The European bison's, *Bison bonasus*; impact on pedunculate oak and Norway spruce in Almindingen on Bornholm

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Abstract

A herd of European bison (*Bison bonasus*) was reintroduced to the Danish nature in 2012 on Bornholm in Almindingen, which is the fifth largest, and least fragmented, forest in Denmark. The bark stripping behaviour of the herd was analysed by the Danish Nature Agency in 2014 and pedunculate oak (*Quercus robur*) and Norway spruce (*Picea abies*) were found to be the species with the highest frequency of damaged trees. Both pedunculate oak and Norway spruce are economically valuable for their forestry. In this study, the research question involved: Does the European bison show a preference for bark stripping of a specific size of pedunculate oak and Norway spruce? Where are the wounds located on the tree and how big are they and not at least, what is the number of wounds per wounded tree? Furthermore, whether bark stripping affects the radial growth of young pedunculated oak, young- and old Norway spruce was analysed. To analyse if the radial growth was affected by bark stripping, linear and mixed linear models were made - both with and without taking the climate's impact on growth into account. The linear model was used for separate years (2013, 2014, 2015) and the mixed linear model was used for pooled years. This study did not show any significant impact on the radial growth by bark stripping.
The vast majority of bark stripped oaks was found on trees with diameter ≤ 15 cm. For spruce, the vast majority of trees bark stripped was found on trees with diameter ≥ 15 cm. The majority of the examined trees were wounded more than once. The size of the wounds indicates that infection with wood destructive fungi and bark beetles might occur with time.

Resumé

I 2012 blev en flok europæisk bison genudsat i en indhegning i Almindingen, som er lokaliseret på Bornholm. Almindingen er den femte største skov i Danmark og den mindst fragmenterede. Flokkens skrælningsadfærd blev undersøgt af Naturstyrelsen i 2014. Deres undersøgelse viste, at de hyppigste skrællede træer var rødgran (*Picea abies*) og stilkeg (*Quercus robur*). Disse træer er af økonomisk betydning for skovdriften. I denne rapport analyseres om europiske bisoner udviser en præference for at skrælle en bestemt størrelse af rødgran og stilkeg, placeringen af skællene, antallet af skræl per træ og ikke mindst størrelsen af skællene. Ydermere bliver det undersøgt om skrælning af bark påvirker den radiære tilvækst af unge og gamle rødgraner og unge stilkege. Dette er blevet analyseret via en lineær og en lineær mixed model. Den lineære model blev anvendt for årene 2013,2014, 2015 enkeltvis, mens den lineære mixed model blev anvendt for den samlede årrække. Modellerne blev lavet både inkluderende og ekskluderen klimaets indvirkning på tilvæksten. Dette studie viser ikke nogen signifikant tegn på, at skrælning af bark påvirker den radiære tilvækst.
Største delene af de skrællede stilkege havde en diameter på ≤ 15 cm, hvor den største andel af de skrællede rødgraner havde en diameter på ≥ 15 cm. Hovedparten af de skrællede træer havde mere end et skræl. Den gennemsnitlige størrelse af skræl indikere at der er risiko for infektion med ved nedbrydende svampe samt bark biller.

Keywords: European Bison (*Bison bonasus*), bark stripping, Norway spruce (*Picea abies*), pedunculate oak (*Quercus robur*)

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1. **Introduction**

The introduction contains a description of the reintroduction of European bison on Bornholm, along with why it might be practical to reintroduce the European bison with the aim of restoring a greater diversity in the nature. Furthermore, the introduction contains a description of the biology of European bison with a focus on food and habitat preference. As the focus in this study is on European bison's impact on Norway spruce (Picea abies) and pedunculate oak (Quercus robur), the introduction contains a section describing the physiology of Norway spruce and pedunculate oak and how they are affected by bark stripping. Throughout this thesis BP year will be used when attributing to geological periods and archaeological bone funds which have been dated with C^{14} BP. B.C. will be used when attributing to cultural time periods. y B.P stands for before present, and the 1 January 1950 is used as commencement date of the age scale. The introduction starts with a description of the reintroduction of European bison on Bornholm and a summary of European bison and how big herbivores can have an impact on ecosystems.

By the end of May 2012, seven European bison, *Bison bonasus,* were released into a 200-hectare enclosure in Almindingen, a forest located on the Danish island of Bornholm. The forest contains habitats with rare, threatened and endemic flora and fauna. According to the EU habitat directive, Denmark is obliged to protect habitats and increase the quality of habitats with rare, threatened or endemic flora and fauna. The reintroduction of European bison is a part of the Danish Nature Agency's plan to restore a better quality of natural environment through natural grazing. Natural grazing by big herbivores such as European bison provides nature with a variety of different habitats (Friese, 2016; Kunstmann, 2003). Furthermore, the Danish Nature Agency hopes that the introduction of the European bison will contribute to the conservation of rare species and increase ecotourism (Friese, 2016; Kunstmann, 2003). Bornholm was chosen for the reintroduction of European bison to Denmark because it contains a contiguous forest area that consists of a mosaic of different forest types and open nature (Friese, 2016). Furthermore, the ownership of the forest may make it probable to reach an agreement concerning a free-living herd of European bison on Bornholm. The herd of European bison will be under enclosure for the first five years (2012 to 2017). What happens after the five-year period is not yet decided; however, one scenario is to remove the fence. This said, the fence will only be removed if studies show that the European bison does not affect the forest negatively.

European bison are mainly grazers, with a tendency to be partly browsers, which means they also browse on trees and shrubs. European bison is believed to eat bark of trees when other more nutrient rich food resources as fresh twigs or buds, and herbs is frugal (Cabon-Raczynska et al., 1987; Gębczyńska et al., 1991; Jønsson, 2014; Kowalzcyk et al. 2011; Krasińska et al., 1987). Confusingly, this behaviour has, throughout the literature, been described using four different terms: debarking, barking, bark peeling, and bark stripping. In the present study, bark stripping will be used. How big a part of the food bark accounts for to the herd on Bornholm is unknown, but a study from Poland showed that bark accounts for 16% of their food in winter, for the herd in the Polish part of Bialowieza (kowalczyk et al., 2011). The herd studied in Poland was given supplementary food in winter, like the herd on Bornholm. The focus in this study will be on the bark stripping behaviour: which trees are bark stripped, do they prefer a specific size of trees, and does bark stripping affect the trees negatively?

The presence of big herbivores such as European bison have, throughout millennia, had an impact on the natural succession. The primeval forest was mostly a closed forest in the early Holocene (10,000-5,000 y B.P), but also contained habitats of semi-closed woodlands, moors, grassland and meadows, maintained by large herbivores and possibly storm damage and forest fires (Nielsen & Buchwald, 2010; Sandom et al., 2014). Today, moors, grassland and meadows are a result of agriculture and grazing by farm animals, whereas natural forests are a result of wild herbivores living in Denmark today. About 6,000 years ago farming and livestock implemented in Denmark. Since then, Denmark has been strongly affected by human agriculture and consequently many of the large herbivores have disappeared. Large herbivores may be key species for ecosystems, as they reshape and maintain habitats for other species. If large herbivores disappear, we may lose the foundation for diversity in ecosystems and thereby the species connected to these systems (Buttenschøn, 2007; Sandom et al., 2014;Van Wieren 1998; Wilhjelmudvalget, 2001; Aaris-Sørensen, 2009;).

Archaeological bone findings of bison in Denmark and Sweden indicate that European bison lived in Denmark in the Preboreal (10,200-8700 y B.P), which is a period in the early Holocene (Table 1) (Bailey,2008; Benecke, 2005). The distribution of European bison in other parts of Europe in the early Holocene is unknown due to lack of bone findings. However, skeletal remains from middle and late Holocene indicate that European bison were widely distributed on the European continent, from France in the west, to Ukraine and Russia in the east (Table 1) (Benecke, 2005).

Table 1 Epochs during the last 5.3 million years (Polly et al, 2011a; Polly et al, 2011b; Sandom et al.,2014).

Epoch	y B.P
Pliocene	5.333 million-2.6 million
Pleistocene	2.6 million-11,700
Early Holocene	10,000-5,000
Middle Holocene	5,000-2,000
Late Holocene	2,000-present

Two subspecies of European bison once existed; lowland bison (*B. bonasus*) and Caucasian bison (*B. caucasicus*). From the Middle Ages, the population of European bison started to decline due to the logging of forest, habitat fragmentation, colonisation of foothills, and hunting. The last wild population of lowland bison became extinct in 1919 in Poland, and the last Caucasian bison was killed in 1927. During the second half of the 19th century, lowland European bison were sent off to zoological gardens in Europe by the Tsars of Russia (Krasinska & Krasinaki, 2007). The lowland European bison was restored from 54 individuals that survived in zoological gardens and breeding centres (Pucek et al., 2004). Today's lowland European bison have descended from only five founder animals, which make the species genetically vulnerable (Krasinska & Krasinaki, 2007). Not a single thoroughbred representative of the Caucasian European bison survived through to modern times (Krasinska & Krasinaki, 2007).

Today, Europe is currently home to approximately 3,230 free-roaming bison. The European bison is listed in the Bern Convention Appendix III for protected fauna species. On the IUCN Red list, it has the status of vulnerable (IUCN, 2016). The species are facing some severe problems, such as previous inbreeding, which has decreased the gene pool and thereby increased the risk for diseases and reproductive difficulty (Pucek et al., 2004). The average inbreeding level in the subspecies lowland European bison is today almost 50%, however no signs of inbreeding depression have been observed (Tokarska et al., 2011). Additionally, their previous habitat is now highly fragmented. European bison need contiguous habitats, which shuld consist of a mosaic of different forest types and open nature, if they are to be able to spread and increase the population size (Kuemmerle et al., 2011(b), Pucek et al., 2004).

1.1 Historic landscape

The Danish environment has not always looked the way it does today. Fifteen thousand years ago most of Denmark was covered with tundra, and the climate was colder than it is today. The cold climate gave rise to completely different flora and fauna. Among others, the fauna included woolly mammoth, steppe bison, reindeer, musk ox, and woolly rhino. Those species were adapted to the tundra steppe, which was rich in dwarf shrubs and grasses (Aaris-Sørensen, 1998). The woolly mammoth, steppe bison, and woolly rhino subsequently became extinct but species such as musk ox and reindeer still thrive further north.

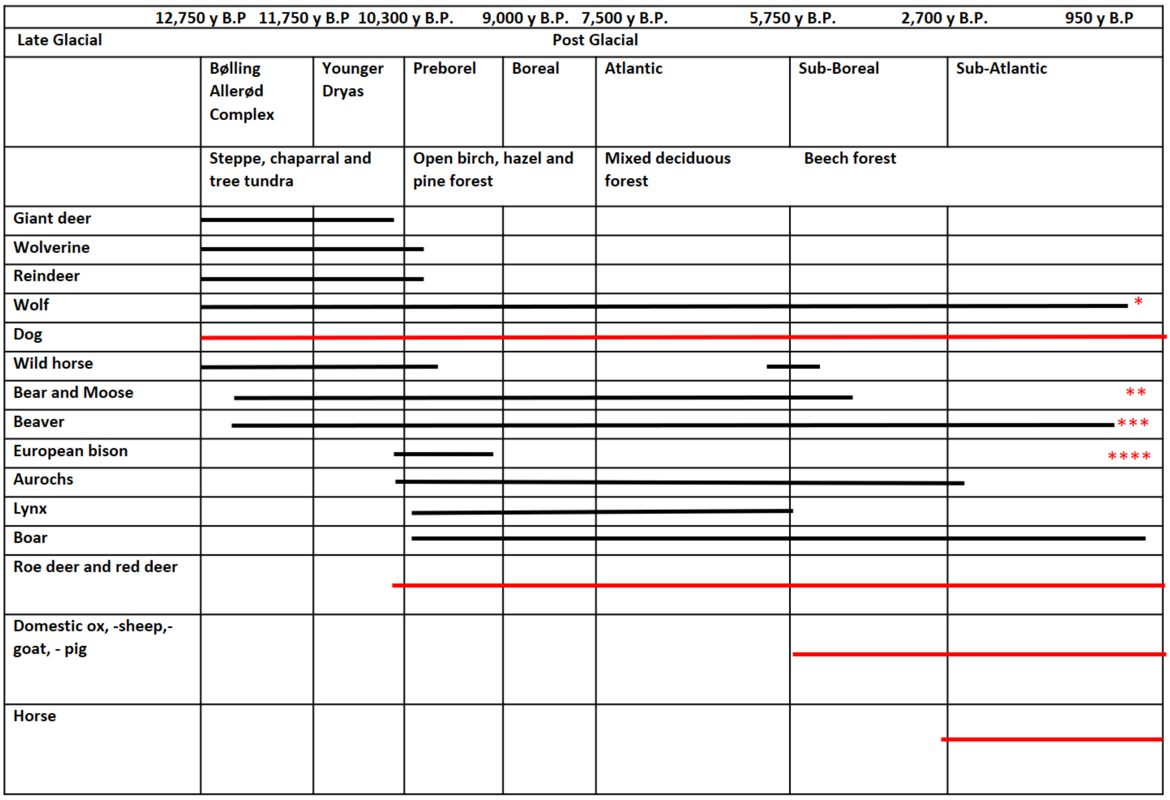

*Figure 1. Distribution of large mammals since the last ice age in Denmark (Buttenschøn, 2007). Black lines indicate animals which have disappeared from Denmark, while the red lines indicate that the animal is still present as either wild or domestic animal. * The wolf immigrated to Denmark in 2012. ** Moose were reintroduced in 2015 to an enclosure located in Lille Vildmose. ***Beavers were reintroduced in 1999 in Klosterheden. **** European bison were introduced to Almindingen on Bornholm in 2012.*

In the period after the last Ice Age, approximately 10,000 y B.P, the temperature increased (Jensen et al., 2000). Due to warmer temperatures, trees immigrated to Denmark, creating a natural environment dominated by open forest with space for herbs and grass vegetation (Aaris-Sørensen, 1998). With the opn forest came habitats for moose, European bison, wild horses, red deer, roe deer, aurochs, and boars (Figure

1) (Aaris-Sørensen, 1998). The forest slowly increased in size, and became denser, and thereby the amount of open land decreased, and consequently reducing herbaceous vegetation. European bison became extinct in Denmark (around 8,700 y B.P) according to archaeological bone findings (Aaris-Sørensen, 1998). There are different theories about the extinction of the European bison. One theory states that the transformation from grasslands to forest-dominated ecosystems during the early Holocene period, together with hunting from the increased human population, likely affected the distribution of European bison (Pucek et al., 2004, Kuemmerle et al., 2012). Another theory states that local extinction in South Scandinavia was mainly caused by the transformation of the mainland into a group of peninsulas and islands due to the Littorina transgression (Benecke, 2005). However, a European bison bone dating back to the Iron Age - approximately 1450 y B.P has been found in Bøgesø bog located on Southern Zealand (Table 2). Whether European bison's recolonized Denmark after approximately 7000 years of extinction or if it was killed somewhere else and transported to Denmark is unknown. However, it was found in proximity to a human settlement and archaeologists believe it was sacrificed to the gods (Thomsen, 2000). According to Kuemmerle et al. (2012), a moderate suitable environment for European bison was found in Southern Scandinavia in the middle and late Holocene, thus the species could potentially have existed in Denmark.

Table 2 Cultural time periods trough out the Holocene (Riis, 2015; Silkeborg kulturhistoriske museum, 2011).

