concerning in light of their conservation and ecosystem service values. Oak regeneration failures are regarded as central to this problem (Annighöfer et al. 2015). Insufficient natural regeneration of oak has been a concern for over a century (Watt 1919; Korstian 1927). It is well-known that pedunculate and sessile oak are light-demanding species (Röhrig et al. 2006; Ligot et al. 2013; Leuschner and Ellenberg 2018; Kohler et al. 2020). Their regeneration therefore depends on relatively open forests, forest edges or savanna-like grasslands with

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abundant light and natural or anthropogenic disturbances that maintain such habitats (Vera 2000; Bobiec et al. 2018; Petersson et al. 2020). Furthermore, the recruitment strategy of light-demanding temperate tree species such as oaks, growing in open habitats in the presence of thorny shrubs, may be viewed as an adaptation to now extinct large browsers and grazers (Bakker et al. 2004). A distracting fact in many European temperate forests of today is that oaks are among the most palatable tree species for ungulates (Kullberg and Bergström 2010; Petersson et al. 2019). In today's denser and darker environments that lack protective thorny shrubs, grazing and browsing from ungulates may severely affect oak seedling growth and survival (Bobiec et al. 2018; Barrere et al. 2021; Dobrowolska et al. 2020).

Besides light availability, grazing and browsing, acorn dispersal and predation by animals are important for natural regeneration (Mellanby 1968). Scatter-hoarding birds and rodents may consume large quantities of acorns but some will survive and germinate in suitable places (Gómez et al. 2019). Birds in particular can carry acorns far from seed-bearing trees to open areas where they may develop successfully (Pesendorfer et al. 2016; Martínez-Baroja et al. 2019).

Open habitats, however, do not guarantee successful establishment in practical forestry. Interference from low-stature herbaceous and woody vegetation may severely reduce growth and survival of young oak seedlings (Jensen et al. 2011). It is often necessary to control competing vegetation using herbicides, mechanical site preparation, mulching or prescribed burning. Numerous studies show a positive correlation between these methods and growth and survival in oak seedlings (e.g., Davies 1988; Löf et al. 2006; Dey et al. 2019). In addition, in habitats with dense herbaceous vegetation, rodents such as voles can damage and consume seedlings which may further reduce survival over time (Manson et al. 2001).

In northern Europe, oak silviculture in pure stands for high-quality timber production combines relatively short rotations (ca 100–130 years) with frequent heavy thinnings and regular high pruning of epicormic branches (Carbonnier 1975; Henriksen 1988). These pure stands are often even aged, with or without an understory of other tree species (Drössler et al. 2012). For various reasons, such stands are considered difficult to regenerate naturally (Löf et al. 1998). For example, acorn removal and consumption by animals, competition from other vegetation and browsing by deer are seen as serious problems (Andersson 1991; Götmark et al. 2005; Jensen et al. 2012). When used, natural regeneration is thought to be most effective following mast years, in a uniform shelterwood system, and sometimes combined with mechanical site preparation (Almgren et al. 1984). However, there are few examples where this method of natural regeneration has been successful (Hansen 1995). Instead, such stands are often clear-cut followed by planting of bare-rooted

seedlings, which probably significantly increases the regeneration costs.

This study, conducted in southern Sweden, was designed to examine effects of fencing and regeneration technique (natural regeneration, direct seeding and planting) on the establishment of oak seedlings. To our knowledge, there is a lack of experience from studies where several regeneration techniques are compared side by side, especially for oaks. The objective is to gain practical insight into differences in establishment success using artificial- and natural-regeneration techniques for reforestation of oak stands. To meet this objective, we present findings about the effects of fencing and regeneration technique on the growth, survival, establishment rate and recruitment rate of seedlings. Additionally, we report and discuss the costs involved for the various regeneration techniques used in this study.

Material and methods

Study site and experimental design

The experiment was carried in a 2.6 ha oak (*Q. robur*) stand on the island Visingsö (58.03° N, 14.29° E, 94 m.a.s.l.) near Gränna in southern Sweden. The island is ca 3 km wide, 14 km long with an area of 25 km². The experiment was initiated in May 2014 and monitored until the autumn of 2018. The stand consisted of a sparse shelter-wood of approximately 100-year-old oaks, without an understory. The mean basal area was 12 m² ha⁻¹ at the end of the study. This corresponds to ca 42% of above canopy light in oak forests according to Petersson et al. (2020). In the beginning of the experiment in 2014, the ground vegetation was already dominated by a dense layer of herbaceous vegetation. During the study period, this vegetation was mainly dominated by grasses, sedges and thickets of *Rubus idaeus* L. In addition, clusters of small naturally regenerated oak seedlings were distributed throughout the stand. These groups of naturally regenerated seedlings were evenly distributed and were estimated to occupy about one third of the area. Only a few individuals of other woody species were present in the seedling/sapling layer. The soil texture of the site is fine sandy till. During the experiment, annual precipitation varied between 331 and 501 mm, and mean air temperature was from -2.1 to 1.8 °C in January and 15.6 to 20.4 °C in July (SMHI 2019). Most years had relatively normal rainfall and temperatures except 2018 when there was little precipitation and higher temperatures compared to the mean of the last 20 years (Table 1). Hares (*Lepus timidus* L. and *Lepus europaeus* P.) and roe deer (*Capreolus capreolus* L.) were abundant. There are no figures on population densities available. However, during the period 2014–2018, a yearly average of 25 roe deer were shot on the island, i.e., 10 roe deer

Table 1 Monthly precipitation (mm) and monthly mean air temperature (°C) during the 2014–2018 growing seasons at Visingsö climate station located 9.6 km north of the experimental site (SMHI 2019)

Month	2014	2015	2016	2017	2018	20-year-mean
<i>Precipitation</i>						
May	52	78	19	20	19	41
June	54	49	13	73	26	69
July	30	53	54	30	23	72
Aug	83	46	54	124	98	66
Sept	87	76	12	51	22	38
<i>Air temperature</i>						
May	11	9	11	10	13	10
June	14	13	15	14	16	14
July	19	16	17	16	20	17
Aug	16	17	16	16	18	16
Sept	14	13	16	13	13	13

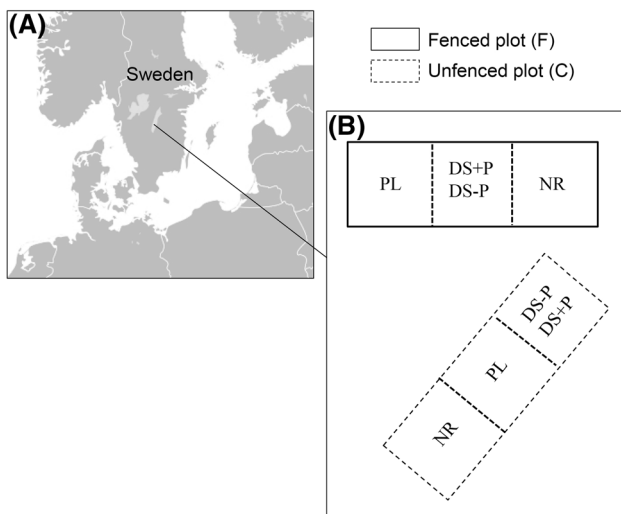


Fig. 1 The location of the site in southern Sweden (a) and an example of design of one out of four blocks (b). Blocks were ca 100 m apart from each other. Main treatments in each block were the fencing (F) and no fencing (C). The sub-treatments were planting (PL), direct seeding with (DS+P) and without protection (DS–P) and natural regeneration (NR)

shot per 1000 ha (Hans Christensson pers. comm.). Roe deer annual harvest is a variable positively related to population abundance (Kahlert 2015). No such figures are available for hares. To our knowledge, there were no other large mammals on the island with the potential to damage seedlings.

The experimental design included four randomized blocks with two treatments along with sub-treatments (split plots) in each of the blocks. Figure 1 shows the location of the site and exemplify the design of one out of four blocks (Fig. 1). Blocks were about 100 m from each other. The treatments were fencing (F) and an unfenced control (C), separated by about 10–20 m within the blocks. Each treatment plot was 8 × 24 m, and around the F treatment a 2-m-high steel wire fence was erected in May 2014 to exclude large herbivores

and hares during the study. Within each block, the two treatment plots were selected so that they were as similar as possible in oak crown coverage and herbaceous species composition. In addition, they were chosen so that a cluster of naturally regenerated oak seedlings was enclosed in each of them. Thus, these naturally regenerated treatment plots were not completely randomized. Each treatment plot was then divided into three subplots (8 × 8 m): planting (PL), direct seeding (DS) and natural regeneration (NR). The NR plots had to be selected to include pre-existing clusters of oak seedlings, whereas the two other plots (PL and DS) were randomly placed in relation to the NR plots. Direct seeding (DS) was done in four rows; two of these rows were randomly selected for direct seeding using an acorn protection device resulting in sub-treatments with (DS + P) and without (DS – P) seed protection. This device costs 0.30 euro each and consisted of two hollow plastic truncated pyramids joined at the bases which physically protected acorns from removal by rodents (see Castro et al. 2015 for more details). Thus, a total of four sub-treatments were applied (PL, DS + P, DS – P and NR) (Fig. 1).

In the PL plots, bare-rooted oak (*Q. robur*) seedlings were planted in May 2014. The seedlings were 2 year old, between 30 and 50 cm tall, originated from Flakulla, Sweden and had not been previously transplanted. The cost per seedling was 0.60 euro (planting procedure excluded). The seedlings were planted manually with a planting auger, at 1 × 1 m spacing. In each PL plot, between 46 and 58 seedlings were planted for a total of 419 seedlings in the experiment. The seedlings were obtained from Ramlösa nursery, Sweden.