Cultural time periods	Year
The Stone Age	12,800-3,900 B.C.
New Stone Age	3,901-1,700 B.C.
Bronze Age	1,701-500 B.C.
Iron Age	501 B.C.-800 A.D.
Viking age	801-1,066 A.D.
Middle Age	1,067-1,535 A.D

Six thousand years ago, most of Denmark was covered by primeval forest. The dominating large mammals were red deer, roe deer, boars and aurochs (Figure 1) (Jønsson, 2014). The primeval forest consisted of a mosaic of closed and semi-closed forest with scrubs and open biotopes. In Jutland, open biotopes such as moors and grasslands are estimated to have accounted for 10-40% of the primeval forest. On the islands, the open biotopes might have comprised a minor percentage of the total area (Nielsen & Buchwald, 2010). The large herbivores, especially the aurochs, are expected to have played an important role in shaping the environment in the past. However, it cannot be ruled out that the open biotopes could have occurred due to something other than the large herbivores, for example, natural or human-made fires could have played a role in formation of open biotopes (Nielsen & Buchwald, 2010). The open biotopes were identified through pollen analyses (Nielsen & Buchwald, 2010). After the Ice Age, the aurochs were the most widespread large mammals in western and northern Europe, based on appearances of bones (Nielsen & Buchwald, 2010; Thomsen, 2000). In Jutland, the aurochs were present until the Iron Age (500 B.C.-800 A.D.), where the most recent bones found are dated to approximately 2,450 y B.P (Thomsen, 2000). European bison and the aurochs resemble each other when it comes to their food preference. Both are classified as grazers with a tendency to be partly browser (Jønsson, 2014). With the beginning of the New Stone Age (approximately 3,900 B.C.), the human impact on nature took a new turn, as the Danes became farmers. The establishment of agriculture entailed deforestation and livestock farming, which resulted in an increase in grassland. Many scientists think that the auroch's role as a key species for maintaining a natural environment consisting of a mosaic of different types of nature was replaced by that of livestock (Aaris-Sørensen, 1998; Thomsen, 2000). This change in Danish nature took place from the Stone Age (3,900 -1,700 B.C.) and has had ongoing fateful consequences for some species.

The loss of forest continued until the beginning of the 19th century, when Denmark reached a minimum of forest of only three percentage of the total area. Since 1850, Denmark has lost 350 species of plants and animals, while a huge number are still acutely endangered or vulnerable due to human activity (Wilhjelmudvalget, 2001). Most of these species are connected to forest habitats, where succession has its own cycle. They would prosper badly in the present time's dark and monoculture forest. With the Forest Reserve Act of 1805, Denmark's forest area has increased and today accounts for 13.5% of the total area (Nord-Larsen et al., 2010). Even though the forest area is increasing, there is a need for forestry that takes the natural development of the forest into account. Earlier, the main focus has been on forest industry, and not biodiversity. Furthermore, Denmark is an intensive agricultural country, and consequently forests are often small and scattered in a highly fragmented landscape. A new trend in forestry shows a tendency towards implementing older methods of management, such as coppice and forest grazing, which are more supportive of biodiversity (Danmarks Naturfredningsforening, 2011). With this tendency and the increasing forest area, it might be possible to use some of the species that previously lived in Denmark to re-establish Danish natural environment. The European bison is one of these species. By reintroducing the European bison to Denmark, the Danish Nature Agency hopes to be able to establish a nature with a higher quality with additional space for rare, threatened and endemic flora and fauna (Nord-Larsen et al. 2010; Petersen &Vestergaard, 2006; Wilhjelmudvalget, 2001).

When considering reintroduction of prehistoric mammals, it is important to be aware that suitable habitats can still be found. As a result, it would not be evident to reintroduce reindeer or musk ox to Denmark. As aurochs are expected to have played an important role in shaping nature before the human impact, it would be logical to reintroduce them, had they not become extinct. However, as European bison and aurochs resemble each other when it comes to food preferences, it might be worthwhile reintroducing European bison to the Danish environment. By comparing pollen analysis with present day flora Denmark can be regarded as suitable for European bison (Kummerle et al., 2012).

1.2 European bison

European bison are a ruminant and eat four times during the day: in twilight before daybreak, twice during the day, and again in twilight after sunset (Pedersen & Stensgaard, 2015). The genus bison includes large and massive herbivore mammals. European bison belong to the order even-toed ungulates (*Artiodactyl*) and the family *Bovidae*, which also includes goats and sheep (Pucek et al., 2004). The genus Bison first appeared in the Pliocene Era (5.333 million to 2.6 million y B.P) in South and East Asia (Krasinska & Krasinaki, 2007). In the Pleistocene period (2.6 million to 11,700 y B.P), the bison extended its range into other parts of Asia and Europe, where it developed into different subspecies (Krasinska & Krasinaki, 2007). The European bison became a distinct species approximately 11,400 years ago and developed into two subspecies; lowland bison (*B. bonasus*), and Caucasian bison (*B. caucasicus*) (Pucek et al., 2004; Krasinska & Krasinaki, 2007; Kunstmann, 2003). European bison show sexual dimorphism, which means that bulls (males) are larger than cows (females). A fully-grown European bison bull is approximately 1.70 metres tall at the shoulder and can weigh up to 920 kg, while the cow reaches approximately 1.50 metre and can weigh up to 640 kg. Their length is approximately 2.5 metres. Both sexes have horns and the fur colour is brownish and provides good camouflage (Krasiński & Krasińska, 2007; Pucek et al., 2004).

Habitat

The natural habitat of European bison before the extinction in 1919 is difficult to pinpoint with certainty as analyses of the habitats have been made after reintroduction. At present European bison are only expected to be present in one percent of their former range (Jønsson, 2014). Traditionally, European bison were considered to thrive only in temperate broadleaved forests. This might simply be because this kind of habitat was the last refuge for the species (Kerley et al., 2012; Krasinska & Krasinski, 2007; Kuemmerle et al., 2012; Pucek et al., 2004). Climate and vegetative information in mid- and late Holocene has been modelled by Kuemmerle et al., (2012) including the European bison's habitat. The model showed that European bison may have utilised a wide range of forest types and have occupied temperate broad-leaved and northern mixed forests, but was most widespread in closed forests during the mid- and late Holocene (Kuemmerle et al., 2012). These findings are in line with both field studies by Perzanowski et al., (2008), assessments from Holocene bone remains (Benecke, 2005), and fine-scale habitat assessments (Kuemmerle et al., 2010, 2011b). Most of the studies carried out on the habitat preferences of European bison took place in the Polish part of the Bialowieza and the Borecka forest. These studies show that European bison spends a large amount of their time in forest areas, and prefer older broad-leaved forests (Krasińska et al., 1987; Kuemmerle et al. 2010). Studies from Lithuania show that European bison prefer more open biotopes (Balčiauskas, 1999). Equally, European bison also prefer open biotopes in the Belarussian part of Bialowieza. This is in agreement with the fact that open biotopes accounting for a larger part of the Belarusian part of Bialowieza than in the Polish part (Daleszczyk et al., 2007). Pedersen & Stensgaard, (2015) performed a study on the habitat preferences of the herd on Bornholm divided into season and time of day (Table 3). The herd on Bornholm spent a greater percentage of time in coniferous and deciduous forests in winter and autumn, both in daytime and at twilight, compared to summer and spring. The herd spent more time in the coniferous forest in summertime than in deciduous forest.

Table 3 Amount of time at daytime and twilight spent in deciduous and coniferous forest, and open habitats pooled together based on Pedersen & Stensgaard, (2015).

Season	Time of the day	Deciduous	Coniferous	Open habitats
Spring	Day	2.3%	15%	82.7%
Spring	Twilight	5.6%	4.3%	98.7%
Summer	Day	15%	20%	65%
Summer	Twilight	6.6%	15%	78.4%
Autumn	Day	38%	20%	42%
Autumn	Twilight	17.8%	19%	63.2%
Winter	Day	28.3%	15%	56.7%
Winter	Twilight	38.3%	23.3%	38.4%

Food- and feeding

European bison, in contrast to the findings of older studies, are not dependent on a specific type of food, but can eat many different plants, and is thereby considered a grazer with tendency to be partly browser (Figure 2). In the Polish part of Bialowieza, a study of the rumen content showed that their food consisted of 131 different plant species, of which 33% were trees and shrubs, and the remaining 67% were grasses, sedges and herbs in summertime (Borowski & Kossak, 1972). The bulk of trees and shrubs consisted of 26.6% bark (Borowski & Kossak, 1972). European bison are considered a grazer with a tendency to be an intermediate browser (Figure 2).

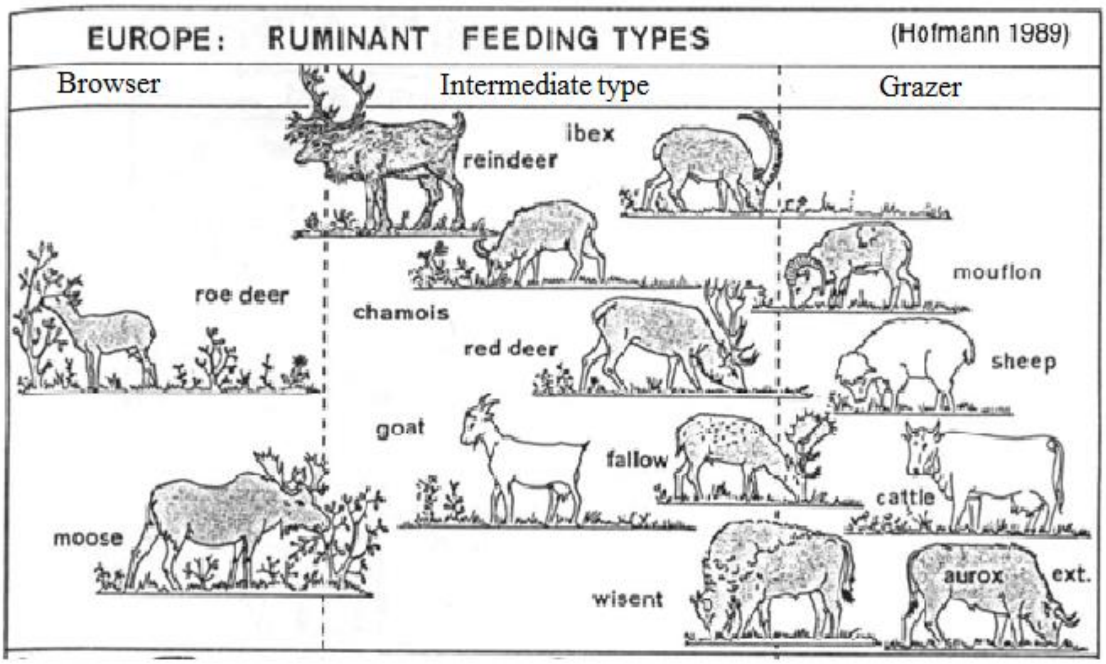

Figure 2. Diet type of ruminant (Hofmann, 1989).

Since the 19th century, in the majority of the areas where European bison are found, they have been given supplementary food during winter, traditionally hay (Kowalzcyk et al. 2011). Supplementary feeding takes place as a means of reducing the destruction of forest, which may occur when European bison strip trees of bark (Kowalzcyk et al. 2011). If supplementary feeding terminated, these relations would likely change significantly. A study by Kowalzcyk et al., (2011) supports this hypothesis. They showed, that with access to supplementary fodder in winter, 16% of the food consumed by European bison consisted of woody materials (trees and shrubs), while it increases to 65% in a non-feed situation (Kowalzcyk et al., 2011). The high intake of woody materials in a non-feed situation interconnects with their ability to digest lignin (Kowalczyk, 1976). A study by Borowski & Kossak, (1972) on European bison bark stripping behaviour carried out in Bialowieza showed that the trees most severely affected were those with a diameter between 4 to 15 cm in breast height (1.30 cm). The percentages of the most frequently bark stripped tree species are shown in Table 4. However, traces of bark stripping were also found on trees with diameter >15 cm, mostly on roots above ground (Borowski & Kossak, 1972). Bark stripped trees of economic interest in the Polish study were pedunculated oak and Norway spruce. The greatest proportion of bark stripping takes place from late autumn to early spring, which is naturally linked to the fact that there are no fresh twigs or buds and the layer of herbs is frugal at this time of the year (Cabon-Raczynska et al., 1987; Gębczyńska et al., 1991; Kowalzcyk et al. 2011; Krasinska et al., 1987; Jønsson, 2014;)

Table 4. Distribution of trees and shrubs bark stripped by European bison in Bialowieza in percentage (Borowski & Kossak, 1972).

Species	Bark stripped
Pedunculate oak (*Quercus robur*)	46.5
Common hornbeam (Carpinus betulus)	21.6
Common ash (*Fraxinus excelsior*)	17.0
European White-elm (*Ulmus laevis*)	4.2
Goat Willow (*Salix caprea*)	3.2
Small-leaved linden (*Tilia cordata*)	3.2
Norway spruce (*Picea abies*)	2.0
Common alder (*Alnus glutinosa*)	1.9
Norway maple (*Acer platanoides*)	0.2
Common hazel (*Corylus avellana*)	0.2

1.3 Spruce and oak

Trees in temperate regions undergo an annual cycle, which consists of a growth period (late spring to early autumn) and a dormant period (late autumn to early spring). The seasonal change in the environmental conditions limits the growth. The environmental features which most affect the growth are precipitation and temperature, but light and relative humidity affect as well (Andreassen et al., 2006; Andersson et al., 2011; Drobyshev et al., 2008). Trees have both primary and radial growth, and they grow by producing new cells by cell division, which only occurs in a very limited number of places, called meristems (Campbell et al., 2008). The radial growth is a growth in thickness and is produced by lateral meristems also called vascular cambium, which are present in roots and stems (Virginia Tech, 2013). Radial growth can be disrupted by transport and storage allocation problems (Virginia Tech, 2013).

The width of the growth positively correlates to energy invested in productivity (Coder, 2011). The size of the circumference correlates negatively with growth, because the same amount of xylem tissue is spread over a larger circumference in a large tree compared to a thinner one (Coder, 2011). As a geometric feature of vascular cambium, energy invested in growth might result in uneven growth across a cross-section (Coder, 2011). In spring, a rapid growth results in cell division producing large secondary xylem cells with a relatively large diameter and thin walled; at the end of the growing season, new cells will be smaller and thick walled (Campbell et.al, 2008; Coder, 2011). The difference in cell size and wall thickness results in a rather distinct line. When viewed on a transverse section, the distinct line makes up a circle (Phipps, 1985). The distinct line is the tree-ring boundary between two annual increments and is referred to as the tree ring (Phipps, 1985). The structure of the early wood cells maximises the delivery of water to leaves (Campbell et al., 2008; Phipps, 1985). The thick walled cells produced in autumn do not transport as much water as early wood cells produced in spring, but contribute to support the core (Campbell et al., 2008; Phipps, 1985). Three types of wood can be distinguished based on the absence or presence of water conducting vessels and their location (Phipps, 1985). The conifer wood contains no vessels or pores and is referred to as nonporous (Phipps, 1985). Nonporous wood is characterised by a distinct colour difference between early wood (thin walled, light-coloured) and latewood (thick walled, darker-coloured) (Phipps, 1985). Angiosperms contain pores and are divided into two types: diffuse-porous and ring-porous. Oak belongs to ring-porous, as the vessels are placed in a ring (Phipps, 1985; Steppe & Lemeur, 2006).

The secondary plant body consists of tissues produced by the vascular cambium and cork cambium (Campbell et al., 2008). Cork cambium is a part of the bark and produces a strong, thick cover, which mainly consists of wax-impregnated cells that protect the stem from water loss, fungi, bacteria and insects (Campbell et al., 2008; Coder, 2011; Virginia Tech, 2013; Teknologisk institut, 2006). Bark refers to all tissues outside of the vascular cambium. Inner bark consists of phloem, the vascular tissue transporting sugar and secondary compounds. The vascular cambium adds secondary xylem and secondary phloem, and increases the vascular flow. Xylem, the vascular tissue transporting water and nutrients in a vertical direction from roots to leaves, grows inward from the vascular cambium. All types of tree have some outer year-rings, sapwood, that consist of some living cells; however, the cells transporting water are dead cells. Water and nutrients get transported from the root to the leaves (Campbell et al.,2008). A transformation of sapwood to heartwood takes place when the tree grows. As sapwood turns into heartwood, the previous living cells die (Campbell et al., 2008).

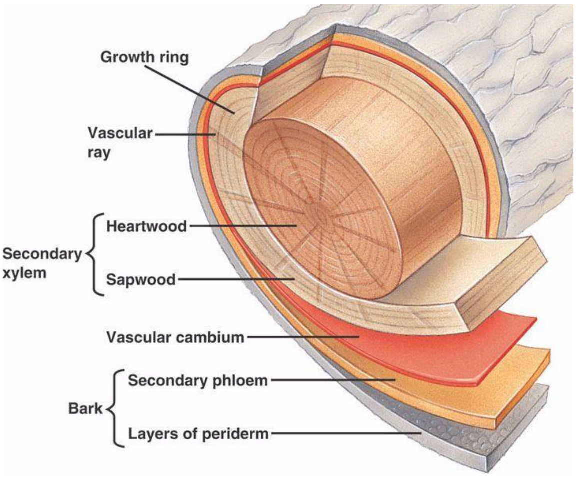

Figure 3. Anatomy of tree trunk (Campbell et al., 2008).