Due to unavailability of acorns in 2014, direct seeding of *Q. robur* acorns in the DS plots was carried out in May 2015. Spring seeding is normal practice in the region, although autumn seeding sometimes also occurs. Acorns cost 7.95 euro per kg (planting procedure of acorns excluded), and there were around 235 acorns per kg with a vitality of 58%. Acorns were sown at a soil depth of five cm in four rows that

were each six m long. We planted two acorns per seeding spot at 20 cm spacing, which resulted in 120 acorns each in the sub-treatments (two rows each) with and without protection. In total, 960 acorns were sown in the experiment. Acorns were collected in Poland (Puszcza, Barlinecka) in 2014 and stored at Levinsen Treeseed LTD, Lynge, Denmark until use.

Data collection

For all living planted seedlings, heights (from ground to shoot apex in cm) and ground level stem diameter (mm) were measured one, two and five growing seasons following planting (May and October 2015 and October 2018). Before planting, the same variables were measured on a subsample of seedlings ($n = 10$). Due to accidentally driving a truck over one unfenced plot with planted seedlings in 2015, some data were missing in October 2015 and 2018. For all living seedlings produced after direct seeding, heights (cm) were measured one and four growing seasons following seeding (October 2015 and 2018). If two seedlings emerged from the same seeding spot, we measured the tallest one. Heights (cm) of all living naturally regenerated seedlings were measured within one circular plot (radius 2 m) on each of the NR plots in May and October 2015 and in October 2018. For all seedlings measured in May and October 2015, we noted if they had been browsed by hares or roe deer (these species' browsing damage is visually similar and was not distinguished). In addition, any other damage (e.g., from voles) that occurred was also noted at the treatment plot scale.

The percentage of ground vegetation (dominated by grasses, sedges and thickets of *R. idaeus*) cover was estimated in all subplots in 40-cm-radius circles close to all the living seedlings in PL and NR plots. In DS plots, vegetation cover was instead measured around the eight plastic sticks that marked the beginning and end of the four rows used for direct seeding. These plots were assigned to one of 11 categories, where 0=0%, 1=1–10% and 10=91–100% vegetation cover. These measurements were conducted in May and October 2015 and in October 2018.

Calculations and statistical analysis

Effect of fencing and regeneration technique on seedling height

Since there were different ages and origins of seedlings in the four regeneration techniques, we evaluated the effect of fencing on height separately for each technique (PL, NR, DS – P and DS + P) using linear mixed models. We included two fixed effects: fencing (factor with two modalities: fenced and unfenced) and the date (ordered factor with three levels: May 2015, October 2015 and October 2018), and an

interaction between these two fixed effects. The block was included as a random effect. If the fencing date interaction was significant, we tested the differences between fenced and unfenced plots for each sampling year using Tukey's post-hoc pairwise comparisons of estimated marginal means.

Effect of fencing and regeneration technique on seedling relative growth rate

To compare growth of seedlings from the different sub-treatments with different initial heights, we computed relative growth rate (RGR) as:

$$\text{RGR} = \frac{H_{\max}(\text{Oct2018}) - H_{\max}(\text{Oct2015})}{H_{\max}(\text{Oct2015})} \times 100$$

H_{\max} is the average of the five tallest seedlings in each sub-treatment; this was used since the NR sub-treatment otherwise would have been biased by adding newly recruited (and thus relatively small) seedlings. By using only the five tallest seedlings, we ensure that no newly established seedlings were involved. We then studied the combined effect of the fencing and of the regeneration technique on the RGR with a linear mixed model. We included two fixed effects: fencing and regeneration technique (the latter is a factor with four modalities: PL, DS – P, DS + P and NR), an interaction between these two fixed effects, and the block as a random effect.

Effect of fencing and regeneration technique on survival, establishment rate and recruitment rate

In the experiment, it was not possible to compare survival rates between sub-treatments. Therefore, for each regeneration technique, we used a different response variable to represent establishment success: survival, establishment rate or recruitment rate. For planted seedlings, we computed survival in plot k , at date j as:

$$\text{Survival}_{j,k} = \frac{n_{\text{seedlings}}(j, k)}{n_{\text{seedlings}}(\text{May2015}, k)} \times 100$$

where $n_{\text{seedlings}}(j, k)$ is the number of seedlings in plot k on date j and $n_{\text{seedlings}}(\text{May2015}, k)$ is the number of seedlings at start of the experiment in that plot.

As mentioned earlier, in DS plots each seeding point could develop two seedlings where only the tallest was measured. Therefore, in the DS plots we calculated the establishment rate, i.e., the number of seeding points with at least one living seedling in Oct 2018 divided by the initial number of seeding points per sub-treatment in May 2015.

In the NR plots, individual seedlings were not followed. Therefore, for the naturally regenerated seedlings in the NR

circular survey plots, we computed the number of new seedlings recruited per m^2 on date j , in plot k ($R_{j,k}$) as:

$$R_{j,k} = \frac{n_{\text{seedlings}}(j, k) - n_{\text{seedlings}}(\text{May2015}, k)}{S_k}$$

where S_k is the surface area of the plot (12.57 m^2).

We then evaluated the effect of fencing on survival (PL seedlings), establishment rate (DS – P and DS + P) and recruitment (NR seedlings) with a separate linear mixed model for each regeneration technique. We included fencing, the date and the interaction between these two factors as fixed effects. In each model, the block was included as a random effect. For DS + P only, we log transformed the establishment rate to meet the assumption that the model residuals are normally distributed. If the fencing date interaction was significant in one of the models, we tested the differences between fenced and unfenced plots for each date using Tukey's post-hoc pairwise comparisons of estimated marginal means.

Effect of regeneration technique on browsing frequency

In each block and for each date, we calculated the browsing frequency as the number of seedlings browsed divided by the total number of seedlings. We tested the influence of regeneration technique and fencing on browsing frequency with three analyses of variance (ANOVA), one per date: May 2015, October 2015 and October 2018. If the regeneration technique factor or the interaction between regeneration technique and fencing was significant, we assessed the significance of differences among the groups with Tukey's post-hoc pairwise comparisons of estimated marginal means.

Regeneration costs

For fencing costs, we used a standard cost of 11.60 euro per meter (Skogforsk 2020) and assumed that one square-shaped hectare was fenced. In the calculations, we used a standard density of 2800 seedlings or seeding points per ha (Bogghed 2018). We assumed relatively high labour costs for the planting procedure, 1266 euro per ha, since larger bare-rooted seedlings of broadleaves are somewhat more difficult to handle than conifer seedlings (Bogghed 2018). Similarly for direct seedling, we assumed higher labour costs for seeding procedure than normal, 633 euro per ha, since the figures in Bogghed (2018) are based on direct seeding of conifers and not large-seeded species such as *Quercus*. Due to labour cost of putting the acorns in the protection devices, we doubled the costs when these were included in the DS + P treatment. Except for any fence, no costs were included for natural regeneration, which occupied about one third of the area.

We conducted all analyses in the R statistical framework, version 3.6.3 (R Core Team 2020). For each model, we verified the Gaussian distribution of the residuals, and the assumption of homogeneity of variance. We performed all linear mixed models with the R package "lme4" (Bates et al. 2014). We used the "emmeans" R package for Tukey's post-hoc pairwise comparisons of estimated marginal means (Lenth et al. 2018). We examined the significance of the fixed effects of all mixed models with a post-analysis of deviance (Wald χ^2 Type II) using the ANOVA function of the R package "car" (Fox et al. 2012). We used an $\alpha=0.05$ significance level for all tests.

Results

Effects of fencing and regeneration technique on seedling height

For both PL and NR seedlings, there was a positive effect of fencing on seedling height (Fig. 2). For PL seedlings, this effect ($\chi^2=37.6$, $df=1$, $p<0.001$) increased with time ($\chi^2=22.3$, $df=2$, $p<0.001$). There was also a significant interaction between these two variables ($\chi^2=38.2$, $df=2$, $p<0.001$). By the end of the experiment in October 2018, PL seedlings were 65 cm tall on average inside fences, whereas unfenced seedlings were 39 cm tall which is only 2 cm taller than their original height at the time of planting. The same significant effects were found for stem diameter of PL seedlings (data not shown). Similar effects were also found for NR seedlings. The height of NR seedlings increased with fencing ($\chi^2=6.61$, $df=1$, $p<0.05$) and with time ($\chi^2=15.79$, $df=2$, $p<0.001$), but there was no significant interaction between the two variables ($\chi^2=3.38$, $df=2$, $p=0.18$). On average, the NR seedlings were smaller than PL seedlings, ranging between 36 (inside fence) and 26 cm (outside fence) at the end of the experiment. The DS seedlings were even smaller, between 16 and 20 cm in October 2018. Here, there was a slight but significantly negative effect of fencing on seedling height in the DS-P treatment ($\chi^2=3.9$, $df=1$, $p<0.05$; Fig. 2). Otherwise there were no other significant direct or interaction effects for height of DS seedlings.