As a self-impregnation resin, triglyceride, sugars, tannin, alkaloids, and wax can precipitate in conifers. Resin ducts occur in both the axial system and in rays (Campbell et al. 2008; Den Store Danske, 2015; Teknologisk institut, 2006). External parameters such as injuries by frost, wind and wounding can stimulate the formation of resin ducts in conifer wood (Den Store Danske, 2015; Teknologisk institut, 2006). In response to wounding, spruce develop axial resin ducts in the secondary xylem, where resin ducts are normally absent or occur in low numbers in unwounded trees (Nagy et al., 2000).
Angiosperms manly use tannin and minerals. Furthermore, angiosperms such as oak can produce tyloses, which is a bladder-like distension of parenchyma cells, into the lumen of vessels, resulting in the occlusion of vessels and, in so doing, the transport to heartwood is blocked. In common, the different compounds are believed to protect trees against insects, fungi infection and herbivores (Den Store Danske, 2015; Teknologisk institut, 2006). Nitrogen is an important component in plant defensive compounds. Nitrogen is

a key factor in determining plant defences, due to boreal forest being limited by, above all, nitrogen (Rokke, 2004).

Norway spruce

Norway spruce was introduced approximately 250 years ago and is now the most prevalent forest tree covering 16% of the forest area and producing 18% of the wood in Denmark (Nord-Larsen, 2010). Norway spruce is easy and cheap to cultivate and, in most locations, produces wood that is considered of high quality by foresters. For the fitness of trees "poor" wood may be equally good. Norway spruce is relatively frugal in regards to nutrients, but has a huge requirement for water (Larsen, 2013). It has a number of natural enemies, parasites, which can be critical. The parasites do not kill the tree, but often result in stem and root rot, which consequently reduces resistance to storm damage and decreases the price of wood (Larsen, 2013; Thomsen, 2010). The parasites include fungi such as *Stereum sanguinolentum*, *Cylindrobasidium evolvens*, *Peniophora pithya*, *Sistotrema brinkmannii, Nectria fuckeliana*, and *Heterobasidion annosum*, bark beetles (*Ips typographus*), giant wood wasps (Urocerus gigas) and steely-blue wood wasps (Sirex juvencus) (Larsen, 2013; Vasiliauskas, 1996). All of these parasites infect wounded trees, which are either stressed or suffer from large wounds.

Pedunculate oak

Pedunculate oak immigrated to Denmark together with the most other large-leaved angiosperms approximately 8,000 years ago (Jensen, 2006). Oak can grow on all types of soil and accounts for 10% of the forest area (Jensen, 2006). Oak is not only an important species for us but also in regard to biodiversity (Jensen, 2006). Around 1,000 to 1,500 organisms are partially or completely dependent on oak (Jensen, 2006). Some of those species are parasites on living oak such as *Armillarialutea*, *Laetiporussulphureus*, oak mazegill (*Daedalea quercina*), and *Ganoderma sp.* (Thomsen & Rune, 1998).

The bark stripping behaviour of European bison might stress both oak and spruce and damage parts of the wood and consequently induce the risk of parasite infection.

1.4 Bark stripping

The greatest damage to forests by European bison is bark stripping, which mostly affects Norway spruce and pedunculte oak with diameter in breast height between 4 to 15 cm (Borowski & Kossak, 1972). Due to oaks' hardening of bark is it mostly young oaks which are bark stripped. Within this age, stem of spruces begins to clear from drying lower branches and smooth bark is exposed. Smooth bark is best suited for bark stripping (Čermak et al., 2004). The bark stripping often takes place in late autumn, winter, and early spring (dormant period) but can also take place in summer (Borowski & Kossak, 1972; Cabon-Raczynska et al., 1987; Gębczyńska et al., 1991; Jønsson, 2014; Kowalzcyk et al. 2011; Krasinska et al., 1987; Nørgaard, 2013). Bark stripping during the dormant period can be fatal, but is not as fatal as bark stripping during summer (Nørgaard, 2013). Bark stripping in winter is more superficial, on the outer part of the bark, which consists of dead cells (Nørgaard, 2013). Bark is loose during the growth season due to high sap tension and bark stripping can destroy both outer and inner bark (Nørgaard, 2013). Formation of new bark take years, and until a bark strip is covered, there is a risk that a wounded tree will be infected with wood-destructive fungi.

Figure 4. Winter bark stripes on the root of an old spruce, the stem of young spruce and on the stem of young oak. Photo: Betina Brender

Fungi infecting Norway spruce

Bark stripping may lead to infections of various wood-destructive fungi. Some of the most important fungi for spruce are presented here. One common wood- destructive fungus is *Stereum sanguinolentum*. *S. sanguinolentum* produces spores in autumn (Čermak et al., 2004). *S. sanguinolentum* colonises both new and old wounds made by red deer and the infection rate was found to be significant higher in wounds made in the winter period compared to wounds made in summer (Čermak et al., 2004). In a study carried out in Norway, 27% of the bark stripped trees by red deer were infected with *S. sanguinolentum* (Veiberg & Solheim, 2000). When it colonises a tree, mycelium will digest the wood and, as an effect, produce rot ranging from 2.5 to 4.5 metres from the wound (Čermak et al., 2004). In the study by Čermak et al, (2004) *S. sanguinolentum* was found to spread at an average rate of 15.6 cm/year (from 1 to 36.4 cm/year) in RD Proklest, and, at an average rate of 23.8 cm/year (from 1 to 70 cm/year) in FD Mořkov.

Trees infected with *S. sanguinolentum* risk infection with *Heterobasidion annosum* (Čermak et al., 2004). *H. annosum* is the most economical important wood-destructive fungus for Norway spruce and can cause stem rot in wood up to eight metres in height (Čermak et al., 2004; Thomsen, 2000). Spores of *H. annosum* are released from apothecium all year round, except for periods with frosty weather (Thomsen, 2000). The production of spores varies throughout the year and is affected by the weather (Nørgaard, 2013; Thomsen, 2000). A damaged tree exposes the highest risk of infection in August and September and the lowest risk when the temperature drops below five degrees (Thomsen, 2000). Spores are transported by the wind and can travel up to several kilometres, but the vast majority of disperse close to the apothecium (Thomsen, 2000). A tree infected with *H. annosum* constitutes a large risk of spreading the fungus to unwounded tress through root contact (Thomsen, 2000). From the roots, it dissipates to the stem (Thomsen, 2000). *H. annosum* can only be dispersed through vegetative formation (Nørgaard, 2013; Thomsen, 2000).

The largest problem with *H. annosum* occurs in a managed forest, due to the fact that stumps making up the main dispersal point through vegetative formations, and *H. annosum* can colonise fresh stumps compared to other wood destructive fungi. In unmanaged forest damages by *H. annosum* is less problematic (Thomsen, 2000). Injuries made by bark stripping and other wounds can also be a source for infection (Thomsen, 2000). Trees infected with *H. annosum* have a high danger of falling (Thomsen, 2000). Bark beetles such as spruce bark beetle colonise stressed trees as secondary parasites (Nørgaard, 2013).

Conifers have developed resin as a chemical defence against bark beetles, but coevolution has made wood wasps able to produce slime which is toxic to trees (Nagy et al., 2000; Thomsen & Harding, 2010). The fresh resin might attract the giant wood wasp (*Urocerus gigas*) or steely-blue wood wasp (*Sirex juvencus*) (Thomsen & Harding, 2010). Norway spruce appears to be their favourite host (Thomsen & Harding, 2010). Both species fly in July and August and lay their eggs on recently fallen trees or in wounded trees, which are either stressed or have large wounds (Thomsen & Harding, 2010). Wood wasps form a symbiotic relationship with wood destructive fungi of the genus *Amylostereum* (Thomsen & Harding, 2010). When laying her eggs, she places spores on the tree and injects a slime which is toxic to trees (Thomsen & Harding, 2010). The function of the slime is to desiccate the sapwood (Thomsen & Harding, 2010). The fungus will disperse in the wood and the mycelium provides food for the larva. By eating mycelium, the larva receives enzymes, which metabolise woody compounds into carbohydrates (Thomsen & Harding, 2010). The larval phase takes between two to three years, and the larva will slowly eat its way through the stem until it reaches the outer bark. Most frequently, it will take years before the rot infection has extended to a level which will bring down the tree (Thomsen & Harding, 2010).

Fungi infecting pedunculate oak

Fungi parasitizing oak are often saprotrophic species, which are efficient heartwood destructives (Møller, 2010). *Armillarialutea*, *Laetiporus sulphureus*, and oak mazegill (*Daedaleaquercina*) are fungi which often parasite oak (Thomsen & Rune, 1998). These fungi feed mostly on dead wood, but they can parasitize stressed trees (Thomsen & Rune, 1998). They all infect the heartwood of living trees through clear cuts of branches or wounds, where heartwood is exposed or in situations where a large wound is covered by callus (Thomsen & Skov, 2011). An extensive rot in the stem will be widespread when the apothecium appears (Thomsen & Rune, 1998).

Both spruce and oak mycelia will most often disperse to wood which already existed when the infection took place, as sapwood can produce chemical defences and change structure which reduce risk of infection (Skov, 2001; Thomsen & Skov, 2011). The infected wood will rot with time (Thomsen & Skov, 2011). In order to be able to use the stem for wood, logging is needed as soon as the infection is discovered. To make sure no mycelium is left in the logged trunk, trimming half a meter above the visible rot is needed (Thomsen & Rune, 1998). A huge amount of the economically important part of the log is lost, and the proportionate cost to logging and transport will increase. Furthermore, it is difficult to find a buyer for trees infected with rot (Nørgaard, 2013; Thomsen, 2000). Wounded trees might, however, be beneficial for biodiversity as wood-destructive fungi weaken trees and consequently provide habitats for e.g. bark beetles, hollow-nesting birds and woodpeckers (Jensen, 2006).

2. Aims of this study

From earlier studies carried out on bark stripping by ungulates, including European bison, we know that ungulates have a preference for trees with smooth bark, as this is the bark most suitable for bark stripping (Čermak et al., 2004). A study conducted on the food preferences of European bison showed that European bison prefer trees with a diameter between 4 to 15 cm (Borowski & Kossak, 1972).
The Danish Nature Agency carried out a field study in 2014, to gather information about the bark stripping behaviour of the herd on Bornholm. The majority of species bark stripped were found to be pedunculate oak and Norway spruce above two metres in height, which are economically valuable for forestry. How big a proportion of their food bark accounts for has, in earlier studies, been found to correlate with food availability (Kowalzcyk et al., 2011). In the Polish part of Białowieza, woody material accounts for 16% of the food for European bison in winter with access to supplementary fodder - where it increases to 65% in a non-fed situation (Kowalzcyk et al., 2011). How large a percentage of the food bark accounts for is, however, unknown for the herd on Bornholm.

Not much is known about how bark stripping by European bison affects pedunculate oak and Norway spruce. One-way bark stripping may affect pedunculate oak and Norway spruce is by reducing the radial growth. From a biological perspective, reduction of the radial growth can indicate transport and storage allocation problems. If bark stripping affects the radial growth negatively, the reintroduction of European bison can cause economic consequences for the forestry. However, there are differing views regarding whether or not bark stripping affects the radial growth (Gill 1992a).

A well-documented effect of bark stripping by moose and red deer is an increased risk of infection by wood-destructive fungi (Čermak et al., 2004; Gill 1992a; Roll-Hansen & Roll Hansen, 1980a; Veiberg & Solheim, 2000). This can be a problem for trees as these fungi will produce rot, thereby causing stability deterioration and increasing the risk of falling (Thomsen, 2000). However, the risk of infection with wood-destructive fungi is dependent on the size and age of wound (Roll-Hansen & Roll Hansen, 1980a). To my knowledge, no earlier studies made on European bison includes the size of wounds and the infection rate of wood-destructive fungi and if the wounds affect the radial growth negatively.

To provide a comprehensive picture on bark stripping’s impact on pedunculate oak and Norway spruce in Almindingen on Bornholm, further information on the bark stripping will be needed. This study aims to provide further scientific knowledge about the effect of bark stripping, by asking the following research questions:

(a) What size of trees are bark stripped by European bison? **(b)** Is tree bark stripped more than once? The location of wounds might have an economic effect due to rot spreading up to several metres from a wound. Therefore, this study asks the research question **(c)** Where are wounds located on the tree? As the size of wounds appears to be an important factor in the risk of infection with wood-destructive fungi in studies conducted on moose and red deer, this study asks the research question **(d)** What is the size of wounds made by European bison? To try to shed light on whether bark stripping has a negative effect on radial growth, increment cores were made from wounded and unwounded trees **(e)**.

Furthermore, this study wants to quantify if any local difference in the bark stripping frequency can be observed within different areas of the study site **(f)**.

3. Materials and methods

3.1 Location

The study site is located in Almindingen, in the central part of the Danish island Bornholm 55.124229 N-14.928299 E (Figure 5).

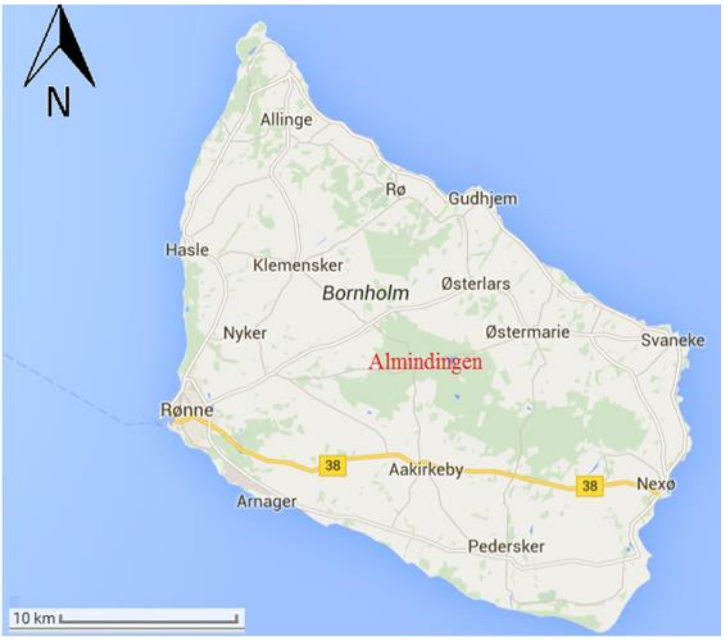

Figure 5 Location of Almindingen on Bornholm

Denmark is a relatively small and densely populated country where the presence of humans has influenced nature and landscape for centuries. Denmark consists of distinct cultural landscapes with open land dominated by agriculture. In 2014, Denmark consisted of 66% agriculture, 10% cities and roads, and 7% lakes, bogs, and meadows, the remaining 16% was forests and heath (Mikkelsen et al, 2014). Almindingen is the fifth largest forest in Denmark and the least fragmented one (Jønsson, 2014). The forest is approximately 5000 ha. and is owned by the Danish Nature Agency, the municipality and private owners (Friese, 2016). A herd of European bison is located in an enclosure with a size of approximately 200 ha. The enclosure is located in the middle of the forest surrounded by gravel roads, Søndre Svinemosevej bounds the enclosure to the south, Rømersvej to the north and west, and, towards the east, it is bound by Nydamsvej (Figure 6). There are no highways on the island and the human population is low, compared to the size of the island (Jønsson, 2014). The enclosure consists of different habitats ranging from coniferous and deciduous forest to patches of grasslands and meadows. The conifers dominate the area of the enclosure by 52.6%, versus 26.7% deciduous forest, and only 15.4% open habitat and the remaining 5.3% land consists of streets and a lake (Jønsson, 2014). The deciduous forests contain habitats with old, middle and young pedunculate oak (*Quercus robur*), beech (*Fagus*), birch (*Betula*), common alder (*Alnus glutinosa*) and the coniferous contain habitats with old and young Norway spruce (*Picea abies*). By winter 2013/2014 the herd consisted of eight animals - one bull, six cows and a first-year calf, while in winter 2014/2015 the herd had increased to twelve animals - one bull, six cows, a second-year calf and five first-year calves (Naturstyrelsen, 2016). Aside from European bison, roe deer (*Capreolus capreolus*) inhabits the enclosure. No larger predators are present in the forest. This makes Bornholm the optimal place to reintroduce European bison to Denmark. The climate is temperate with a mean annual temperature of 7.9 °C, the warmest month being August (mean temperature 16.7° C) and the coldest being February (mean temperature -0.3 °C) (DMI, 2015). The mean annual rainfall was 692 mm, measured from 2013 to 2015 (DMI, 2015). The growing season, defined as the period with average mean air temperature above 5 °C, lasts between 184-–275 days (DMI, 2015; Drosbyhev et al., 2008).