Effects of fencing and regeneration technique on seedling relative growth rate

Except for seedlings in the DS-P treatment, there was a trend toward higher relative growth rate (RGR) in the fenced plots from October 2015 to October 2018 (Fig. 3). This was, however, not significant at the $p<0.05$ level ($\chi^2=2.71$, $df=1$, $p=0.1$), and there were no significant effects of fencing on RGR in any of the sub-treatments. Neither the effect of the

Fig. 2 Mean seedling heights following planting (PL), natural regeneration (NR) (top boxes), direct seeding without protection (DS-P) and with protection (DS+P) (bottom boxes) from 2014 to 2018 in fenced (F, gray dots) and unfenced (C, open dots) plots; error bars show \pm SE

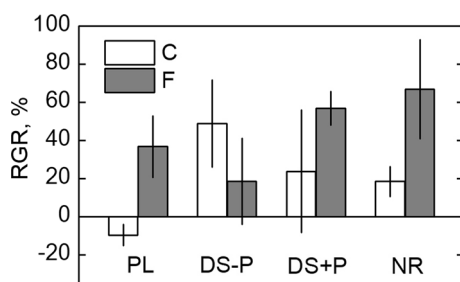
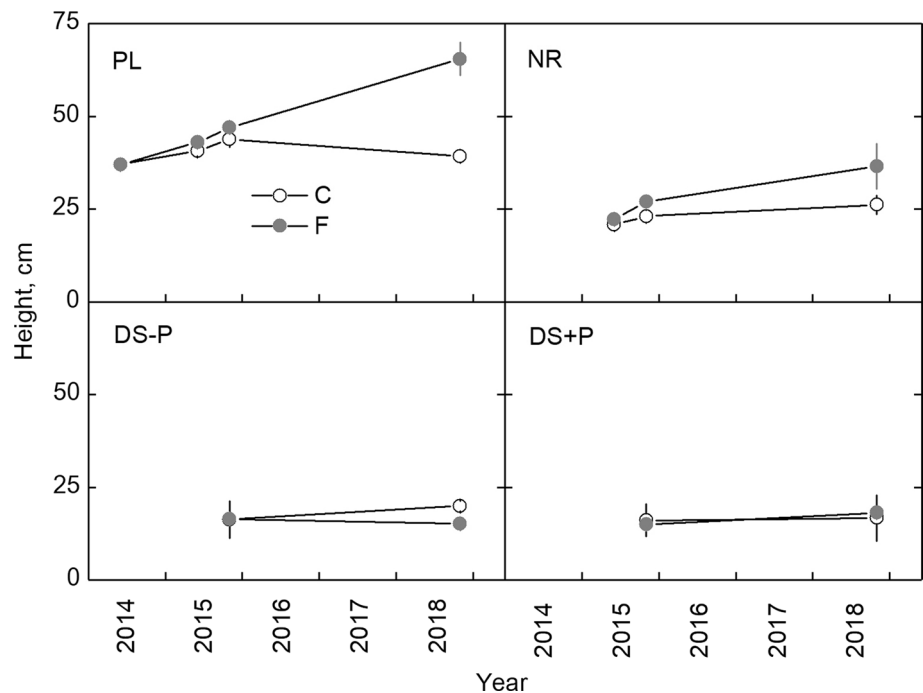


Fig. 3 Relative growth rate (RGR) between 2015 and 2018 of the five tallest seedlings per treatment plot following planting, direct seeding and natural regeneration in fenced (gray bars) and unfenced control plots (open bars) (mean \pm SE)

regeneration technique ($\chi^2=2.02$, $df=3$, $p=0.6$), nor the fencing–regeneration technique interaction ($\chi^2=4.26$, $df=3$, $p=0.2$) were significant.

Effect of fencing and regeneration technique on survival, establishment rate and recruitment rate

Survival in PL-seedlings decreased ($\chi^2=27.4$, $df=2$, $p<0.001$) so that survival was ca. 51% five growing seasons after planting, but there was no effect of fencing ($\chi^2=0$, $df=1$, $p=0.99$) on survival of these seedlings (Fig. 4). Across both DS treatments, the average establishment rate in October 2018 was 21%. However, for the DS-P treatment there were no significant effects of fencing or time, and no significant interaction between the two variables. In contrast, the DS+P treatment showed a significant interaction

between fencing and time ($\chi^2=6.86$, $df=1$, $p<0.01$). In October 2018, the establishment rate was higher in fenced plots than in unfenced plots (Tukey's post hoc test, $p<0.01$). From October 2015 to October 2018, we observed a slight trend of increased recruitment of naturally regenerated seedlings ($\chi^2=2.72$, $df=1$, $p=0.1$; Fig. 4). However, there was no effect of fencing on recruitment ($\chi^2=0.23$, $df=1$, $p=0.63$). In October 2018, there were on average 1.9 naturally regenerated seedlings per m^2 in our fenced and non-fenced experimental plots (data not shown).

Effect of regeneration technique on browsing frequency

Browsing damage from roe deer and hare was mainly observed in the unfenced plot. In May 2015, browsing frequency was higher in C compared to F plots ($F=48.7$, $df=1$, $p<0.01$), and with a significant interaction between fencing and regeneration technique: PL seedlings suffered more browsing than NR seedlings ($F=7.1$, $df=1$, $p<0.05$; Fig. 5). In October 2015, there was a similar but non-significant trend between C and F plots ($F=3.8$, $df=1$, $p=0.06$) but without any interaction or effect of regeneration technique. Browsing frequency was higher in May (on average 38%) compared to October 2015 (on average 11%). In the two first years (2014 and 2015), the lower stems parts of many seedlings were damaged by voles. In addition, we observed many small seedlings established from direct seeding (both inside and outside fences, and from both DS-P and DS+P treatments) that were clipped ca 1 cm above the ground, probably by voles.

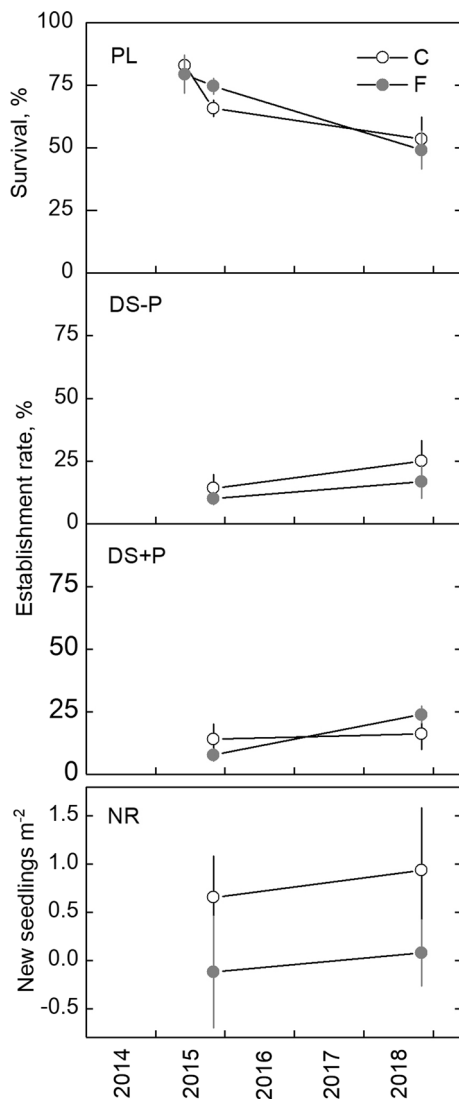


Fig. 4 Mean establishment success represented by different variables for each regeneration technique: survival percentage of planted seedlings (PL) from May 2015 to Oct 2018 (top box), establishment rate in Oct 2015 and 2018 following direct seeding in May 2015 (middle boxes, without and with acorn protection) and number of new naturally regenerated seedlings per square meter during the same period (bottom box). Gray dots show fenced plots and open dots represent unfenced control plots; error bars show standard errors. See Material and Methods for calculations

Throughout the monitoring period of this experiment, there was a high cover (81–90%) of ground vegetation in all plots (data not shown).

Regeneration costs

Irrespective of regeneration technique, costs per hectare increased substantially when fencing was included (Table 2). Planting bare-rooted seedlings inside a fence was the most expensive regeneration technique in our study, whereas

natural regeneration without fencing cost the least (i.e., no costs). The per-hectare cost of direct seeding without acorn protection or fencing was 28% of the cost of planting. However, when acorn protection devices were used, the costs increased to 78% that of planting.

Discussion

Our results indicate that fencing has a strong positive effect on height growth during the first five years after installation of the experiment, and we found similar trends for diameter growth and relative growth rate (Figs. 2 and 3). This is in line with several other studies on the subject in Europe and elsewhere (e.g. Jensen et al. 2012, Churki et al. 2016, Dey et al. 2019, Ramirez et al. 2020, Petersson et al. 2020, Barre et al. 2021). In the long run, however, the protective effect from fences can be complicated by competition from other woody vegetation (Leonardsson et al. 2015). Compared to oak seedlings, other woody and faster-growing species that are also protected from browsing inside the fences may then out-compete the young oaks. Thus, growth and survival can also be reduced inside fences. Therefore, and in addition to fencing, management interventions such as pre-commercial thinning may be needed, but in our case few naturally regenerated individuals of other woody species were present.