Figure 6 Map of plots inside the enclosure and control plots.

3.2 Previous study

Before the introduction of the European bison, the Danish Nature Agency performed vegetation mapping based on forest maps, air photos and ground surveys. Based on this mapping, they selected a 200 –ha. area for the enclosure. The vegetation inside the enclosure was classified into 12 habitats based on the dominant species. Out of the 12 habitats, 10 were selected for analysis (Table 5).

Table 5 Monitored habitats inside the enclosure and control arears (Jønsson, 2014).

Habitat	Tree dominance	Area (ha)
2.1-2.10	Common alder and silver birch	3.037
3.1-3.10	Beech	12.41
5.1-5.10	Old pedunculate oak	7.38
6.1-6.10	Middle age pedunculate oak	20.26
7.1-7.10	Young pedunculate oak	2.76
11.1-11.10	old Norway spruce	63.78
12.1-12.10	Young Norway spruce	30.79
13.1-13.10	Cleared	17.64
16.1-16.10	Meadow	11.17
20.1.20.10	Bushgrass	1.51
4.1-4.10	Control beech	
8.1-8.10	Control old pedunculated oak	
10.1-10.10	Control old spruce	

In each habitat, analyses were made within 10 plots. A plot consisted of a circle with a radius of 15-metre (equivalent to 706 m^2) and a circle with a radius of five-metre (equivalent to 78.5m^2) located in the centre of the 15-meter circle (Figure 7). Each plot was marked with a stick located in the centre of the 15-meter circle.

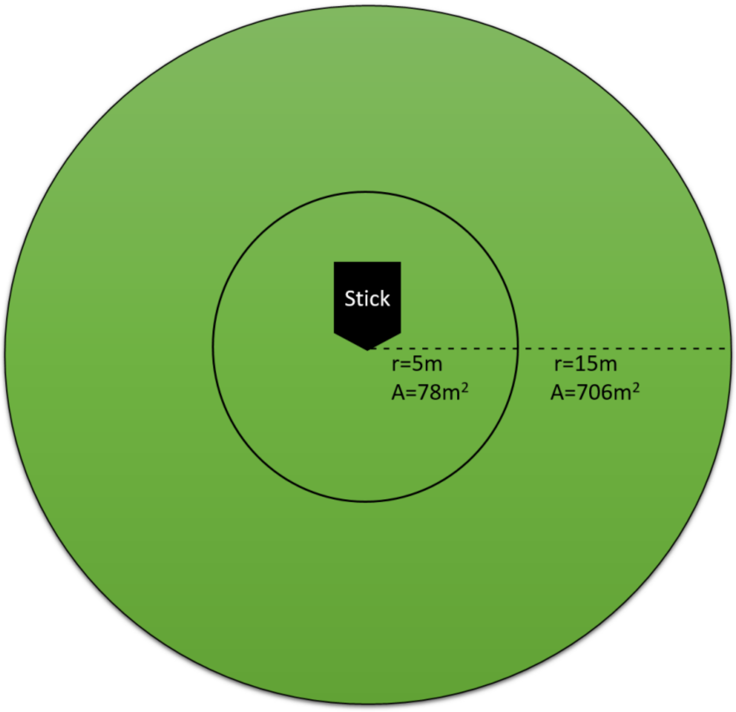

Figure 7 Study design.

In 2014, the plots selected in 2012 by the Danish Nature Agency were re-examined to record bark stripping. All bark stripped trees were counted in the 15-metre circles, as well as the total number of trees. In the five-metre circles**,** the size was measured for all trees with a diameter in breast height equal to or larger than 10 cm.

3.3 This Study

For this study, pedunculate oak and Norway spruce were selected, as these were the species with the highest frequency of trees bark stripped in 2014. As only one species of the genus spruce and oak being included in the present study, the genus name will be used throughout the rest of the thesis. The fieldwork was carried out during three periods: Two in 2015: July 6th - 20th 2015, and July 5th – 15th 2015, and one in 2016: January 18th - 21st. Data collection was carried out in the habitats 5, 6, 7, 8, 10 11, and 12 (Table 5) plus in two new control habitats containing young spruce and young oak. Each habitat established by the Danish Nature Agency contains 10 plots. In addition to this, five plots in the new control habitats were established. The purpose of the fieldwork in this study was to quantify if European bison prefer trees of a specific size, and to determine the position of wounds and the number of wounds per tree. Furthermore, the study would quantify if bark stripping had a negative effect on the radial growth, and the percentage of bark stripped trees in each plot, to locate regional distribution differences in percentage of trees bark stripped between plots within a habitat and among different habitats. Plots in control habitats were used to check for misjudged wounds in plots inside of the enclosure. To locate plots established by the Danish Nature Agency a GPS, GerminGPSmap 78s and the free software BaseCamp™ were used. The stick marking of the centre of the five- and 15-metre circles were absent in plots 7.10, 10.3, 10.5, 11.10, 12.5, and 12.7. Therefore, new sticks were re-established according to the GPS coordinates. Due to uncertainty in the accuracy of the GPS, new GPS coordinates were made. The new control plots were chosen randomly. When a plot was located, using measuring tape, a circle with a radius of 15-metres and five-metres was made (Figure 7). This method is useful in my case, where the focus is not on vegetation analysis on the species' composition, but on bark stripping of oak and spruce.

3.4 Bark stripping

Five metre-circles

In the five-metre circles, the total number of trees was noted, as well as the number of bark stripped ones. The diameter of each tree was measured with a diameter tape measure, and with log diameter- measuring callipers in breast height. The number of wounds on each tree was noted, and the length and width of each wound was measured. Pictures was taken with Canon 1000 D with a lens of 18-270 mm. The location of each wound was divided into three categories:

1. Root up to 15 cm
2. Stem under breast height
3. Stem above breast height

To quantify which age group of trees European bison prefer to bark strip, the map made by the Danish Nature Agency was consulted to find the age of trees within each habitat (Figure 6).

15-metre circles

In the 15-metre circles, the total number of trees was noted, as well as the number of bark stripped ones. This data was used to compare the amount of bark stripped trees in each habitat, with data collected by the in 2014. Furthermore, the 15-metre circles were used to locate regional distribution differences in the percentage of bark stripped trees between plots within a habitat and between different habitats. The percentage of bark stripped trees was divided into five categories:

0= 0% bark stripped

0.5= 0% < x ≤ 10% bark stripped

1=10% x ≤ 50% bark stripped

2=50% < x ≤ 90% bark stripped

3=90%<x≤ 100% bark stripped

3.5 Growth

To quantify if European bison affected the radial growth of oak and spruce with their bark stripping behaviour, increment cores were randomly taken from 12 bark stripped and 12 control trees within the habitats young oak, old spruce and young spruce between September 7th-16th 2015 using increment borer Mora-Coretax 200 mm. Control trees and bark stripped trees were taken from the same plot to ensure the same growing conditions. For analysis, plot 7.7 was chosen for young oak, plot 11.9 for old spruce, and plot 12.10 for young spruce. Two increment cores were taken at breast height ±10 cm from each tree perpendicular to each other, as trees do not always grow homogeneously.

3.6 Tree-ring analyses

The increment cores were glued onto wood mounts with wood fibres perpendicular to the field of view, and sanded with a belt sander using 100, 150, and 220 P sanding paper followed by hand sanding with 300, 800, and 1000 P sanding paper, if the year-rings were not notable after belt sanding (Figure 8). Prepared samples were scanned at 1200 dpi resolution using Canon Scan 9000F. Year rings were defined as rather distinct lines, which are created by the generally sharp contrast between small, thick walled cells formed at the end of a

Figure 8 Increment cores from study site 7.7 (young oak) glued onto wood mounts.

growing season, and large, thin walled cells made in the next growing season. The width between two-year rings was measured by placing a help line perpendicular between two-year rings using CooRecorder 7.7 (Figure 9). CooRecorder 7.7 gave the width in coordinates. To transform the width to mm CDendro 7.7 was used. The mean of the two increment cores from the same individual were calculated using Excel 2013. In addition, I performed cross-dating on the 12 tree-ring series belonging to the same species and age group by manual comparison of ring-width graphs (appendix 1).

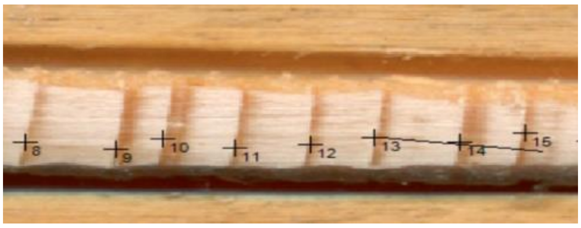

Figure 9 Measurement of year rings. The line between year ring 13 and 14 indicates the help line.

To quantify if there is a significant difference in growth between trees bark stripped and control trees, linear models were constructed for the years 2013, 2014, and 2015: separate and mixed linear models were constructed for pooled years. For separate years, a linear model with ring-width as a response variable, bark stripping (yes or no) as a predictor variable were constructed to test for statistical significance between bark stripped and control trees. For pooled years, a mixed linear model was constructed with ring-width as a response variable, bark stripping (yes or no) as a predictor variable, and with intercepts allowed to vary among individuals as a random factor. P-values for separate years were calculated using a t-test, where P-values for pooled years were calculated using likelihood ratio test. The statistical analyses were carried out using the free software R (R development team 2016) and R Studio Version 0.99.878 – © 2009-2016 R Studio, Inc.

3.7 Climate correlations

Yearly growth is affected by climate conditions, precipitation and temperature (Andreassen et al., 2006; Andersson et al., 2011; Drobyshev et al., 2008). To take the climate impact on growth into account I constructed three different mixed linear regression models for both spruce and oak based on previous cited studies. Three different studies were consulted, two on oak growth in the southern part of Sweden and one on Norway spruce growth in the southern part of Norway (Andreassen et al., 2006; Andersson et al., 2011; Drobyshev et al., 2008).

Spruce

Three different types of linear mixed regression models were constructed for spruce, with the radial growth as a function of climate (temperature and precipitation) with intercept allowed to vary among individuals as a random factor.

Model 1: According to Andreessen et al., (2006), precipitation in June correlated to growth as well as the previous year's temperature in July-September.

Model 2: According to Andreassen et al., (2006), May, July and August precipitation also showed a correlation on the growth. This model includes precipitation from May to August as well as the previous year's temperature in July to September.

Model 3: According to the Bornholm Danish Nature Agency, the growth season of Norway spruce starts in April on Bornholm. This model includes precipitation from April to August as well as the previous year's temperature in July to September.

By running a likelihood ratio test, the model showing the lowest AIC (Akaike information criterion, measuring the relative quality of a model) was chosen as the best fitting model.

Different variations of the best fitting model were made linear, including or not including interactive effects and a non-linear, with intercepts allowed to vary among individuals as a random factor. The different variations of the best fitting model were compared using a likelihood ratio test. The model with the lowest AIC value was chosen for further analysis.

To predict the growth in 2013, 2014 and 2015 precipitation and temperature data from 1997 to 2012 for Bornholm were used (DMI, 2015). The measured growth was subtracted from predicted growth.

To quantify if there was a significant difference in growth between bark stripped trees and control trees, linear models were constructed for the years 2013, 2014, and 2015; separate and mixed linear models were constructed for years pooled. P-values for separate years were calculated using a t-test where the P-values for years pooled were calculated using likelihood ratio test.

Oak

I based my set of possible climate models on two previous studies, one was conducted on Gotland (Andersson et al., 2011) and the other was performed over a larger area containing study sites in Skåne, Halland, Blekinge, Kronoberg, Kalmar, Västra Gotland, Jönkoping, and Östergötland (Drobyshev et al., 2008). The two studies did not come to the same conclusion on which month´s precipitation and temperature had the greatest impact of the secondary growth.

Three different types of linear mixed regression models were constructed for oak, of the radial growth as a function of climate (temperature and precipitation) with intercepts allowed to vary among individuals as a random factor.

Model 1: According to Drosbyhevet et al., (2008) summer temperature plus temperature in October the previous year correlated to growth. Precipitation in June and July plus the previous year's precipitation during the growth season also correlated to growth.

Model 2: According to Anderson et al., (2011) the previous year's temperature in September and October correlated to growth. Precipitation from March to June plus the previous year's precipitation in August and September also correlated to growth.

Model 3: According to Anderson et al.et al., (2011) the previous year's temperature in September and October correlated to growth. Precipitation in the full growing season plus the previous year's precipitation in August and September also correlated to growth.

The best fitting model (lowest AIC) was found by running a likelihood ratio test.

Different variations of the best fitting model were made, linear including or not including interactive effects and a non-linear, with intercepts allowed to vary among individuals as a random factor. The different variations of the best fitting model were compared using a likelihood ratio test. The model with the lowest AIC was used.

To predict the growth in 2013, 2014 and 2015 climate data on precipitation and temperature from 1997 to 2012 for Bornholm were used (DMI, 2015). The measured growth was subtracted from predicted growth.

To quantify if there is a significant difference in growth between bark stripped trees and control trees, the same procedure was used as for spruce.

4. Results

4.1 Previous study 2014

From raw data collected by the Danish Nature Agency, the number of trees of each species monitored in the enclosure and the percentage bark stripped by European bison in 2014 was calculated (Figure 10).

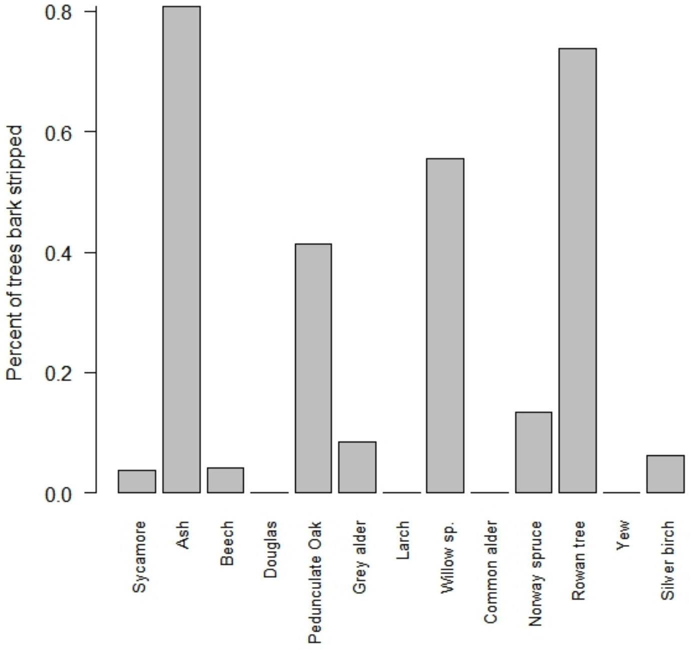

Figure 10. Percentage of bark stripped trees of sycamore, ash, beach, douglas, pedunculated oak, grey alder, larch, willow sp., common alder, Norway spruce, rowan tree, yew and silver birch. In total, the population size of the species was: sycamore N = 183, ash N = 26, beech N = 495, douglas N = 14, oak N = 1745, grey alder N = 98, larch N = 81, willow sp. N= 25, common alder N = 140, spruce N = 2130, rowan tree N= 132, Yew N = 14, silver birch N=492.