Although we tested the effect of fencing on height separately for each regeneration technique, our study indicated that the growth benefit of fencing was somewhat stronger for the planted seedlings, which were taller than the naturally regenerated and especially direct-seeded plants. In October 2018, the height differences between seedlings in fenced and unfenced plots were 26, 10 and 3 cm for planted, naturally regenerated and direct-seeded seedlings, respectively. Similar results for oaks were found by Kittredge and Ashton (1995) and Götmark et al. (2005) although their research included browsing from other ungulates. In addition to browsing by roe deer, browsing by moose (*Alces alces* L.) and to a lesser extent red and fallow deer (*Cervus elaphus* L., *Dama dama* L.) occurred in the study of Götmark et al. (2005). They found that young oaks shorter than 20 cm were much less frequently browsed than taller individuals. In addition, roe deer, as most cervid species, have been shown to preferentially browse near their shoulder's height, i.e., around 75 cm (Duncan et al. 1998; Nichols et al. 2015) which often results in the observation that small seedlings are less frequently browsed by cervids (Hartley et al. 1997; Renaud et al. 2003). This correlates with our findings in May 2015 of lower browsing frequencies on the small seedlings following natural regeneration (Fig. 5). One important implication from this could be that fencing is not necessary during the first few years of regeneration techniques that

Fig. 5 Mean browsing frequency on planted (PL), directly seeded (DS) and naturally regenerated seedlings (NR) in May (left box) and Oct (right box) 2015. The DS-P and DS + P seedlings were not yet established in May 2015, so they aren't shown in the first box. Fenced (gray) and unfenced control plots (open). Error bars show standard errors, and small letters indicate significant differences at $p < .05$

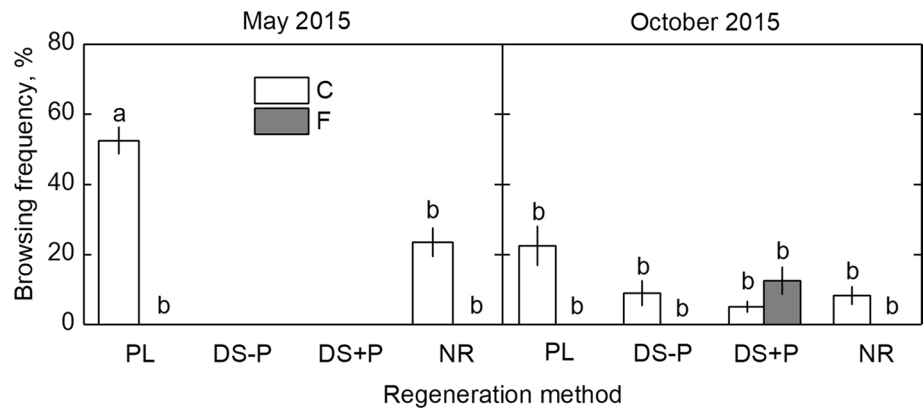


Table 2 Costs (euro ha⁻¹) in the various treatments and sub-treatments including plant and seed material, any acorn protection devices and fencing and labor costs for planting and direct seeding procedure. For planting and direct seeding, 2 800 seedlings or seeding points per hectare have been used for calculations. For description of treatments and costs, see text

Treatment	Sub-treatment			
	PL	DS - P	DS + P	NR
C	2 946	823	2 296	0
F	7 586	5 463	6 936	4 640

initially produce small seedlings, i.e., natural regeneration and direct seeding. However, more research is needed before any practical recommendations could be given.

In addition, and in line with previous research in the same region (Pettersson et al. 2020), more seedlings in our study seemed to have been browsed during the winter and spring (included in the May measurements) than in the summer and autumn (included in the October measurements). Short et al. (1975) found that the digestibility and nutrient content are optimal during the early spring, which might explain why deer preferentially browse deciduous shoots at that time. However, we only measured browsing frequency during two occasions in 2015, and therefore more observations are needed to support this result.

In contrast to seedling growth, there was little effect of fencing on survival of planted seedlings, establishment rate following direct seeding or on recruitment rate of new naturally regenerated seedlings (Fig. 4). Although oak seedlings in many places are preferentially browsed by ungulates, they are also considered browsing-tolerant because they can survive moderate browsing through re-sprouting (Harmer 2001; Bergqvist et al. 2018; Bobiec et al. 2018). Our experiment was, however, rather short (five years). In the long run, we could probably expect that browsing will reduce survival and establishment and ultimately prevent unprotected seedlings from growing into the overstorey (Churki et al. 2016,

Dey et al. 2019). Despite the fact that roe deer may eat large quantities of acorns (Barrere et al. 2020), there was no effect of fencing on the recruitment rate of naturally regenerated seedlings. However, deer mainly consume acorns placed above the soil surface (Garcia et al. 2002). In natural regeneration of oaks, scatter-hoarding animals are often responsible for the dispersal and burial of acorns, and buried acorns face less risk to be consumed by other animals, or to desiccate during dry weather (Watt 1919, Garcia et al. 2002, Bogdziewicz et al. 2020). This may explain why fencing had little effect in our study since small scatter-hoarding animals may search for food and bury acorns both inside and outside fences.

From the start of the experiment herbaceous vegetation cover was close to 90% in all treatments. Therefore, our results for growth, survival and establishment rates of oak seedlings are heavily influenced by interference from herbaceous vegetation. When oak seedlings of similar initial heights following planting and direct seeding are grown in treatments where herbaceous vegetation is controlled, and in relatively open conditions, they grow taller than in the present study (Davies 1985; Löff et al. 2004). The height of seedlings is, however, not the best indicator of biomass accumulation under these circumstances and most likely underestimates growth reductions due to competition. For example, open-grown oak seedlings tend to invest more resources in roots, branches and leaves compared to height (Jensen et al. 2011). Most likely, seedlings in all our study treatments would have been larger without competing herbaceous vegetation.

The survival rate of planted seedlings at the end of the experiment was only about 50% (Fig. 4). Similar results have been found in previous research when oak seedlings are planted into already established herbaceous vegetation (Löff et al. 2006). If some form of vegetation control had been applied, the survival would probably have been higher. Abundant natural ground vegetation may decrease soil water content and nutrient availability while exacerbating initial water stress that seedlings undergo following planting (Löff

et al. 1998). Thus, competing ground vegetation probably weakened the seedlings and partly explains the low survival even though precipitation during the first years following planting was normal. Furthermore, we observed extensive vole damage, possibly causing high mortality during the first years following planting. Earlier research on broadleaved seedling survival and establishment in herbaceous environments has shown that a substantial number of seedlings can be damaged or consumed by rodent herbivores, and thus disappear over time (Lüpke 1987; Manson et al. 2001; Hytönen and Jylhä 2005).

Similar to survival of planted seedlings, the number of established seedlings following direct seeding was rather low. Establishment rates following direct seeding vary due to differences in rodent populations (mice and voles) and the presence of habitats that provide them shelter (Birkedal et al. 2009, 2010). For example, removal rates of buried acorns by rodents correlate with the amount of herbaceous vegetation at the regeneration site (Villalobos et al. 2020). Since we had a high coverage of herbaceous vegetation, it is probable that many acorns were removed before they could germinate. Surprisingly, there was no effect of the acorn protection device. In contrast, Castro et al. (2015) and Leverkus et al. (2015) found that the same device reduced removal significantly to almost zero. Our establishment rates in both DS-treatments were, however, much influenced by the fact that many small seedlings established by direct seeding were clipped about 1 cm above the ground which even out any differences. This was probably caused by voles since dense herbaceous vegetation is a suitable habitat for voles which feed on plants, seeds and insects (O'Brien 1994, Manson et al. 2001). Especially during winter, they may feed on woody vegetation (Chitty et al. 1968). Therefore, the effect of acorn protection was negligible in this study. Most likely, the acorn protection device would have worked much better in combination with vegetation control or where herbaceous vegetation is not yet established.

What regeneration technique in this study was the most cost effective? (Table 2) When roe deer and hare populations cannot be reduced within a reasonable timeframe, it seems difficult to regenerate oak without fencing. In unfenced areas, seedling height growth was negligible in this study. Thus, and in this region, investing in fences is expensive but necessary as soon as seedlings reach browsing height. The per-hectare cost of direct seeding without acorn protection or fencing was 28% of the cost of planting. This is somewhat lower compared to figures in Grossnickle and Ivetic (2017). Cost comparisons can differ much depending on the amount of seedlings and acorns used for reforestation. For example and compared to our numbers, many more seedlings and seeding points are often used in central Europe, whereas there are normally much fewer in North America (Röhrig et al. 2006; Dey et al. 2008). In addition, cost comparisons

differ due to a number of other factors such as size of seedlings, type of fences and the regeneration conditions such as any need of site preparation and inclination in the terrain etc. Anyway, five years after the start of this experiment, in areas fenced to exclude browsers, planting, direct seeding (without an acorn protection device) and natural regeneration resulted in 1375, 467 and 6333 seedlings per ha, respectively. Not only did natural regeneration produce the highest density of seedlings, it had the lowest cost per ha of any treatment, making it by far the most cost-effective regeneration method. Since many seedlings and saplings eventually die for various reasons, it is important to start with many seedlings during regeneration of oak stands (Kohler et al. 2020). However, in our study the naturally regenerated seedlings were somewhat smaller than the planted ones, and clustered over the area, potentially prolonging the regeneration phase. In addition, where there is more competing woody vegetation, the planted seedlings would likely be more competitive in the beginning. Furthermore, the outcome of planting and direct seeding depend heavily on vegetation control measures. A small additional investment in, for example, mechanical site preparation, might have improved the planting and direct seeding methods.

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Author contributions ML initiated the study, led the evaluation together with JB and wrote the first draft of the manuscript. ML and LKP prepared material and collected data. JB performed the statistical analysis. All authors contributed to and discussed the previous versions of the manuscript. All authors read and approved the final manuscript.

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Compliance with ethical standards

Conflict of interest All authors declare that they have no conflict of interest.

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APPENDIX

B

BARRERE ET AL. 2021

This appendix presents the latest version of an article of science popularization written in French for the review *Biodiversité, des clés pour agir* (to be published in late 2021). It focuses on the two experimental studies presented in chapters 4 and 5.

La simulation d'abrutissement : un outil pour mieux comprendre l'influence des cervidés sur la régénération forestière.

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En 2011, le rapport sur l'état des forêts en Europe (FOREST EUROPE, UNECE FAO, 2011) classait les cervidés comme la 3ème principale menace au renouvellement durable des forêts européennes, derrière les insectes et les pathogènes. Les cervidés abrutissent les jeunes plants et en France, le niveau des dégâts constatés sur les jeunes peuplements remet en cause le renouvellement de nombreuses essences d'intérêt économique, et écologique. Dans ce contexte, l'OFB étudie en collaboration notamment avec l'Office National des Forêts (ONF) les interactions entre la régénération forestière et les populations de grands herbivores afin d'appréhender du mieux possible les conséquences de la hausse des populations pour la dynamique forestière. Dans cet article, nous présentons une méthode de simulation de l'abrutissement – section artificielle de la plante combinée à l'application de salive animale – qui peut s'avérer particulièrement pertinente pour répondre à certaines questions de recherche sur les conséquences de l'abrutissement sur la régénération forestière.