4.2 Which size trees were bark stripped?

During a previous study in summer 2014, 1633 oaks and 1866 spruces were examined in the 15-metre circles. During the present study, 1407 oaks and 1852 spruces were examined (Table 6). For all habitats, an increase in number of trees bark stripped from 2014 to 2015 was observed. The highest increase was found for old spruces and the lowest increase was observed for old oaks. A proportion test was carried out and a significant difference was found between 2014 and 2015 $p<0.05$, for all groups.

Table 6. Years of planting, Number of trees, and percentages of trees bark stripped in 2014 and 2015 for young, middle age, old oak, and old and young spruces.

Plots	Planted (year)	2104 No. trees	2014 No. trees bark stripped	2014 % trees bark stripped	2015 No. trees	2015 No. trees Bark stripped	2015 % trees bark stripped
5. Old oak	1897-1933	99	0	0	99	8	8.1
6. Middle-aged oak	1951-1965	271	6	2.2	271	29	10.7
7. Young oak	1985-1996	1263	471	37.3	1037	486	46.9
11. Old Spruce	1939-1972	477	120	25.2	477	216	45.3
12. Young Spruce	1977-1996	1389	154	11.1	1375	326	23.7

In the five-metre circles, the size in breast height was measured for 165 oaks and 201 spruces. The size of the trees was plotted and divided into groups (bark stripped or not) (Figure 11). To predict the risk of bark stripping as a function of size a logistic regression line was constructed. For spruce, the risk of bark stripping increased with size, whereas it decreased for oak. Bark stripping reaches a minimum when oak trees reach a diameter of 40 cm. It took approximately 90 years for an oak tree to have a diameter of 40cm (Figure 12). A logistic regression was also constructed as a quadratic equation (Figure 13). No difference was seen in the diameter of bark stripped spruces when using the logistic regression run as a quadratic equation compared to the logistic regression based on a linear equation. However, by using the logistic regression run as a quadratic equation, oaks shift towards smaller trees being bark stripped. The quadratic term of the logistic regression was significant, $p<0.001$, for oak. The lowest risk of bark stripping when using the logistic regression based on a linear equation is expected to occur when oak reach 30 cm (Figure 13). It takes approximately 70 years before the examined oaks reach a diameter of 70 cm (Figure 12).

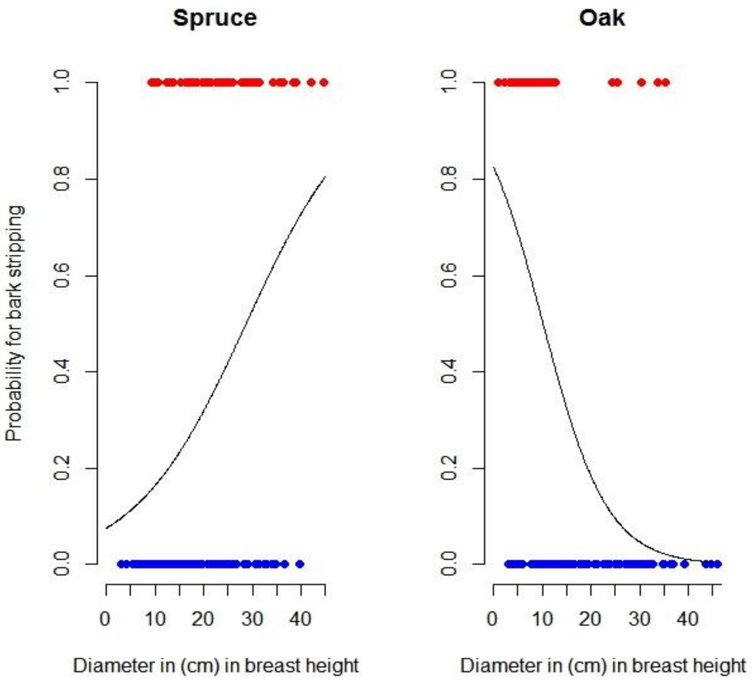

Figure 11. Probability of bark stripping of oak and spruce as a function of size. Red circles indicate individuals which have been bark stripped and blue circles indicate individuals that have not been bark stripped. The black line shows the predicted probability of being bark stripped versus size, and is made by a generalized linear model.

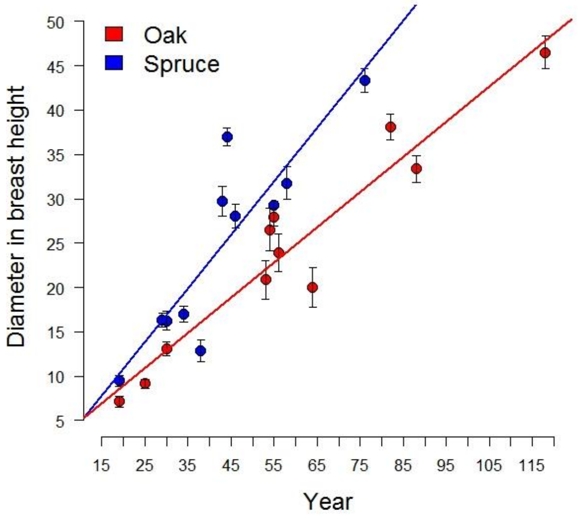

Figure 12 Diameter of oak and spruce as a function of year with SEM (standard error of the mean).

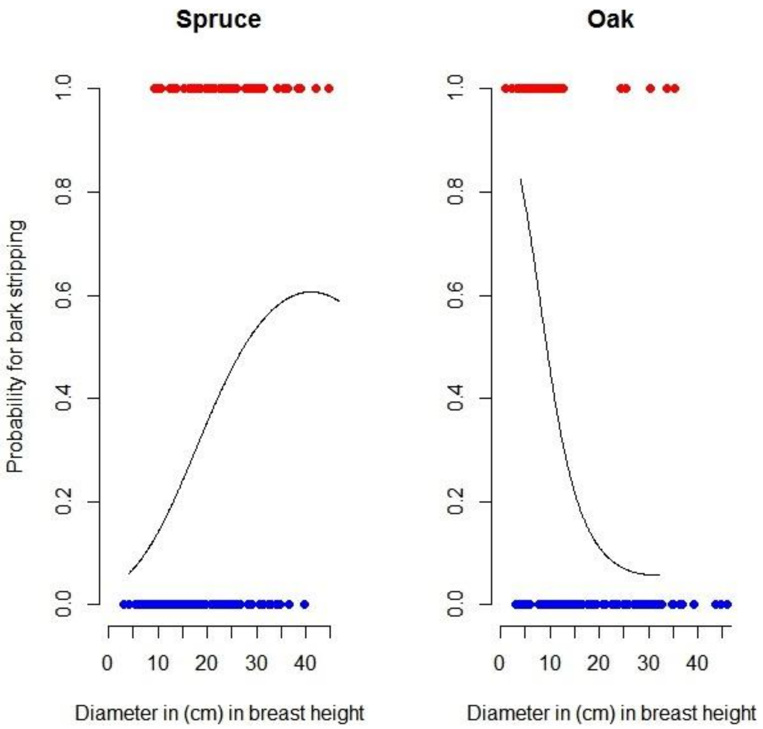

Figure 13. Probability of bark stripping of oak and spruce as a function of size. Red circles indicate individuals which have been bark stripped and blue circles indicate individuals which have not been bark stripped. The black line shows the predicted bark stripping percent versus size of the trees (logistic regression), and is made by a generalised linear model with a quadratic equation with size as the quadratic term.

4.3 The location of wounds, number of wounds on each tree bark stripped

The vast majority of bark stripped oaks were found among oaks with a diameter ≤ 15 cm. For spruces, the vast majority of bark stripped trees were found on trees with a diameter ≥ 15 cm. For trees with a diameter ≤ 15 cm, the most frequent place for bark stripping was found to be on the stem below breast height for both oaks and spruces. An approximately equal distribution of trees with wounds on roots and stem below breast height was examined for trees with a diameter ≥ 15 cm.

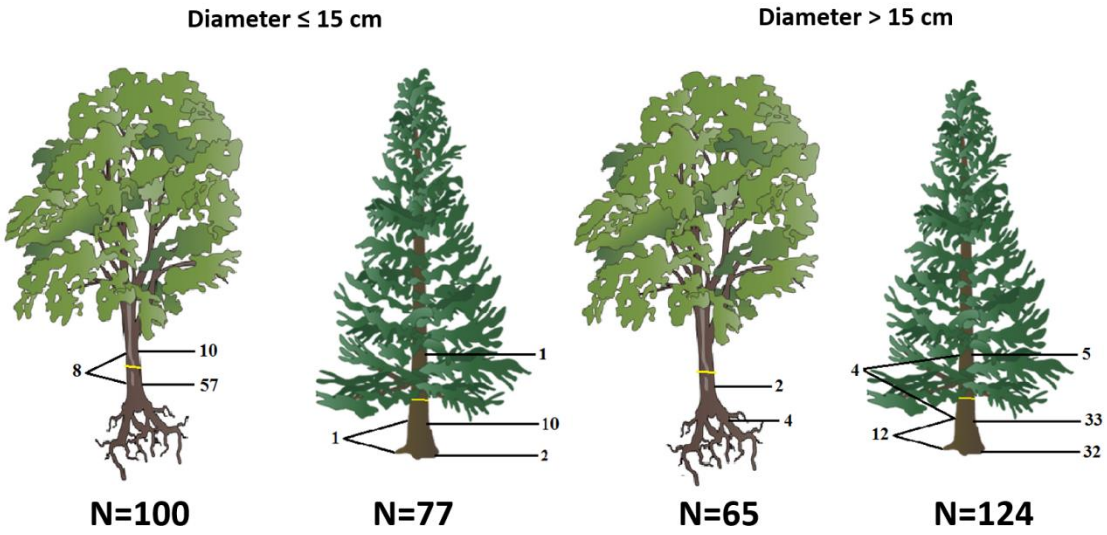

Figure 14 Number of bark stripped trees grouped into two groups, diameter ≤ 15 cm or dimeter >15 cm. Location of wounds divided into three categories: on roots, stem under breast height, and stem above breast height. The yellow line indicates breast height.

For each tree bark stripped, the number of wounds was counted. The number of wounds was divided into four categories: one, two, three, or more than three wounds (Figure 15). For both oak and spruce, the vast majority of trees had more than one wound. However, for each category independently, the highest number of both oak and spruce were found to have one wound.

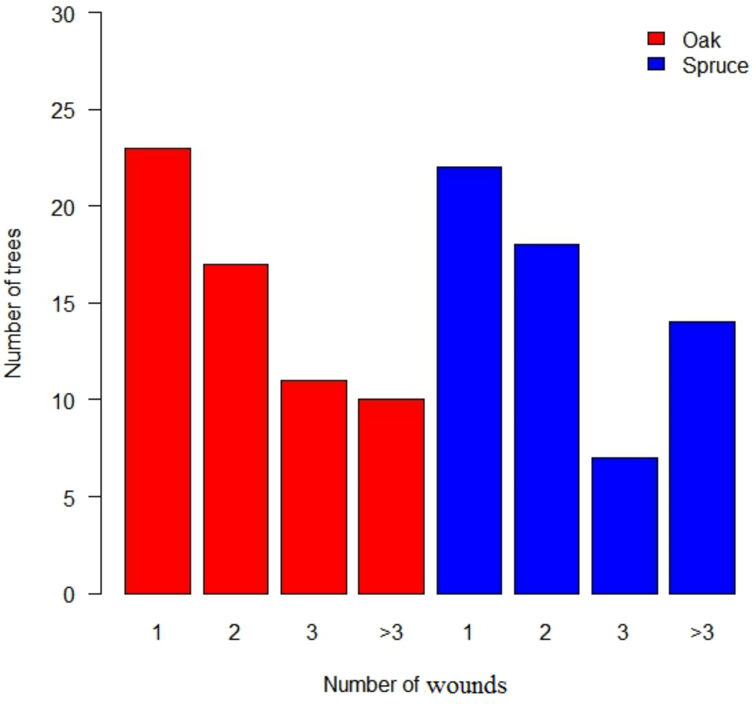

Figure 15 Number of wounds categorised in four categories: one, two, three, and more than three wounds.

4.4 Is the radial growth affected by bark stripping?

The mean size of wounds in cm^2 was calculated for the groups: young oak, young , and old spruce (Table 7). Less than ten bark stripped trees were found within old and middle-aged oaks and are therefore not included. A high standard deviation of the cm^2 of wounds was found for both young oak, young, and old spruce.

Table 7 Mean size of wounds (cm^2) for spruce and oak grouped into: young, middle age, and old oak, young, and old spruce.

Spices	Mean ± SD of wound (cm^2)	Mean ± SEM of wound (cm^2)	Mean ± SD of size of trees in cm	Mean ± SEM of size of trees in cm
Young oak	66 ± 96	66 ± 8	7 ± 3	7 ± 0.3
Young spruce	161 ± 299	161 ± 36	18 ± 6	18 ± 1
Old spruce	111± 172	111 ± 17	30± 7	30.20 ± 1

The average radial growth for the 12 control and 12 bark stripped trees within the habitats young oak, and young and old spruce used to quantify the putential effect of bark stripping on the growth is showen on Figure 16. The curve for control and bark stripped trees followed the same pattern for all of the three groups analysed: young oak, young and old spruce.

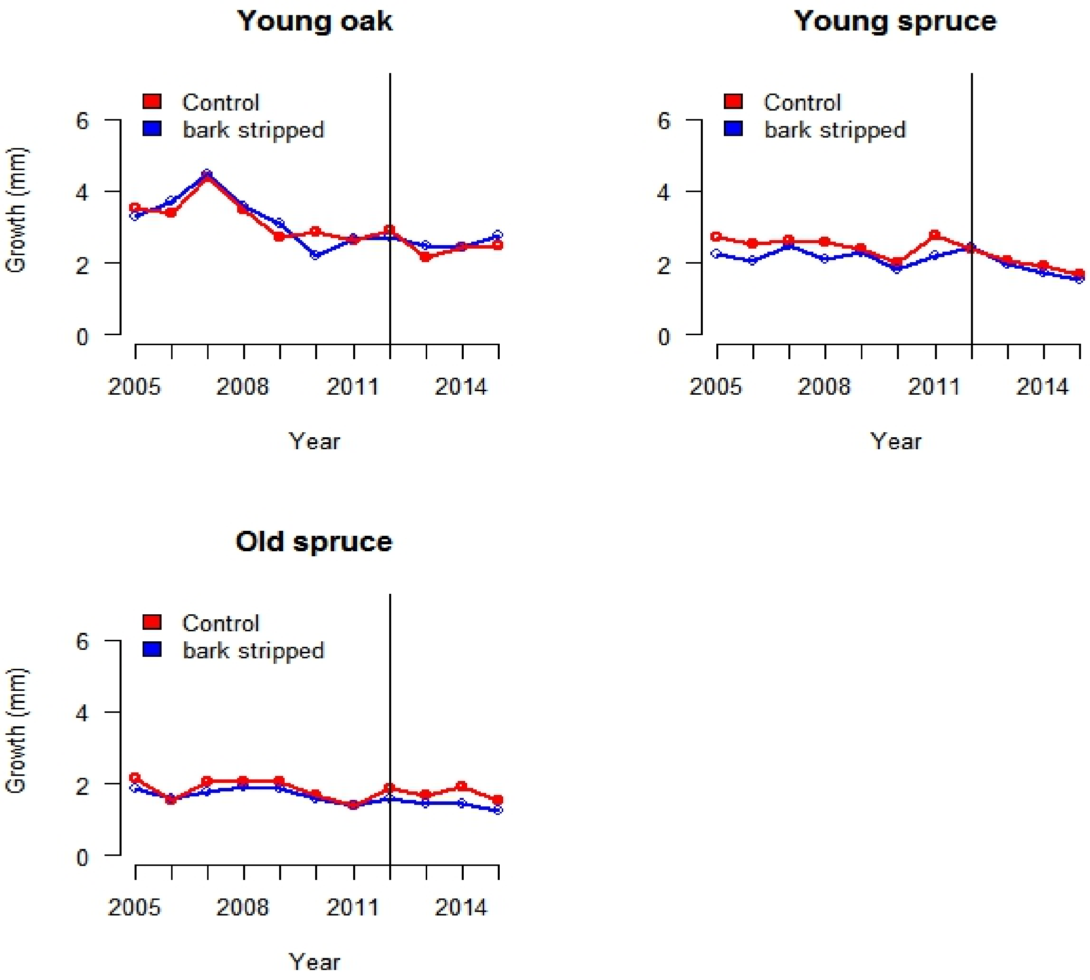

Figure 16. Average growth curve for 12 control and 12 bark-stripped treees of young oak, young and old spruce over time. The vertical line at year 2012 indicates the year of introduction of the European bison

The average growth between non-bark stripped trees and bark stripped trees were compared for separate years and pooled years and no difference was observed (Figure 17). No significant differences were found for either oak or spruce for years separated or pooled (Table 8).