B.1 Pourquoi et comment étudier l'influence des cervidés sur la régénération forestière ?

B.1.1 La question de l'équilibre sylvo-cynégétique en France

Depuis plusieurs décennies, les populations de cervidés augmentent de manière considérable en France. L'essor des principales espèces de cervidés s'observe notamment par une hausse marquée des prélèvements de chasse, qui ont été multipliés par 9 pour le chevreuil (*Capreolus capreolus*) (Fig. B.1) et par 8 pour le cerf (*Cervus elaphus*) sur les 40 dernières années (Réseau Ongulés Sauvages OFB/FNC/FDC). Bien que la relation ne soit pas linéaire, on peut aujourd'hui affirmer que la hausse des prélèvements observée reflète une augmentation réelle et notable de ces populations (Kahlert *et al.*, 2015). Ce phénomène, qui suit une tendance globale dans la majorité des pays de l'hémisphère Nord (Côté *et al.*, 2004), s'explique entre autres par la mise en place de mesures de gestion en faveur de ces espèces (plans de chasse, réintroductions, restauration d'habitats, nourrissage), ainsi que par une expansion de leur aire de répartition notamment permise par la déprise agricole.



Figure B.1: Le chevreuil est l'une des principales espèces de grands herbivores en France.
Photo : J. Barrere

Le maintien d'une faune sauvage riche et diversifiée est largement encouragée par les ac-

teurs du monde de la chasse, une activité de loisir qui compte 1.03 millions de pratiquant en France (FNC 2020). La densité et la diversité des populations de grand gibier contribue en effet fortement à l'attractivité d'un territoire de chasse, ainsi qu'aux ressources financières des propriétaires de territoires de chasse. Cependant, la hausse des populations de cervidés s'accompagne aussi d'une augmentation des dommages causés par ces espèces sur les peuplements forestiers, particulièrement dans les stades jeunes. La consommation des graines et des jeunes plants, ou encore l'écorçage des arbres adultes, sont les dégâts usuels, dont l'intensité et la fréquence augmentent avec les populations, allant parfois jusqu'à compromettre le renouvellement d'un peuplement. La présence d'une densité importante de cervidés peut notamment induire une réduction du taux de survie et de la vitesse de croissance des semis de l'essence « objectif » (*i.e.* l'essence que l'on souhaite majoritairement régénérer), deux indicateurs utilisés par les forestiers pour juger l'avancée de la régénération. Sur le long terme, ces effets peuvent aboutir à un allongement des durées de régénération de plusieurs années, ainsi qu'à une réduction importante de la densité de semis par rapport aux objectifs fixés par les forestiers. Par ailleurs, les mesures pour faire face à une pression d'herbivorie importante (*e.g.* pose d'enclos, plantations compensatoires) représentent un coût additionnel conséquent. D'un point de vue économique, la présence de fortes populations de cervidés peut ainsi fortement compromettre la rentabilité des investissements forestiers, d'où la nécessité de trouver un équilibre entre activités cynégétiques et sylvicoles. L'article L425-4 du code de l'environnement définit ainsi l'équilibre sylvo-cynégétique comme « la compatibilité entre d'une part la présence durable d'une faune sauvage riche et variée et, d'autre part, la pérennité et la rentabilité économique des activités sylvicoles ». La mise en place de mesures de gestion sylvicoles et cynégétiques efficaces pour se rapprocher de cet équilibre rend ainsi indispensable la réalisation d'études scientifiques pour mieux comprendre les interactions écologiques en jeu.

B.1.2 Quelques réponses apportées par la recherche

La majorité des études scientifiques s'accordent sur l'idée que des surdensités de cervidés comme observé dans des territoires fermés et sans prédateurs comme les îles d'Anticosti (autour de 16 cerfs de Virginie.km⁻²) ou d'Haida Gwaii (jusqu'à 33 cerfs à queue noire.km⁻²) au Canada sont incompatibles avec un renouvellement forestier dans des conditions satisfaisantes (Potvin *et al.*, 2003; Stroh *et al.*, 2008). A des densités intermédiaires, les conséquences de la présence de cervidés sur le renouvellement forestier sont plus contrastées, et dépendent fortement du contexte biotique (*e.g.* espèces animales et végétales présentes) et abiotique (*e.g.* conditions climatiques ou édaphiques). Il existe en particulier de fortes différences entre les espèces d'arbres en terme d'appétence pour les herbivores, et en terme de tolérance à l'abrutissement. Du fait de ces différences, les essences ne sont pas impactées de la même façon par les cervidés.

A des densités intermédiaires, les cervidés contraignent principalement le renouvellement des essences les moins tolérantes à l'abrouissement, et/ou les plus appétentes. Dans les forêts françaises, de nombreuses essences à fort intérêt sylvicole telles que l'érable (*Acer pseudoplatanus*), le sapin (*Abies alba*) ou le chêne (*Quercus sp*) sont ainsi particulièrement sensibles à l'abrouissement. En contexte de forêts mélangées, de nombreuses études ont ainsi pu mettre en évidence que la présence de cervidés pouvait induire une modification du cortège d'essence dans le sens d'un remplacement de l'essence objectif par des essences moins touchées par l'abrouissement, mais à moindre valeur sylvicole. A titre d'exemple, dans les sapinières-pessières de moyenne altitude, la pression d'abrouissement avait causé le remplacement progressif du sapin par l'épicéa (*Picea abies*) (?), une essence certes moins appétente mais moins viable sur le long terme du fait, entre autres, de sa forte sensibilité aux scolytes et à l'écorçage.

B.1.3 Vers une évolution et une diversification des méthodes de recherche

La majorité des études conduites sur l'influence des cervidés sur la végétation forestière utilisent des dispositifs d'enclos-exclos, c'est-à-dire la comparaison de la dynamique de la végétation dans des parcelles clôturées et dans des parcelles témoins accessibles aux cervidés (Mârell *et al.*, 2012). Ce type d'étude, utilisé depuis plusieurs décennies partout dans le monde, est particulièrement pertinent pour apporter des réponses locales (ou générales si répliqués à suffisamment grande échelle) sur les effets de l'abrouissement sur la végétation et est aujourd'hui encore largement mobilisé en France sur la question de l'interaction Faune-Flore, et plus particulièrement sur l'équilibre sylvo-cynégétique.

Les récentes innovations technologiques et l'avancée des travaux de recherche permettent aujourd'hui de creuser de nouvelles questions scientifiques sur la question de l'équilibre sylvo-cynégétique. A titre d'exemple, l'ADN environnementale (ADN collecté dans l'environnement plutôt que directement sur un organisme) permet, à partir de la salive déposée sur les plants abrouis, d'identifier quelle espèce de cervidé a abroui une plante donnée (van Beeck Calkoen *et al.*, 2019). Similairement, la comparaison de la végétation dans des exclos et des enclos sélectifs (enclos ne laissant entrer qu'une seule espèce d'herbivore) peut permettre d'isoler les effets des différentes espèces de cervidé sur la végétation (Saïd *et al.*, 2019). Concrètement, ces deux approches peuvent permettre l'identification des espèces de cervidés causant le plus de dommages aux jeunes peuplements, et ainsi d'adapter les tableaux de chasse pour réguler en priorité ces espèces.

Une autre approche de plus en plus en vogue ces dernières années est l'utilisation de traits

fonctionnels qui se définissent comme toute caractéristique morphologique, phénologique ou physiologique mesurable à l'échelle de l'individu. Les traits fonctionnels sont utilisés pour décrire les stratégies des plantes en terme de reproduction, de dispersion ou d'allocation des ressources (Wright *et al.*, 2004). A titre d'exemple, la taille et la masse des graines permet de discerner les espèces produisant beaucoup de descendants avec une faible probabilité de survie, ou un faible nombre d'individus avec une forte probabilité de survie. De récentes études ont ainsi pu décrire un certain nombre de traits fonctionnels permettant de décrire la stratégie des différentes espèces de plantes pour faire face à l'herbivorie (tolérance vs résistance) (Carmona *et al.*, 2011). L'étude de l'influence de l'abrouissement sur les traits fonctionnels d'une espèce permet aussi de caractériser sa capacité à supporter et réagir suite à cette perturbation. L'étude de ce type de mécanisme peut ainsi permettre d'identifier le potentiel des différentes espèces d'arbre à faire face à une pression d'abrouissement croissante.

Que ce soit pour l'étude des traits fonctionnels, ou plus généralement pour des études à l'échelle de l'individu, la principale limite des expériences en conditions d'herbivorie réelle est la difficulté de maîtriser la fréquence, le timing ou encore l'intensité de l'abrouissement. Cette nécessité d'appliquer un traitement d'abrouissement standardisé pour ce type d'étude a ainsi amené le développement de la méthode de la simulation d'abrouissement.

B.2 La simulation d'abrouissement

B.2.1 Apports par rapport aux autres approches existantes

Les cervidés peuvent abrouiter des plants tout au long de l'année et d'un plant à l'autre, la quantité de tissu prélevée est variable mais difficilement mesurable. Ainsi, la simulation d'abrouissement se définit comme l'imitation d'une action d'herbivorie par une section artificielle du plant, pouvant être combinée ou non à une application de salive au niveau de la zone où la plante a été sectionnée (Figure B.2). Cette approche est notamment utilisée pour l'étude des réponses des plantes à l'abrouissement à l'échelle de l'individu, et a été inventée en raison de plusieurs avantages par rapport à l'observation de l'abrouissement naturel (Baldwin, 1990). Elle offre la possibilité de connaître et de contrôler à la fois le timing et la quantité de tissu prélevée. Cela représente de plus un gain de temps conséquent dans la mesure où, en situation d'herbivorie réelle, il n'y a aucune garantie que les cervidés viennent rapidement consommer les plants suivis. Enfin, la simulation d'abrouissement permet de limiter les effets confondants liés au choix de l'herbivore. A titre d'exemple, si un cervidé ne consomme que les plants appartenant à une certaine classe de hauteur, il est impossible de dissocier les effets de la hauteur et de l'abrouissement.