Table 8. P-values of growth for young oak, young and old spruce for years separate and pooled. P-values for years separate were calculated using a T-test where the P-values for the years pooled were calculated using likelihood ratio test.

Species	Year	p-value
Young oak	2013-2015	0.518
Young oak	2013	0.341
Young oak	2014	0.999
Young oak	2015	0.506
Young spruce	2013-2015	0.843
Young spruce	2013	0.605
Young spruce	2014	0.498
Young spruce	2015	0.520
Old spruce	2013-2015	0.531
Old spruce	2013	0.420
Old spruce	2014	0.160
Old spruce	2015	0.342

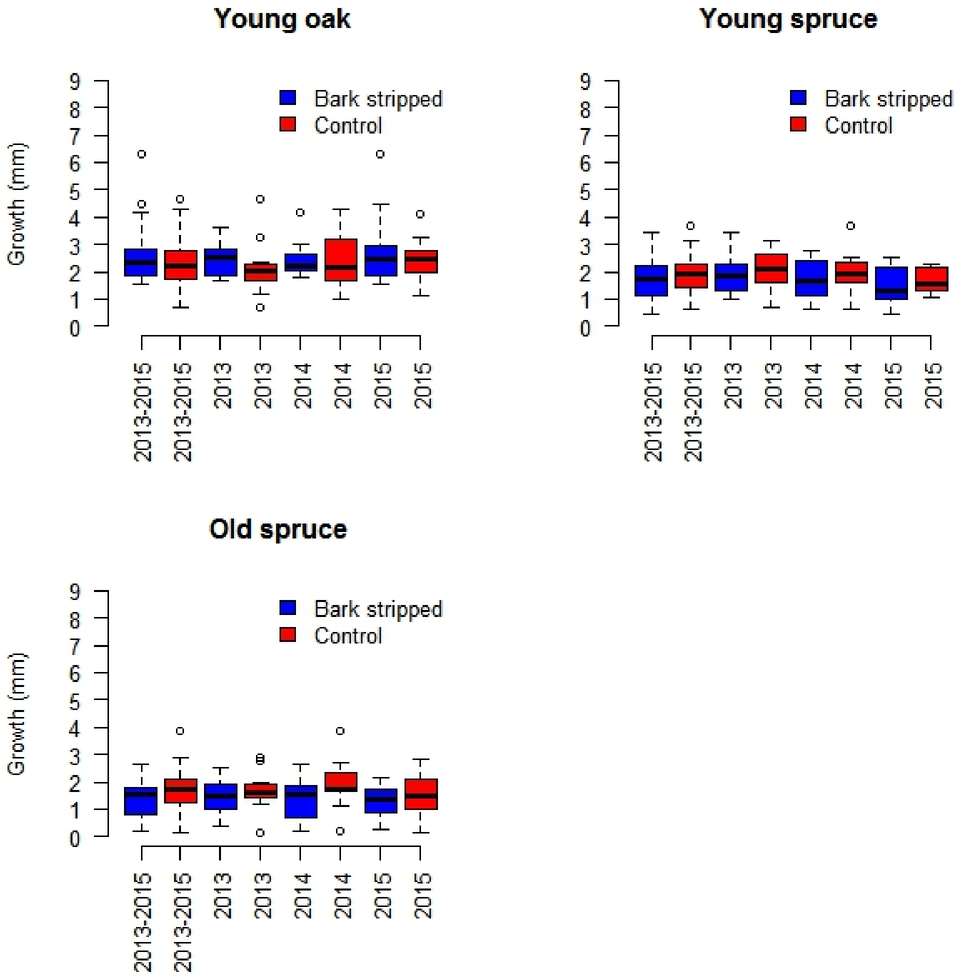

Figure 17. Boxplot for the distribution of growth in mm for years pooled and years separate for young oaks, young and old spruces. Outliers are marked with circles.

The yearly growth of both oak and spruce was affected by climate. For both species, precipitation had the greatest impact on growth, but temperature also played a role. For both spruce and oak, three possible climate models were constructed based on previously cited studies. By running a likelihood ratio, test model 1 proved to be the best fitting model for spruce and model 3 proved to be the best fitting model for oak.

Spruce: Model 1: According to Andreessen et al., 2006, precipitation in June correlated to growth as well as the previous year's temperature in July-September.

Oak: Model 3: According to Anderson et al.et al., 2011 the temperature the previous year's September and October correlated to growth. Precipitation in the full growing season plus the previous year's precipitation in August and September also correlated to growth.

Different variations of the best fitting model were made, linear including or not including interactive effects and a non-linear, with intercepts allowed to vary among individuals as a random factor. A non-linear regression including both precipitation and temperature as the quadratic term gave the lowest AIC value for oak. As this model's t-values of temperature and water as a quadratic term were neither above two or below minus two, a linear model was used not including interactive effects. For spruce, a nonlinear model with precipitation as the quadratic term gave the lowest AIC value. To account for the effect of climate on growth, the predicted growth was subtracted from the measured growth. No big difference is seen between the boxes for bark stripped and non-bark stripped trees (Figure 18). No significant differences on average growth were found between non-bark stripped and bark stripped trees (Table 9).

Table 9. P-values of growth for young oak, young and old spruce for years separate and pooled. P-values for years separate were calculated using a T-test where the P-values for the years pooled were calculated using likelihood ratio test

Species	Year	p-value
Young oak	2013-2015	0.295
Young oak	2013	0.124
Young oak	2014	0.419
Young oak	2015	0.468
Young spruce	2013-2015	0.217
Young spruce	2013	0.328
Young spruce	2014	0.487
Young spruce	2015	0.265
Old spruce	2013-2015	0.612
Old spruce	2013	0.513
Old spruce	2014	0.177
Old spruce	2015	0.542

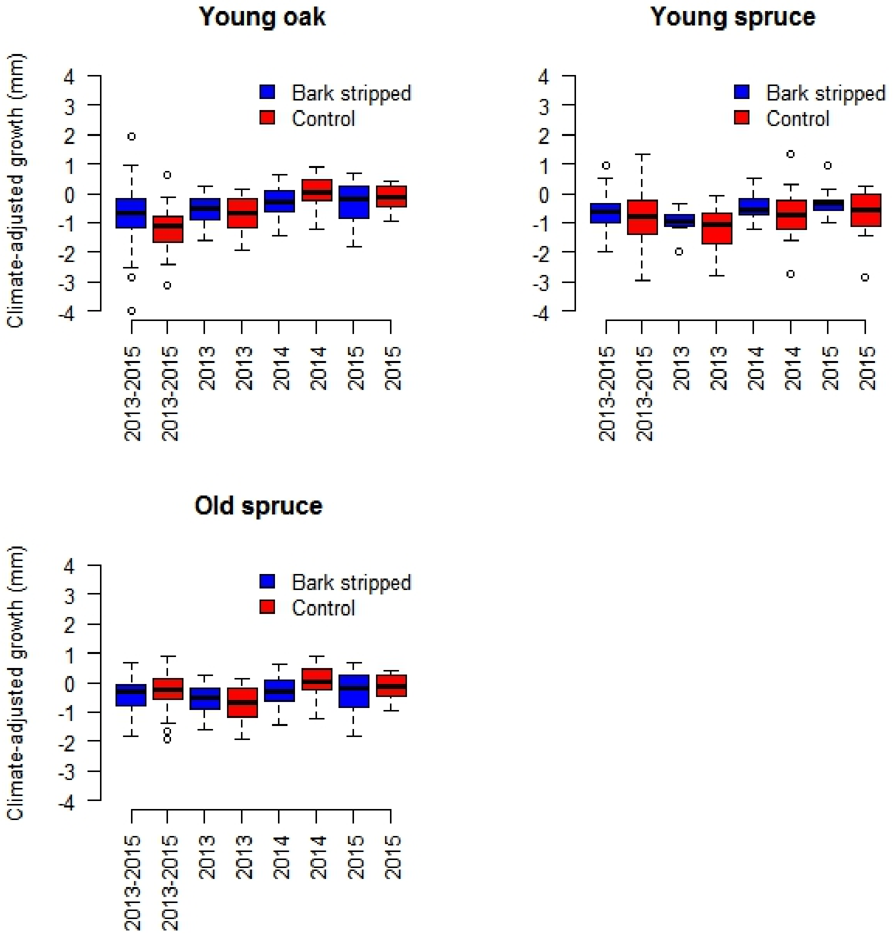

Figure 18. Boxplot for the distribution of growth in mm adjusted for climatic effect for years pooled and years separate for young oaks, young and old spruces. Outliers are marked with circles.

4.4 Site distribution

For each plot in the habitats: young, middle aged, and old oak, and young and old spruce, the respective bark stripping percentages were calculated in 2014 and in 2015 based on data from the 15-metre circles. No plots were found with more than 90% of the total trees' bark stripped. Overall, the percentage of bark stripped trees increased from 2014 to 2015 except for plots 7.4 and 6.1. The highest number of trees bark stripped was found in the habitat young oak for both 2014 and 2015 (Figure 19).

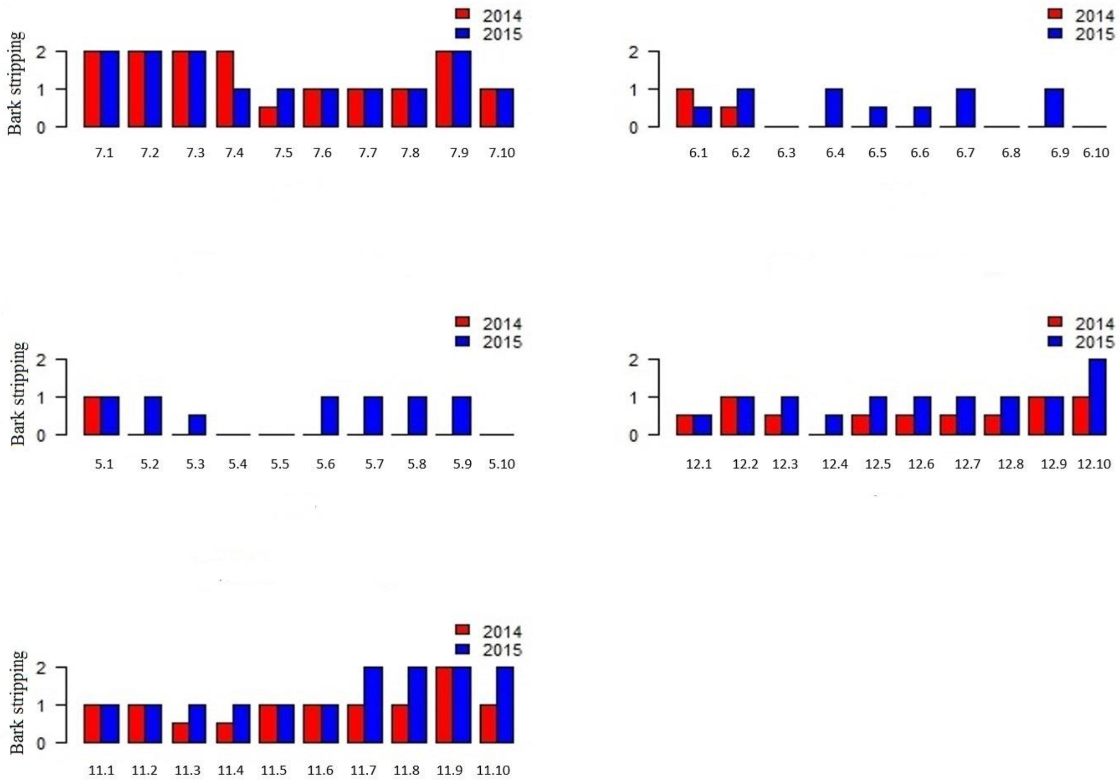

Figure 19. Percentage of trees bark stripped divided into five intervals: 0= 0% bark stripped ,0.5= 0% < x ≤ 10%, 1=10%< x ≤ 50%,2= 50% < x ≤ 90%, and 3= 90% < x ≤ 100% bark stripped for each 15-metre circle within the habitats young-, middle aged and old oak, and young and old spruce.

5. Discussion

Results on size of trees bark stripped by European bison showed that diameter at breast height, hardening of bark and tree density and branchiness of trees are important factors explaining a considerable distribution proportion of the variance in bark stripped trees among young, middle aged, and old oak, and young, and old spruce. The highest frequency of bark stripped oaks was found within young oaks, where the highest frequency for bark stripped spruces was found within old spruces.

5.1 Which trees were bark stripped?

The percentage of trees bark stripped was found to increase from 2014 to 2015 for all plots except plots 7.4 and 6.1. In regard to plot 7.4, the explanation is that plot 20.6 (bushgrass, *Calamagrostis epigejos*) was accidentally mistaken for plot 7.4. This mistake occurred because the GPS was inaccurate up to 15 metres and the two plots were located close to each other. Plot 20.6 contained oaks but not in the same numbers as plot 7.4. For plot 6.1, I have no other explanation than that I must have overlooked some wounds.

The vast majority of wounds were found on oaks ranging from approximately 2 to 15 cm in diameter. This is in line with a study of the food preferences of European bison carried out in Bialowieza (Borowski & Kossak, 1972), where a herd of European bison were found to prefer trees with a diameter between 4 and 15 cm

(Borowski & Kossak, 1972). The logistic regression run as a quadratic equation predicts that the lowest risk of bark stripping will take place when oak reaches a diameter of 30 cm. As trees grow, a hardening of the bark takes place (Campbell et al., 2008). The hardening of bark with age might be a natural explanation. According to the study in Bialowieza, the vast majority of bark stripped spruces should have a diameter between 4 and 15 cm too. However, the bark stripped spruces in this study was found to have a diameter ≤ 30 cm. This shows that the herd of European bison on Bornholm shows a clear preference for larger spruce, which are located in the habitat old spruce. The habitat of old spruce is approximately twice as large as the habitat of young spruce in the enclosure (Jønsson, 2014). A study on the habitat and food preferences of the herd on Bornholm carried out in 2014, revealed that the herd spends more time from October to April in habitats with old spruce in proportion to habitats with young spruce (Jønsson, 2014). As bark stripping is more frequent from late autumn to early spring, the herd's habitat preference could explain the more frequent bark stripping of old spruce (Jønsson, 2014). Another explanation of the abnormal preference for old spruce compared to earlier cited studies could be the high density of young spruces within the plots examined in the present study. A total of 1375 young spruces were examined in 10 plots compared to 477 old spruces. Between 15 to 30 years of age, stems of spruces begin to clear from drying lower branches and smooth bark is exposed according to Čermak et al., (2004). In plots of young spruces, there was approximately 1.5 metres between each tree trunk and the branchiness was high (Jønsson, 2014). This indicates that the young spruces have not yet cleared from drying lower branches even though the trees are between 19-38 years old. The dense vegetation in these plots might make them almost inaccessible for European bison, and consequently reduce the number of bark stripped trees. This hypothesis is supported by a study on red deer bark stripping behaviour made by Sjöström, (1959). As the young spruces are approximately between 15 to 30 years of age, a clear from drying lower branches and smooth bark is exposed to take place soon according to (Čermak et al., 2004). This, together with a thinning which will take place when the majority of the trees reach 30 years, might induce a shift towards a preference for smaller spruces, as the distance between each tree increases and the number of branches decrease (Naturstyrelsen, 2016).

No old oaks were found bark stripped in 2014. Not all wounds examined on old oaks in this study looked new to me (Figure 20). The greatest increase in the percentage of trees bark stripped from 2014 to 2015 was examined within old spruces. The percentage increased by 20.1% from 2014 to 2015 for old spruce. The forest floor within the habitat old spruce were covered with a thick layer of old needles and therefore wounds could have been hidden and consequentially been overlooked (Figure 20). The percent of trees bark stripped in 2014 might had been higher than the data collected by the Danish Nature Agency states, at least for the habitat old oak and spruce.