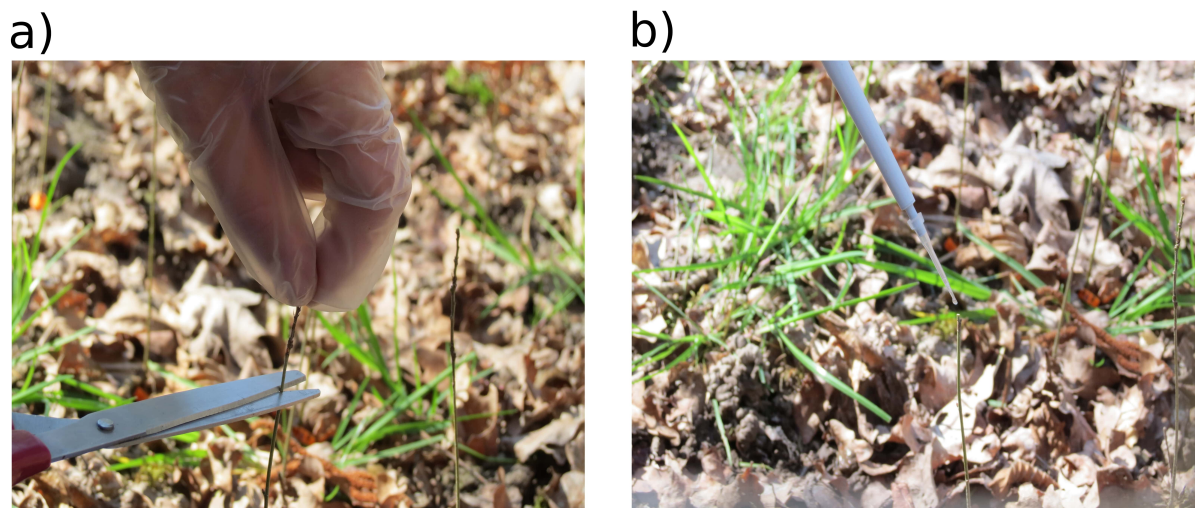


Figure B.2: Application du traitement d'abroustissement simulé sur un jeune semis de chêne à la Fondation Pierre Vérots : a) section de 5 cm de la tige apicale et b) application de 5 μ L de salive de chevreuil. Photo : T. Beroud

Pour les études présentées dans la suite de cet article, les échantillons de salive ont été récoltés sur des chevreuils capturés lors des campagnes de capture organisées chaque hiver par l'OFB sur le Territoire d'Etude et d'Expérimentation (TEE) de Trois-Fontaines (51). La salive peut être récoltée en plaçant des cotons conçus pour le prélèvement de salive (125mm SalivaBio's Children's Swab, Salimetrics) dans la bouche de l'animal durant 30 secondes à 1 minute (selon la fréquence de mastication de l'animal) (Figure B.3). Le coton est ensuite centrifugé pour en extraire la salive qui est congelée jusqu'à utilisation pour le traitement d'abroustissement simulé.

B.3 Deux exemples d'application sur le modèle chêne-chevreuil

En France, les chênes sessile (*Quercus petraea*) et pédonculé (*Quercus robur*) – ci-après dénommés « Chêne » - sont ancrés dans le paysage forestier français (23% du volume de bois sur pied total d'après l'IGN). Ces deux essences sont particulièrement appréciées pour la qualité de leur bois et occupent ainsi une place de choix dans la filière sylvicole française : en 2017, le Chêne représentait 40% des recettes de vente de l'ONF. Par ailleurs, de nombreuses études ont mis en lumière le rôle écologique de ces espèces en tant qu'habitat ou ressource pour des populations d'oiseaux, d'invertébrés, de lichens ou de champignons. La régénération du chêne représente donc un enjeu considérable à la fois d'un point de vue écologique, économique, et social.



Figure B.3: Prélèvement de salive sur un chevreuil capturé au TEE de Trois Fontaines.
Photo : J. Barrere

Le chevreuil est présent dans l'intégralité du territoire français. Etant particulièrement sélectif par rapport à d'autres espèces de cervidés, son alimentation se base en grande partie sur les rameaux, bourgeons et feuilles des jeunes ligneux et semi-ligneux. Les jeunes semis de Chêne font donc intégralement partie du régime alimentaire de cette espèce. Les interactions entre l'essence Chêne et le chevreuil sont ainsi au cœur des travaux de recherche de l'OFB sur l'équilibre sylvo-cynégétique.

B.3.1 Impact de l'abrouissement du chevreuil sur le taux de survie d'une cohorte de semis

En forêt tempérée, la fin de l'hiver et le début du printemps correspondent à la période à laquelle les jeunes ligneux sont le plus consommés par les cervidés. C'est à cette période, avant le flush de croissance, que la teneur en nutriments et la digestibilité des tiges sont les plus élevées: les ligneux constituent alors une source d'alimentation de bonne qualité. Après la première année de croissance durant laquelle les semis peuvent s'appuyer sur les réserves de la graine, les jeunes ligneux sont particulièrement vulnérables car en plus d'être fréquemment abrouistés, ils doivent faire face à une forte compétition avec les plantes voisines pour les ressources et ne disposent que de très peu de réserves pour se défendre contre les herbivores. Sous des densités d'herbivores importantes, le succès de la régénération d'une essence va donc être largement conditionné par sa capacité à atteindre une hauteur suffisante pour échapper à la dent du gibier.

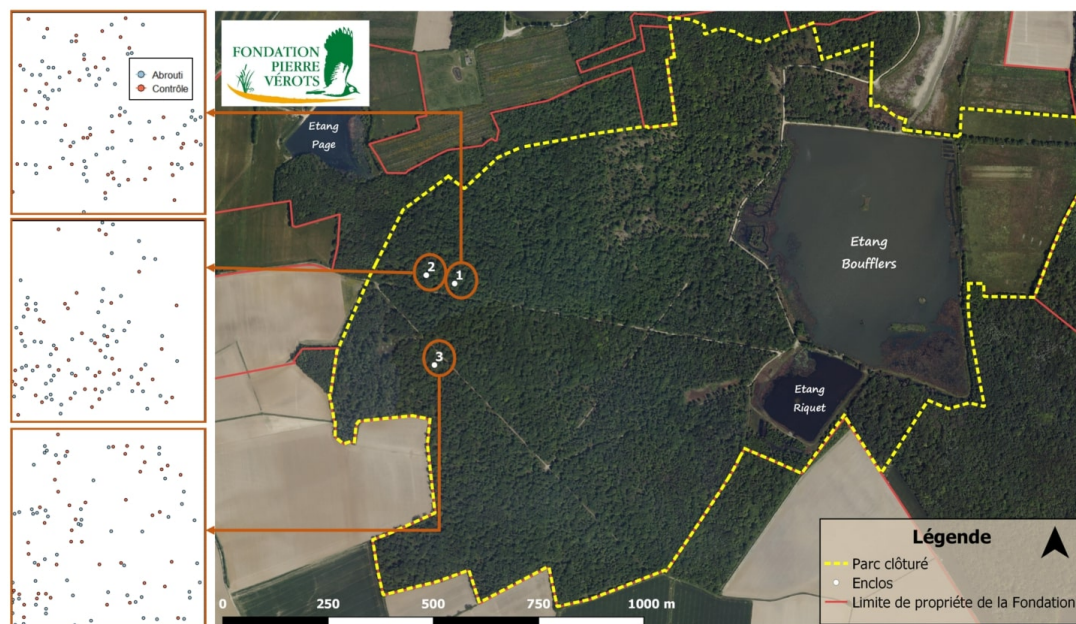


Figure B.4: Localisation des 3 enclos au sein du parc clôturé de la Fondation Pierre Vérots, et répartition spatiale des 100 semis sélectionnés dans chaque enclos.

Pour comprendre dans quelle mesure un épisode d'abrutissement par le chevreuil affecte la croissance et la survie de jeunes semis de Chêne, nous avons mis en place une expérimentation à la Fondation Pierre Vérots (cf. encadré B.1). Dans ce territoire, pendant l'hiver 2018/2019, nous avons sélectionné 3 sites d'une surface variant entre 12 et 17 m² abritant une forte densité de semis de chêne âgés d'un an. Nous avons délimité ces 3 sites par des clôtures permettant de protéger les semis d'un abrutissement naturel par les cervidés présents sur le territoire. Au sein de chaque enclos, nous avons identifié et cartographié 100 semis répartis de manière homogène dans l'enclos et présentant des caractéristiques morphologiques comparables (taille entre 18 et 30 cm de haut) (Figure B.4). Nous avons arraché tous les autres semis qui étaient présents dans l'enclos. Les 100 semis par enclos ont été répartis en deux modalités : 50 semis recevaient un traitement d'abrutissement simulé à la fin de l'hiver (modalité « Abroutis »), et 50 semis ne subissaient aucun traitement (modalité « Contrôle »). Tous les deux mois de mars à décembre 2019, nous avons suivi la survie des semis, et leur hauteur.