Figure 20 Wounds on root of old oak and old spruce.

5.2 The location of wounds, number of wounds on each tree bark stripped

The vast majority of wounds were examined on the stem below breast height for both oak and spruce with diameter ≤ 15 cm. For trees with diameter ≥ 15 cm, an approximately equal distribution of trees with wounds on roots and stem below breast height were found. Only two spruces with diameter ≤ 15 cm had wounds on their roots. This is in line with Borowski & Kossak, (1972), where the bulk of wounds located on roots were examined on trees with diameter ≥ 15 cm. One explanation for bark stripping on roots of old trees could be that European bison might eat tree moss (*Isothecium sp.*) which grows on the roots and stems of old trees. European bison might therefore unintentionally bark strip while eating tree moss (Figure 21). Further studies would be needed to confirm this. I have not been able to find information in previous studies on the food preferences of European bison regarding whether they eat moss. Whether this indicates that, it is a local behaviour of the herd on Bornholm to eat moss, or if moss was simply not included in the earlier studies on the food preferences of European bison for other unidentified reasons, is unknown.

Figure 21. Stem moss and indication of bark stripping by European bison

The vast majority of bark stripped trees had more than one wound. This may reflect the habit of European bison to return to the same area, which increases the risk of bark stripping. In addition, bark stripping by red deer in one-year seems to increase the probability of bark stripping the next year (Vaspernik, 2006). I was unable to identify the age of wounds with further details than old or new and thereby it cannot be concluded if wounds on trees with more than one wound were made dependent or independently of time. The amount of trees with more than one wound could indicate that either trees do not use chemical defences, such as tannin, to protect the phloem and xylem against bark stripping or European bison are simply not affected by tannin due to coevolution, which have made browsers able to produce tannin-binding proteins (Rooke et al., 2004). The hypothesis of low tannin content is supported by a study made by Robbins et al., (1987) where they conclude that tree stems have a very small amount of tannin and it does not appear important in the defence of the stem. Instead of tannin, trees use bark as a physical defence to protect xylem and phloem against damage (Robbins et al., 1987). Bark of several species of trees has been found to have a high content of micro minerals and vitamins, but no correlation was found with vulnerability to bark stripping reviewed in Gill, 1992a. Vitamins can be synthesised by ruminants with exception of vitamin A (Gill, 1992a). A study of bark stripping by cattle showed that bark stripping on rowan was linked to a magnesium deficiency, since this element was often deficient in the area but appeared in high concentrations in the bark (Gill, 1992a). Even without tannins, the value of bark as food is low due to the poor nutrient content, slow rate of breakdown and digestion, and, not least, high lignin- content. This supports that the highest frequency of bark stripping takes place in the period from late autumn to early spring, where more nutritious food is scarce. In the current situation, where the herd is supplementary feed in winter the amount of bark as a source of nutrients is expected to hold at an artificial level.

5.3 Is the radial growth affected by bark stripping and does the size of wounds matter?

Bark stripping can be critical for trees and complete girdling was traditionally used as a management method to kill trees. It usually kills trees by preventing sugars reaching the roots (Gill, 1992c). Bark stripping of European bison however, results only in partial girdling and translocation is not completely interrupted. The trees used for sampling increment cores were selected in light of the size of the wounds. The trees with the largest area wounded were selected. Several early European studies have been made on whether or not bark stripping affects the growth and there are differing views (Grill, 1992c). Several studies on red deer bark stripping reported that growth losses could occur, and if bark stripping was serious, growth losses could be as high as 35% (Gill, 1992c). However, many of these studies were poorly designed and lacked controls for environmental effects or had inadequate replication (Gill, 1992c). More recent studies have failed to reveal any significant effects of bark stripping on growth (Grill, 1992c). Many of these previous studies did not report size of wound; probably the most significant factor affecting the growth. Studies based on simulated bark stripping which did take wound size into account showed that a temporary growth reduction can appear but only in the most severe levels of damage (Gill, 1992c).

This study failed to reveal any significant effect of bark stripping on the radial growth, both with and without taking climate into account. This indicates that the level of damage is not severe enough to cause growth reduction, at least in a short-term perspective. If the increment cores had been taken directly in the wounds, a local reduction in radial growth might have been detected due to a local transport allocation problem.

In this event, infection with photogenes such as wood-destructive fungi are likely to be more serious problem of bark stripping than growth loss. How seriously a species is affected, is linked to the growth rate of protective cork tissue (Vorspernik, 2006). Bark stripping by red deer is concentrated to a relatively short period for trees with rapidly thickening bark such as oak, at approximately 5–12 years (Vorspernik, 2006). In contrast, species with slowly thickening bark, such as Norway spruce, can be bark stripped by at least red deer for 15–60 years, and consequently these species are more seriously affected (Vorspernik, 2006). How serious the effect is, is dependent on the size of the wound, the age of the wound and for spruce production of axial resin and, not least, how fast the spices heal (Vorspernik, 2006). Oak heals more rapidly than spruce (Vorspernik, 2006). Wounds on spruces can remain for 15-30 years or even longer. The average of a new cork layer covering bark stripped areas is according to Vasiliauskas, (1996) between 1.5 to 2 mm per year for spruce, and it normally takes more than 20 years to heal a wound 10 cm wide. This factor creates different environmental conditions and may have profound effects on the fungi flora (Vasiliauskas et al., 1996).

Several factors may influence the occurrence of wood-destructive fungi in open wounds. The size has been shown to correlate positively to the occurrence of wood-destructive fungi. Roll-Hansen & Roll- Hansen (1980a) found that infections take place more often in large wounds (80 cm^2) than in small ones (10 cm^2). The mean size of wounds in this study was found to be 66±96cm^2 for oak, 161±299cm^2 for young spruce, and 111±172cm^2 for old spruce. The high standard deviations, indicating a huge size difference between wounds. The wounds contribute to different infection risks correlating to size. High concentrations of resin were found in some of the wounds on spruces, which might prevent infection of wood-destructive fungi and bark beetles. However, fresh resin might attract giant wood wasps (Urocerus gigas) or steely-blue wood wasps (Sirex juvencus) (Thomsen & Harding, 2010). When wood wasps lay their eggs, they place spores of *Amylostereum* on the tree and inject a slime which is toxic to trees (Thomsen & Harding, 2010). As it takes two to three years for the lava of the wood wasp to develop and eat their way through the stem, some of the trees examined might be infected with *Amylostereum* (Thomsen & Harding, 2010).

It would require increment cores from wounds to quantify if the bark stripped trees are infected with wood-destructive fungi, which was not included in this study. How many of bark stripped trees there might be or is infected with wood-destructive fungi on Bornholm is dependent on the quantity of wood destructive fungi in the forest and the number of bark stripped trees logged when thinning takes place.

Previous studies of bark stripping by moose indicates that 16% of Norway spruce bark stripped by moose was infected with the fungus *S. sanguinolentum* five to seven years after wounding and 39% of the bark stripped trees were infected after 15-20 years (Vasiliauskas et al., 1996). The frequency of *S. sanguinolentum* is site specific, 88% of spruces in Poland and 51.9% in Russia was infected (Vasiliauskas et al., 1996). Vasiliauskas et al., 1996 found 5.2% of spruces bark stripped to be infected with *H. annosum* where other authors found the infection rate to be 7– 11%, but it does not necessarily mean infection took place via wounds, because the largest part of the infection with *H. annosum* is via root contact with diseased stumps (Vasiliauskas et al., 1996). Infection with wood-destructive fungi can be beneficial for biodiversity as trees infected with rot provide new habitats for beetles and thereby increase biodiversity, but if too many trees are infected, the stability of the remaining uninfected trees can be affected (Møller, 2010).

On a forest community scale, the introduction of European bison might have an economic effect for forestry - but how large the effect will be is difficult to predict. If the herd is released into the wild, the effects might be minor due to the relatively low number of European bison compared to the size of Almindingen, which is approximately 5000 ha. Furthermore, the behaviour of European bison is unpredictable. Analysis on bark stripped trees in Berleburg showed that the main species damaged after releasing the herd into the wild was beech, at around 80%-90% of the total damage. Spruce was damaged to a small extent even though both are dominant tree species (Trägerverein Wisent-Welt-Wittgenstein e.V, 2016)

5.4 local difference in the bark stripping frequency

Distance to winter feeding areas, forest density, size of trees, branchiness of trees, distance to fence or forest path and tourism are all factors which have been found to affect the likelihood of bark stripping by moose and red deer (Borowski & Kossak; 1972; Vaspernik, 2006). This study cannot conclude with statistical significance if these factors also affect the local differences in percentage of bark stripping by European bison observed in this study, due to the low number of plots. However, the local differences can perhaps show a tendency.

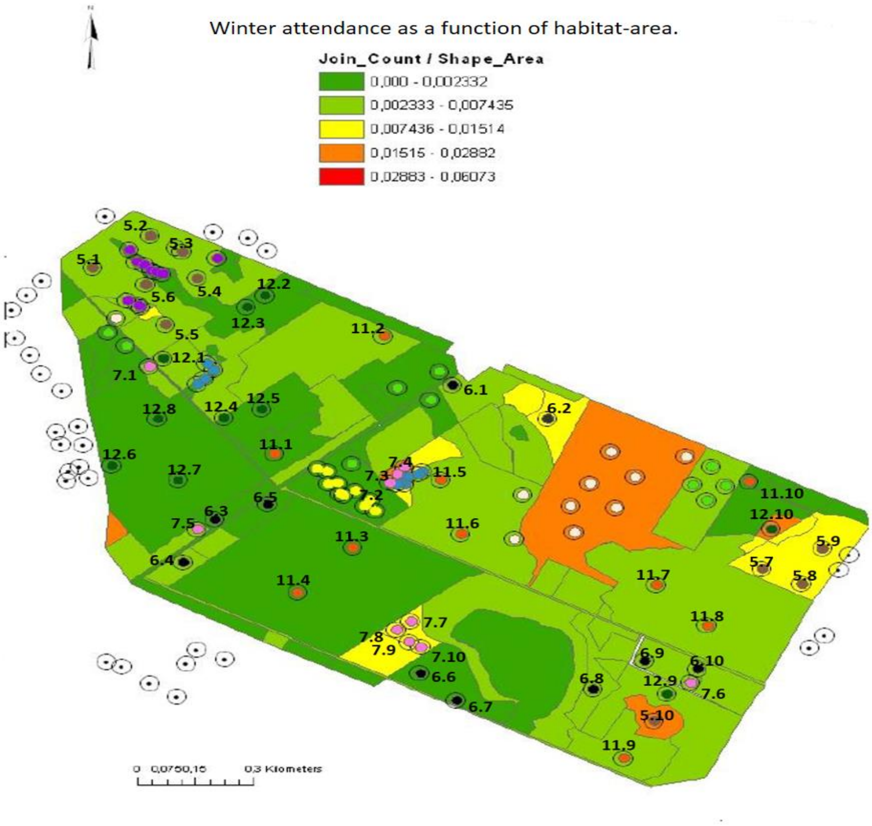

Figure 22 Location of plots within the enclosure (Jønsson, 2014)

This study indicates that factors affecting the likelihood of bark stripping for oaks could be size of trees, distance to fence or forest paths. The highest bark stripping percentage for old spruces was found within areas close to the edge of the fence or close to forest paths. This correlates well with behaviour of red deer and moose (Borowski & Kossak; 1972; Vaspernik, 2006). For young spruces, the main factor controlling local differences in the percentages of trees bark stripped in this study might be the forest density and the number of branches on each tree. The local variations within the frequency of bark stripping might shape islands of highly bark stripped areas within the forest. This might, from a long-term perspective, lead to a more dynamic forest with increasing biodiversity. Stems infected with rot will provide habitats for beetles which provide food for many birds if they are not removed.

This study failed to show any effect of bark stripping on the radial growth of both spruce and oak, with and without taking the climate into account.
The mean size of wounds in this study was found to be be 66±96cm^2 for oak, 161±299cm^2 for young spruce, and 111±172cm^2 for old spruce. According to Roll-Hansen & Roll Hansen, (1980a) infection will occur more often in large bark strips (80 cm^2) than in small ones, (10 cm^2).
The size of bark strips found in this study indicates that the greatest impact of bark stripping on a forest community scale can be expected to be the increased risk of infection with wood-destructive fungi and, as a result, reduction in wood quality. From a biological perspective, the infection with wood-destructive fungi can induce new habitats for, e.g. bark beetles and birds.

6. Conclusion

In this study, an analysis was carried out on whether bark stripping affects the radial growth of spruce and oak. This analysis contributes to the knowledge of effects of bark stripping as it had controls for environmental effects. As the radial growth differs between different individuals within a plot, more replication could have been made if I had had more time. This study has not found any significant impact on the radial growth. This study provides information on the size of wounds, the amount of wounds per tree and the location of wounds which, to my knowledge, have not been analysed before for European bison. This information provides useful knowledge, both on a forest community scale, and from a biological perspective on how European bison might affect spruce and oak, as wound size has been documented to correlate with infection rate of parasitic fungi and bark beetles.
The Danish Nature Agency wants to protect and increase the quality of habitats with rare, threatened and endemic flora and fauna and to provide the natural environment with different habitats. Wood-destructive fungi might, from a long-term perspective, contribute to a more open forest as some of the infected trees might fall. To quantify if bark stripping could contribute to this by infection, further longer-term analyses would be needed.
As a management plan to be able to quantify if bark stripping might positively contribute to the formation of different habitats, I suggest that increment cores are taken within large wounds in each plot within the habitats of old, young spruce, and young oak every second year. As Roll-Hansen & Roll-Hansen (1980a) found infection to take place more often in large bark strips (80 cm^2) than in small ones (10 cm^2). I might suggest only taking increment cores from wounds ≥ 80 cm^{2,} as it is a time-consuming process. As the amount of bark stripping differed in different parts of a forest in studies made on moose and red deer, due to distance to winter feeding areas, forest density, size of trees, branchiness of trees, distance to fence or forest path, or tourism (Borowski & Kossak; 1972; Vaspernik, 2006) I suggest making more plots to be able

to provide information on if the distribution of bark stripping in different local areas made by Europeans are affected by the same factors on a statistical level.

Another important factor in correlating how large the effect of European bison will be is to find out how large a part of the food intake bark accounts for in the current situation where supplementary feeding takes place in winter. This can be done by DNA analyses of the faeces. Perhaps, before the herd is released into the wild I suggest ceasing the supplementary feeding to establish how large a part of the food bark accounts for in a natural situation and to see if the herd changes behaviour in regard to preference of specific species of trees or size of trees bark stripped.

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Appendix

Appendix 1.

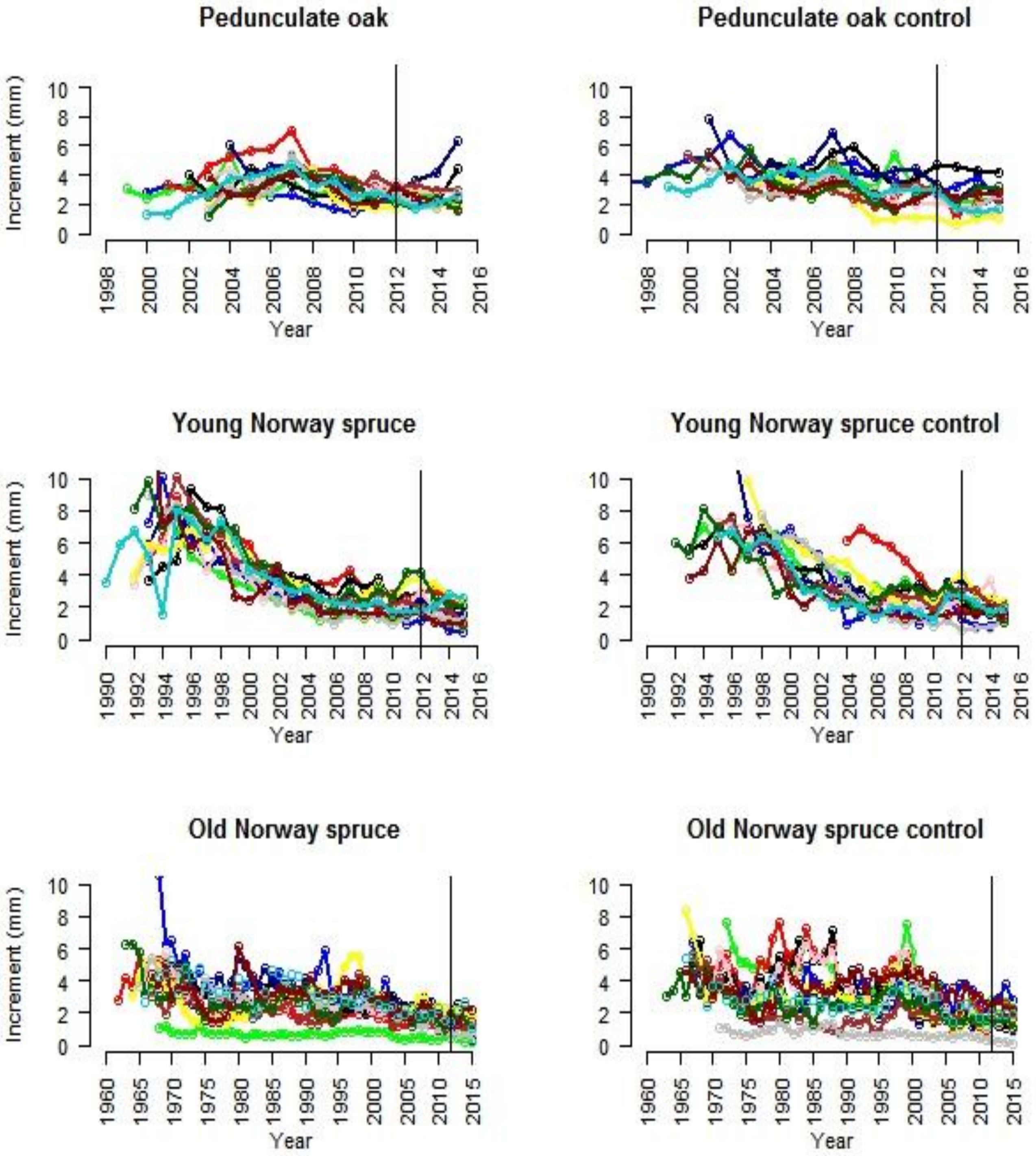

Figure 23 Growth curve for 12 control and 12 bark-stripped treees of young oak, young and old spruce over time. The vertical line at year 2012 indicates the year of introduction of the European bison. Colour of samples and controls: 1= black, 2=red, 3= light green, 4= light blue, 5= turkis, 6=pink, 7=yellow, 8= 9= dark grey, 10= orange, 11= dark green, 12= dark blue

Appendix 2

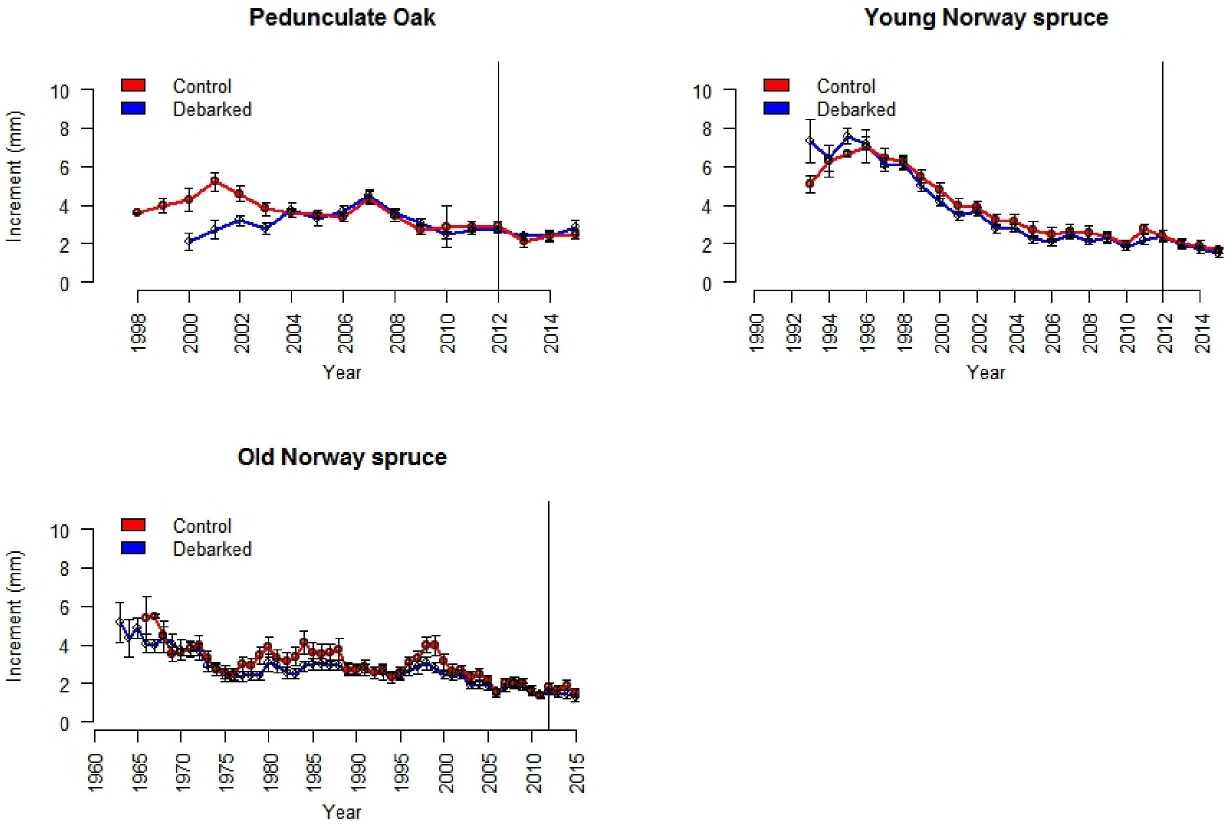

Figure 24 Average growth curve for 12 control and 12 bark stripped treees of young oak, young and old spruce over time with SEM (Standard mean of error). The vertical line at year 2012 indicates the year of introduction of the European bison

Appendix 3

Table 1: Size of bark strips for young oak, young and old spruce

Young oak size of bark stripes (cm^2)	Young spruce size of bark stripes (cm^2)	Old spruce size of bark stripes (cm^2)
30	140	6
30	700	115
81	195	70
26	40	95
40	57	171
108	140	270
77	32	112
14	8	65
42	30	390
40	16	18
195	12	4
132	98	8
184	160	10
70	52	138
68	224	12
12	104	12
552	60	120
76	56	12
60	52	1380
27	120	36
24	32	40
10	200	4
540	175	245
40	45	48
6	21	52
72	930	72
250	2000	120
52	60	96
10	50	60
5	1062	84
10	102	88
124	30	60
312	40	380

24	18	24
30	20	60
12	320	138
9	80	66
20	105	414
43	100	182
175	24	18
52	14	24
8	54	660
48	15	81
9	60	216
54	288	48
32	36	70
6	27	144
8	84	15
78	21	40
64	21	126
32	196	50
18	27	9
10	266	350
1	300	64
3	240	63
85	98	144
24	116	289
36	36	160
16	120	360
5	24	66
10	583	182
99	30	18
36	39	80
10	72	16
18	91	65
30	27	48
8	18	66
24	304	182
20		18
264		80
117		16
64		65
12		48
4		12
117		182

64	24
312	4
44	24
16	21
16	33
72	28
44	9
24	9
48	8
87	4
150	12
177	80
72	40
84	60
60	12
5	570
32	175
102	60
52	18
4	296
18	200
30	56
100	42
468	48
18	30
30	48
14	36
5	132
12	99
7	
22	
3	
3	
3	
9	
1	
10	
22	
215	
25	
50	
9	

40
2
6
8
2
22
8
24
312
12
60
45
45
39
186
51
100
20
261
138

Appendix 4

spruce

Model 1: According to Andreessen et al., (2006), precipitation in June correlated to growth as well as the previous year's temperature in July-September.

Model 2: According to Andreassen et al., (2006), May, July and August precipitation also showed a correlation on the growth. This model includes precipitation from May to August as well as the previous year's temperature in July to September.

Model 3: According to the Bornholm Danish Nature Agency, the growth season of Norway spruce starts in April on Bornholm. This model includes precipitation from April to August as well as the previous year's temperature in July to September.

Mod1= temp1 and precipitation1
Mod2= tem1 and precipitation2
Mod3= temp1 og precipitation3

```
anova(mod2, mod1)
refitting model(s) with ML (instead of REML)
Data: Climate
Models:
mod2: inc ~ precipitation2 + temp1 + (1 | ind)
mod1: inc ~ precipitation1+ temp1 + (1 | ind)
    Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod2  5 1278.3 1297.6 -634.13   1268.3
mod1  5 1134.6 1154.0 -562.32   1124.6 143.62      0  < 2.2e-16 ***
---
```

```
anova(mod3,mod1)
refitting model(s) with ML (instead of REML)
Data: Climate
Models:
mod3: inc ~ precipitation3 + temp1 + (1 | ind)
mod: inc ~ precipitation1 + temp1 + (1 | ind)
    Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod3  5 1286.0 1305.3 -638.00   1276.0
mod1  5 1134.6 1154.0 -562.32   1124.6 151.36      0  < 2.2e-16 ***
```

```
anova(mod3,mod2)
refitting model(s) with ML (instead of REML)
Data: Climate
Models:
mod3: inc ~ precipitation3 + temp1 + (1 | ind)
mod2: inc ~ precipitation2 + temp1 + (1 | ind)
    Df    AIC    BIC  logLik deviance Chisq Chi Df Pr(>Chisq)
mod3  5 1286.0 1305.3 -638.00   1276.0
mod2  5 1278.3 1297.6 -634.13   1268.3 7.741      0  < 2.2e-16 ***
```

Continues with mod1
Different version of mod1

mod: temp1 + precipitation1
mod2:temp1* precipitation1
mod3: precipitation1 + temp1 + I(temp1^2) + I(precipitation1^2)

```
Data: Climate
Models:
mod: inc ~ precipitation1 + temp1 + (1 | ind)
mod2: inc ~ precipitation1 * temp1 + (1 | ind)
    Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod   5 1134.6 1154.0 -562.32   1124.6
mod2  6 1131.4 1154.6 -559.72   1119.4 5.2063      1    0.02251 *
---

anova(mod1,mod3)
refitting model(s) with ML (instead of REML)
Data: Climate
Models:
mod: inc ~ precipitation1 + temp1 + (1 | ind)
mod3: inc ~ precipitation1 + temp1 + I(temp1^2) + I(water1^2) + (1 | ind)
    Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod   5 1134.6 1154.0 -562.32   1124.6
mod3  7 1112.7 1139.8 -549.36   1098.7 25.921      2  2.352e-06 ***


> summary(mod3<-lmer(inc~ precipitation1+temp1+I(precipitation1^2)+I(temp1^2)+ (1|ind) , data=Climate))
Linear mixed model fit by REML ['lmerMod']
Formula: inc ~ precipitation1 + temp1 + I(precipitation^2) + I(temp1^2) + (1 | ind)
   Data: klima

REML criterion at convergence: 1142.6

Scaled residuals:
    Min       1Q   Median       3Q      Max
-3.06180 -0.61389 -0.07014  0.59798  3.04992

Random effects:
 Groups   Name        Variance Std.Dev.
 ind      (Intercept) 0.3784   0.6151
 Residual             1.1864   1.0892
Number of obs: 353, groups:  ind, 24

Fixed effects:
             Estimate Std. Error t value
(Intercept) 10.3418011 12.6249376   0.819
water1      -0.0253048  0.0116346  -2.175
temp1       -0.1587523  0.5073459  -0.313
I(water1^2)  0.0005252  0.0001018   5.160
I(temp1^2)   0.0001202  0.0051156   0.023
```

As the t value for temp^2 is not either above or below minus two it is not included.

```
AIC(modz5<-lmer(inc~ precipitation1+temp1+I(precipitation1^2)+ (1|ind) , data=Climate))

[1] 1145.845
```

Without temp^2 a lower AIC value was obtained and therefor this model was used.

Oak

```
Climate=read.csv("C:/Users/Betina/Dropbox/bison/rapport/Climate 7.csv", header= TRUE)
```

Model 1: According to Drosbyhevet et al., (2008) summer temperature plus temperature in October the previous year correlated to growth. Precipitation in June and July plus the previous year's precipitation during the growth season also correlated to growth.

Model 2: According to Anderson et al., (2011) the previous year's temperature in September and October correlated to growth. Precipitation from March to June plus the previous year's precipitation in August and September also correlated to growth.

Model 3: According to Anderson et al.et al., (2011) the previous year's temperature in September and October correlated to growth. Precipitation in the full growing season plus the previous year's precipitation in August and September also correlated to growth.

Mod1= temp1 and precipitation1
Mod2= tem2 and precipitation2
Mod3= temp2 og precipitation3

```
anova(mod2,mod1)
Data: Climate
Models:
mod2: inc ~ Precipitation2 + temp2 + (1 | ind)
mod1: inc ~ Precipitation1 + temp1 + (1 | ind)
     Df    AIC    BIC  logLik deviance Chisq Chi Df Pr(>Chisq)
mod2  5 768.54 786.57 -379.27   758.54
mod1  5 778.45 796.48 -384.23   768.45     0      0          1
```

```
anova(mod1,mod3)
Data: klima
Models:
mod1: inc ~ Precipitation1 + temp1 + (1 | ind)
mod3: inc ~ Precipitation3 + temp3 + (1 | ind)
     Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod1  5 778.45 796.48 -384.23   768.45
mod3  5 761.91 779.94 -375.95   751.91 16.545      0  < 2.2e-16 ***
refitting model(s) with ML (instead of REML)
```

```
anova(mod2,mod3)
Data: klima
Models:
mod2: inc ~ Precipitation2 + temp2 + (1 | ind)
mod3: inc ~ Precipitation3 + temp3 + (1 | ind)
     Df    AIC    BIC  logLik deviance  Chisq Chi Df Pr(>Chisq)
mod2  5 768.54 786.57 -379.27   758.54
mod3  5 761.91 779.94 -375.95   751.91 6.6364      0  < 2.2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Model 3 the bedst model

Different version of mod3

mod: temp1 + precipitation1
mod2:temp1* precipitation1
mod3: precipitation1 + temp1 + I(temp1^2) + I(precipitation1^2)

```
AIC(modz1<-lmer(inc~ precipitation3+temp3+ (1|ind) , data=klima))
[1] 782.7828
AIC(modz2<-lmer(inc~ precipitation3*temp3+ (1|ind) , data=klima))
[1] 792.9949
AIC(modz3<-lmer(inc~ precipitation3+temp3+I(water3^2)+ (1|ind) , data=klima))
[1] 806.4272
AIC(modz4<-lmer(inc~poly(precipitation3,2)+poly(temp3,2) + (1|ind) , data=klima))
[1] 759.3778
summary(modz4)
Linear mixed model fit by REML ['lmerMod']
Formula: inc ~ poly(precipitation3, 2) + poly(temp3, 2) + (1 | ind)
   Data: klima

REML criterion at convergence: 745.4

Scaled residuals:
    Min      1Q  Median      3Q     Max 
-2.1098 -0.6315 -0.0688  0.4864  3.5434 

Random effects:
 Groups   Name        Variance Std.Dev.
 ind      (Intercept) 0.3136   0.5600  
 Residual             0.8181   0.9045  
Number of obs: 272, groups:  ind, 23

Fixed effects:
                         Estimate Std. Error t value
(Intercept)                3.3843     0.1300  26.029
poly(precipitation3, 2)1   2.9689     1.3496   2.200
poly(precipitation3, 2)2   0.9651     1.1090   0.870
poly(temp3, 2)1            4.9299     1.0030   4.915
poly(temp3, 2)2           -0.2373     1.2598  -0.188
```

```
AIC(modz5<-lmer(inc~ precipitation3+temp3+I(precipitation3^2)+I(temp3^2)+ (1|ind) , data=klima))
[1] 815.2315
```

Model 4 gave the lowest AIC, but as the t- value for both precepitaion^2 and temp^2 was not either above or below minus 2 model 1 was used.