Du fait d'une faible disponibilité en lumière combinée à une sécheresse importante durant l'été 2019, la croissance des semis a été quasiment nulle, confirmant ainsi la difficulté des semis de chêne à gagner en hauteur après la première année lorsque les conditions sont peu favorables. Le traitement d'abrutissement a ainsi réduit la croissance des semis de Chêne (Figure B.6.a) qui, contrairement à d'autres espèces d'arbres, n'a ici pas montré de croissance compensatoire pouvant compenser la perte de tissu due à l'herbivorie. Ces conditions peu favorables ont aussi entraîné une mortalité importante des semis (taux de survie après un

an de 40% pour les semis contrôle, 20% pour les semis abroustis) (Figure B.6.b). Dans chacun des 3 enclos, le traitement d'abroustissement a réduit de moitié le taux de survie, confirmant ainsi que l'abroustissement sur de jeunes semis peut constituer un facteur de mortalité non négligeable en conditions édaphiques et climatiques contraignantes.



Figure B.5: Jeune semis de chêne suivi dans le cadre de l'étude à la Fondation Pierre Vérots.
Photo : J. Barrere

Dans le contexte de la régénération du Chêne, ces résultats confirment que l'espèce est fortement sensible à l'abroustissement durant ses premiers stades de vie. Cette perturbation réduit à la fois la croissance et la survie des semis. Plus généralement, ce protocole en conditions de régénération naturelle combinant protection de l'abroustissement naturel et simulation d'herbivorie illustre le potentiel de ce type d'expérimentation pour identifier dans un contexte donné l'influence de l'abroustissement sur la régénération d'une essence indépendamment des autres facteurs environnementaux.

B.3. Deux exemples d'application sur le modèle chêne-chevreuil

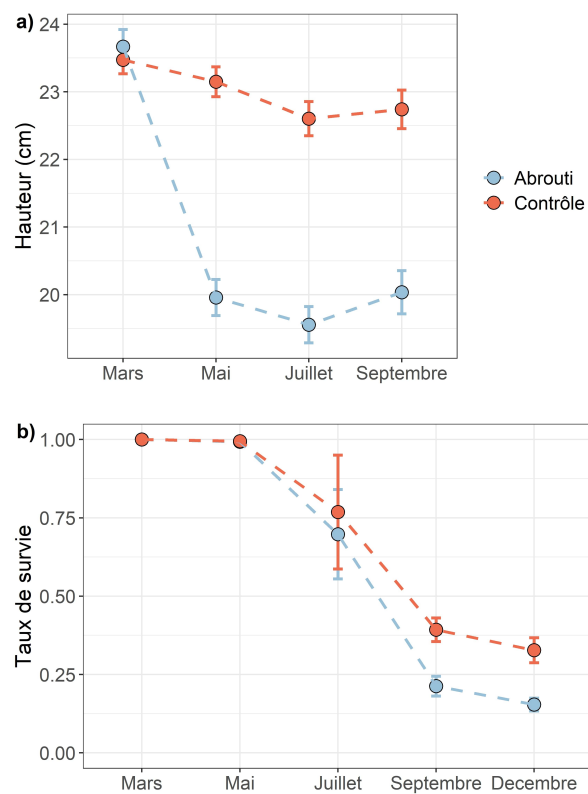


Figure B.6: Evolution a) de la hauteur et b) du taux de survie (moyenne \pm erreur standard) des semis dans les 3 enclos suivis à la Fondation Pierre Vérots.

Encadré B.1. Présentation du site d'étude

La Fondation Pierre Vérots (4°55' 30'E, 45°57' N), située au sud-ouest du plateau de la Dombes (01), est propriétaire et gestionnaire d'un domaine de plus de 300 ha (dont un parc clôturé de 148 ha) dédié à la conservation et à l'étude de la faune et de la flore. Le domaine est constitué de 3 types d'habitats principaux : des prairies et friches, des étangs et une partie boisée (figure ci-dessous). La partie forestière est une futaie irrégulière de chêne pédonculé, dans laquelle on trouve aussi en quantité importante d'autres espèces de feuillus telles que le tremble (*Populus tremula*), l'aulne (*Alnus sp*), le bouleau (*Betula pubescens*), et le charme (*Carpinus betulus*). La forêt est actuellement laissée en libre évolution.



Aperçu aérien du domaine de la Fondation Pierre Vérots. Photo : P. Grandjean

L'étude décrite dans cet article a été réalisée dans la partie clôturée du domaine, qui abritait au début de l'expérimentation une population de daims (*Dama dama*) d'une dizaine d'individus. A la fin de l'expérience, en décembre 2019, la population avait été réduite à un unique individu suite à la décision de la Fondation de remplacer cette population par des chevreuils, seule espèce de cervidé naturellement présente en Dombes. La fin de l'expérimentation a donc coïncidé avec l'introduction d'une dizaine de chevreuils, issus du TEE de Trois-Fontaines (51) et de la Réserve Biologique Intégrale de Chizé (79) dans le but de maintenir une pression d'herbivorie sur la végétation.

B.3.2 Conséquences d'un épisode d'abrouissement sur les traits fonctionnels

Pour faire face à l'herbivorie, les plantes peuvent utiliser des stratégies diversifiées, réparties le long d'un gradient allant de la tolérance (l'herbivorie n'affecte pas ou peu le fonctionnement de la plante) à la résistance (la plante investit dans les défenses pour éviter l'herbivorie) (Hermes & Mattson, 1992; Wright *et al.*, 2004). Plusieurs études ont ainsi identifié un certain nombre de traits fonctionnels qui permettent de caractériser la stratégie d'une espèce de plante donnée. A titre d'exemple, une forte teneur en métabolites secondaires (*e.g.* tannins, alcaloïdes) dans les feuilles ou la présence d'épines indiquent une forte investissement des ressources dans la défense et donc une stratégie de résistance. Au contraire, une faible teneur en fibres dans les feuilles, ou un ratio surface foliaire / masse foliaire sèche (SLA) élevé traduit un investissement dans la production de tissu, et donc dans la tolérance à l'herbivorie. Pour un espèce donnée, l'étude de la variation de ces traits suite à un épisode d'herbivorie permet de mieux comprendre la stratégie de cette espèce, et d'identifier sa capacité à s'adapter à cette perturbation en modifiant ses patrons d'allocation des ressources.

Afin d'étudier la stratégie d'investissement des ressources du Chêne suite à un abrouissement par le chevreuil, une expérimentation a été conduite à la pépinière expérimentale de l'ONF située à Saint Paul-lez-Durance (13). Cette expérience inclut 150 semis de chêne pédonculé, répartis dans 5 traitements selon la durée du suivi (1 ou 2 ans), et l'application d'un traitement d'abrouissement simulé (Tableau B.1).

Table B.1: Nombre de semis, durée de suivi et application du traitement d'abrouissement pour les 5 traitements inclus dans l'expérience en pépinière. Le nom du traitement indique pour la ou les années de suivi si le plant a subi (*T*) ou non (*C*) le traitement d'abrouissement (par exemple pour C_1T_2 : pas de traitement l'année 1, traitement l'année 2).

Nom du Traitement	Nombre de semis	Durée de suivi	Application du traitement d'abrouissement simulé	
			Année 1	Année 2
C_1	30	1 an	Non	-
T_1	30	1 an	Oui	-
C_1C_2	30	2 ans	Non	Non
T_1T_2	30	2 ans	Oui	Oui
C_1T_2	30	2 ans	Non	Oui

L'expérience a débuté en hiver 2018/2019 et sera clôturée fin 2020. Pour les traitements C_1 et C_1C_2 en 2019 et les traitements T_1T_2 et C_1T_2 en 2020, nous avons appliqué les traitements d'abrouissement simulé à la fin de l'hiver. Durant la phase de croissance des semis (de Mars à Octobre) nous avons mesuré tous les 1 à 2 mois la hauteur, le diamètre et le nombre de ramifications des semis. L'été 2019 pour les traitements C_1 et T_1 , et l'été 2020 pour les

autres traitements, nous avons prélevé l'intégralité des feuilles afin de mesurer des traits relatifs à l'investissement dans la croissance (SLA, teneur en chlorophylle et en azote) et des traits relatifs à l'investissement dans la défense contre l'herbivorie (teneur en fibres). Les traits chimiques ont été mesurés par la méthode de la Spectroscopie en Proche Infra-Rouge (SPIR) au CIRAD de Montpellier.

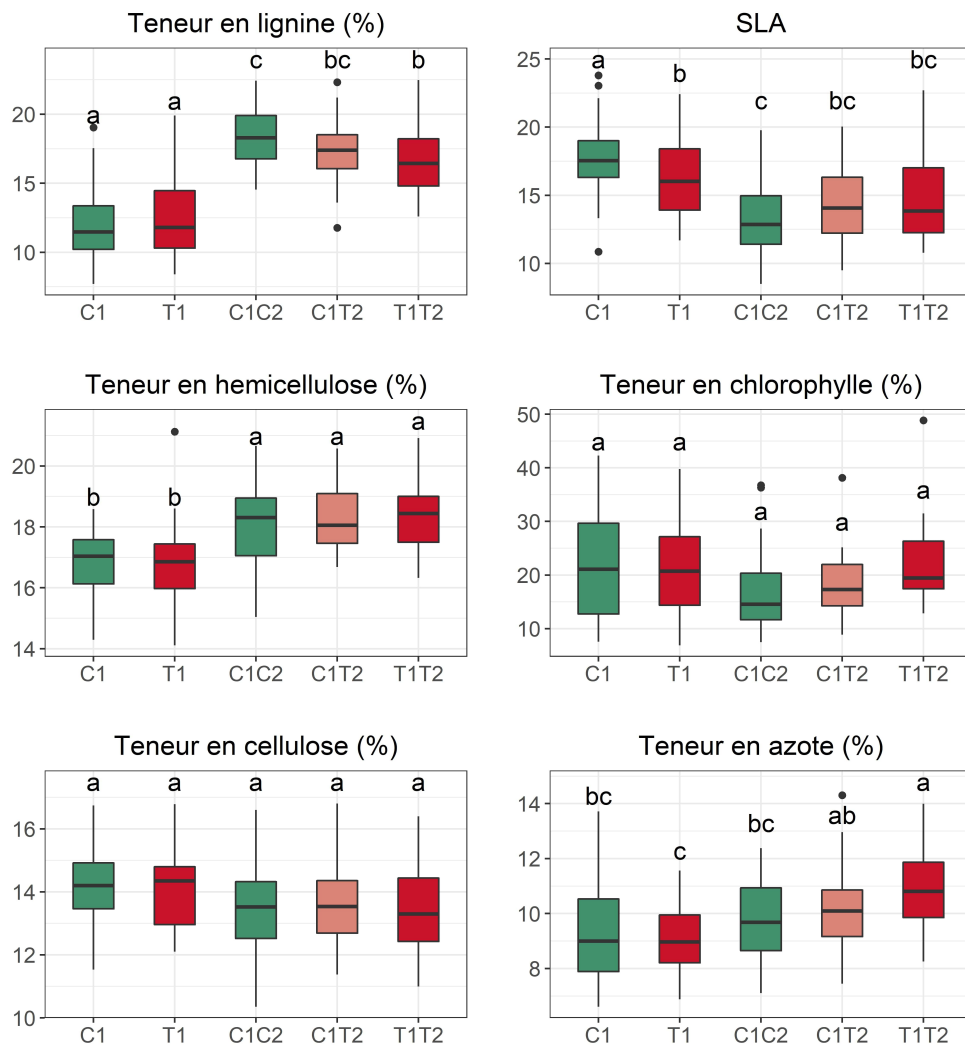


Figure B.7: Diagramme en boîte à moustache des valeurs de traits mesurées sur les plants en pépinière par traitement (cf. tableau B.1). Deux traitements sont significativement différents lorsqu'ils n'ont aucune lettre en commun. Les couleurs vert, rouge clair et rouge signifient respectivement non abrouiti, abrouiti une année sur deux, et abrouiti à chaque année de suivi.

Le suivi de la morphologie des semis a permis de montrer que l'abrouitissement réduit la hauteur, le diamètre et le nombre de ramifications des semis, en particulier pour les semis de petite taille. A l'heure de l'écriture de cet article, nous ne disposons que de résultats préliminaires des analyses SPIR. Peu de différences de traits sont observées la première an-

née de l'expérimentation (traitements C_1 et T_1) (Figure B.7). En revanche, la 2^{ème} année, les plants ayant été abrouvés ($T_1 T_2$) ont présenté une teneur en lignine plus faible que les plants non abrouvés ($C_1 C_2$), et une teneur en azote et une SLA plus élevées (tendance non significative pour ce dernier trait). Ces premiers résultats semblent montrer qu'un abrouvage répété tend à augmenter l'investissement de la plante dans les traits relatifs à la croissance (SLA, teneur en azote), au détriment des traits relatifs à la protection contre les herbivores (lignine).

Le fait que l'abrouvage par le chevreuil augmente l'investissement des ressources de la plante dans la croissance au détriment de la défense structurale montre ainsi une certaine capacité d'adaptation du Chêne qui est capable de modifier ses patrons d'allocation des ressources suite à cette perturbation. Ce résultat confirme aussi que la stratégie du Chêne s'apparente plutôt à de la tolérance qu'à de la résistance. Le suivi de croissance dans ces deux études montre cependant que malgré sa capacité d'adaptation, le Chêne n'est pas capable de compenser complètement la perte de hauteur due à l'abrouvage, ce qui peut avoir pour conséquence, sur le long terme un retard de croissance de plusieurs années du fait de la présence de cervidés.

B.4 Conclusion

Ces deux études ont permis d'illustrer une partie des possibilités offertes par la méthode de la simulation d'abrouvage. Dans le cadre de l'interaction entre l'essence Chêne et le chevreuil, nous avons ainsi pu mesurer la réduction des taux de croissance et de survie de jeunes semis de Chêne induite par l'abrouvage, et relier ces observations à la stratégie d'allocation des ressources de cette espèce. Il est toutefois important de préciser que la simulation d'abrouvage ne doit pas se soustraire à des études populationnelles de type enclos-exclos qui permettent de prendre à compte l'ensemble des effets que peut avoir l'animal sur la végétation forestière (consommation des autres espèces végétales, piétinement, fertilisation du sol via dépôt de fèces, dispersion de graines, etc.). Cette approche représente toutefois une solution robuste pour répondre à diverses questions de recherches spécifiques sur la réponse individuelle d'une plante à un épisode d'abrouvage, comme illustré dans les deux exemples présentés dans cet article.

B.5 Remerciements

Nous remercions chaleureusement la Fondation Pierre Vérots de nous avoir offert la possibilité de conduire cette étude sur leur territoire, et tout particulièrement Jean-Philippe

Rabatel qui aura grandement contribué à la mise en place de l'expérimentation. Nos remerciements vont aussi à toute l'équipe de la pépinière ONF de Saint Paul-lez-Durance (Patrice Brahic, Jérôme Reilhan, Baptiste Delor et Marie De Castro), ainsi qu'à l'équipe du CIRAD de Montpellier (Denis Bastianelli et Elodie Baby) pour leur contribution aux analyses SPIR.

Résumé

Les cervidés ont vu leur abondance et leur distribution spatiale augmenter fortement depuis les dernières décennies, en France, et plus généralement à l'échelle de l'hémisphère Nord. Si ces espèces jouent un rôle clé dans le fonctionnement des écosystèmes forestiers, le niveau actuel des populations compromet le processus de régénération forestière de certaines essences cruciales pour la filière sylvicole telles que les chênes sessile et pédonculé (*Quercus robur* et *Q. petraea*). L'objectif de cette thèse est de quantifier et décrire les mécanismes sous-jacents de la contrainte exercée par les cervidés sur la régénération et d'identifier dans quelle mesure certaines opérations sylvicoles (coupe, dégagement et pose d'enclos) influencent cette contrainte. L'analyse de la composition de panes de cerf et de chevreuil sur le site de La Petite Pierre (Vosges) a permis de montrer que les glands de chêne représentaient une ressource significative dans le régime alimentaire de ces deux espèces, mais que leur consommation de gland saturait les années de forte fructification. Par des approches expérimentales, nous avons mis en évidence que l'abrutissement de la pousse apicale réduisait toujours la croissance en hauteur des semis que ce soit en condition de terrain, ou en pépinière, et que ce phénomène s'expliquait par une faible plasticité d'allocation des ressources pour compenser la perte de tissu. L'analyse des résultats d'un réseau d'enclos-exclos répartis sur plusieurs sites en France et en Suède a permis de montrer que la coupe d'arbre adulte pour augmenter l'ouverture de la canopée accentuait l'effet négatif des cervidés sur la croissance et la survie de jeunes semis de chêne, via une plus forte fréquentation des cervidés dans les patches de régénération ouverts. Enfin, suite à l'implémentation du processus d'herbivorie dans un modèle de dynamique forestière (bibliothèque Régénération de CAPSIS), j'ai effectué des simulations suggérant que sous une forte pression d'herbivorie, des opérations de dégagement moins fréquentes et maintenant des espèces accompagnatrices appétentes comme le charme permettrait de réduire l'influence négative des cervidés sur la croissance du chêne. En conclusion, les résultats de cette thèse étayent l'hypothèse que les cervidés représentent une contrainte significative pour le processus de régénération du chêne, mais suggère qu'une gestion de la végétation de sous-bois adaptée permettrait de réduire cette contrainte et de se rapprocher d'un équilibre plus durable entre faune sauvage et activités sylvicoles.

Mots-clés : régénération forestière, herbivorie, chêne, cerf, chevreuil.

[A noter qu'un résumé de 10 pages en Français est inclu à la fin du manuscrit, chapitre 9, page 203]

Abstract

The abundance and spatial distribution of cervids have drastically increased in France, and more generally in the Northern hemisphere over the last decades. These species play a crucial part in the functioning of forest ecosystems, but the current level of their populations compromises the process of forest regeneration for many tree species of crucial importance such as pedunculate and sessile oak (*Quercus robur* et *Q. petraea*). The objectives of this thesis are to quantify and unravel the mechanisms underlying the constraint exerted by cervids on oak regeneration through the consumption of acorns, of oak saplings and of admixed understory species, and (ii) to identify how specific forest management operations (i.e. fencing, felling, and clearing) can limit or enhance this constraint. The analysis of a long-term dataset of red and roe deer rumen content sampled in the study site of La Petite Pierre (Northeastern France) showed that acorns represented a significant resource in the diet of these two species, but that their acorn consumption saturated years of high fructification. Using experimental approaches, we showed that simulated deer browsing on the apical shoot systematically reduced oak sapling height growth both in situ and ex situ, and this was explained by a relatively poor plasticity in resource allocation following browsing to compensate for the loss of tissues. The analysis of a network of fenced-undefended plots located in several sites in France and in Sweden showed that felling to increase canopy openness enhanced the negative effect of cervids on oak sapling growth and survival through a higher frequentation of cervids under open canopies. Lastly, after implementing the process of herbivory in a forest dynamic model (i.e. Regeneration library of CAPSIS modelling tool), I conducted simulations that suggested that under a high browsing pressure, less frequent clearing operations maintaining highly palatable sapling species such as hornbeam could reduce the negative influence of cervids on oak regeneration. To conclude, this thesis results confirm that cervids exert a significant constraint on the process of oak regeneration, but also suggest that adapted management of the understory vegetation could reduce this constraint and contribute to restore a balance between wildlife and silvicultural activities.

Key-words : Forest regeneration, herbivory, oak, red deer, roe deer.

