Factors affecting regeneration of *Quercus robur* in Białowieża Primeval Forest

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Abstract/Summary

Reasons for the apparent low density of *Quercus robur* recruits in Białowieża Primeval Forest are unclear. In this study we investigated the effects of facilitation by protective structures, negative effects of presence of mature *Quercus robur* and effects of forest type on the regeneration of oak saplings in the forest. Data was collected from 47 km of transects and on two scales: a large scale survey of forest characteristics using plots every 50 metres along the transects and a local scale survey of sapling characteristics and environment using plots centred on all of the 161 saplings found along the transects and nearby paired control plots. The study area consisted of a strictly protected area, and an area subject to limited management. Facilitation by protective structures, predominantly dead *Picea abies* debris, was shown to be particularly important for larger saplings due to their higher vulnerability to browsing. Presence of mature *Quercus robur* had no significant effect on sapling success. Saplings showed a strong tendency to be found in coniferous forest types as measured on the large scale but not necessarily to be found in proximity to coniferous individuals at the local scale. This forest type preference can be attributed to greater abundance of *Picea abies* debris as a source of protection in coniferous forest types; a weakened preference for these forest types was found in areas where tree debris was removed indicating that forest type preference is caused by high levels of tree debris in coniferous forest types.

Introduction

The post-germination phase during which a seedling grows to be an established young tree is a time of great vulnerability for most tree species. At this time even the upper-most leaves are reachable for browsing herbivores, fast growing competitors may deprive the sapling of light and young trees are at risk from disease and parasites from the parent. An understanding of the dynamics of this process of establishment is central to determining the future canopy composition of wooded areas and would help in making management decisions should regeneration of specific tree species be desirable.

A much discussed aspect of the process of tree recruitment is its relationship with herbivory. Studies in both established forests and forest restoration areas have shown that the impact of herbivory, particularly that of ungulates, on regeneration of palatable tree species can be severely limiting to sapling growth (Fuller and Gill 2001). Conversely it has also been proposed that certain tree species cannot regenerate without specific herbivore driven vegetation dynamics (Vera 2000). Other studies have suggested that herbivory has a marked effect on vegetation (Didion, Kupferschmid et al. 2009; Kuijper, Cromsigt et al. 2009).

The phenomenon of facilitation, by which one species positively contributes to the survival of another, has been shown to be important for tree sapling regeneration in various open woodland environments (Callaway 1992; Rousset and Lepart 2000; Smit, Vandenberghe et al. 2007; Smit, Béguin et al. 2009; Smit, den Ouden et al. 2009). Likewise physical structures such as logs and rocky outcrops may also provide a degree of protection to young trees (Smit, Béguin et al. 2009). These so-called 'nurse structures' and 'nurse plants' shelter growing saplings from extreme weather and excessive browsing by herbivores, increasing their chances of survival. Such protection is considered to be most important in high stress environments (Smit, Vandenberghe et al. 2007), such as heavily browsed wood pastures or arid areas but may also be crucial in moderately browsed closed canopy forest. An exposed sapling will benefit from extra light, but suffer from its vulnerability to grazing and harsh weather whereas a protected sapling will grow slowly from lack of light but be less accessible to grazers and benefit from a sheltered micro-climate. Sapling size has also been shown to be a factor, with larger saplings being more limited by browsing than smaller ones. (Kuijper et al. in prep.)

Another effect to be considered has been outlined in the Janzen and Connell hypothesis, whereby tree recruitment occurs preferentially away from the parent tree, due to disease, seed predation and parasitism (Janzen 1970; Connell 1971). This effect causes greater spatial variety of tree species since clumping of trees is not favourable. The hypothesis was applied especially to tropical forests but a similar effect could appear in particularly dense temperate forest.

In the Białowieża Primeval Forest *Quercus robur* is a major component of old growth stands, but since 1936 numbers of new oak recruits have decreased significantly (Bernadzki et al. 1998, Kuijper et al. in prep.). Understanding facilitation, the effects of mature tree presence and any preferences for forest type could be crucial in explaining the dynamics of *Quercus robur* regeneration in the area. According to the Janzen and Connell hypothesis it could be the presence of mature oaks that is preventing sapling growth. There have been cases where tree regeneration has failed due to grazing pressure (Palmer, 2002), and others where it has succeeded in the presence of grazers. The key difference could well be a factor such as facilitation by certain shrub species or protective structures. An oak sapling has the disadvantage of being both palatable and light demanding, meaning that it requires a certain degree of protection from grazers to outgrow other species, but such protection cannot be so dense as to deprive it of light. Is the decline in oak dominance caused by such conditions being rare in the forest?

This perceived lack of oak regeneration may also be a result of any regeneration that is occurring being in an unexpected place. Not only could the effect of mature trees of the same species described by Janzen and Connell and mentioned above be driving oak regeneration away from forest types containing mature oak, but there are also other effects to be considered. The first of these is a documented case of preferential acorn dispersal by Jays to coniferous forest types (Healy 2002) which could also be occurring in Białowieża. Secondly, since oak is a light demanding species, the high levels of disturbance typically found in coniferous forest types as a result of pine beetle activity may favour its regeneration.

In this paper we focus on the effect of mature *Q. robur* presence, forest type and presence of protective structures on recruitment of *Q. robur* saplings. Many other forest characteristics were measured to give a broader description of favourable recruitment conditions. Specifically we tested:

1) Does the presence of protective structures positively impact sapling presence and height?

2) Does proximity to mature *Q. robur* have a negative impact on sapling presence?

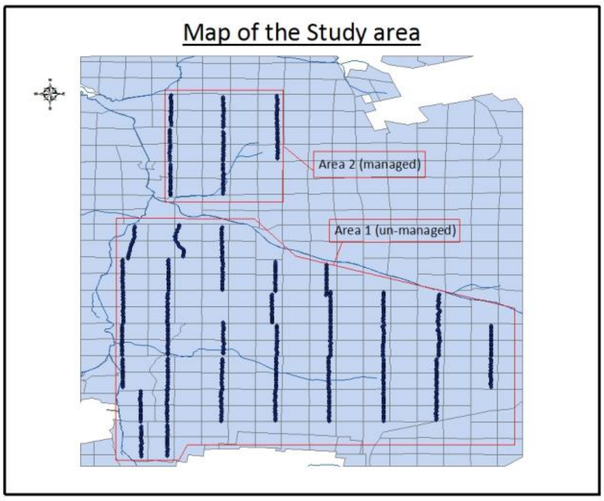
3) Is successful sapling establishment more likely in coniferous forest types?

Methodology

Study site

The Białowieża Primeval Forest (BPF) stretches across eastern Poland and into Belarus covering a total area of over 145,000 hectares, making it the largest lowland, old growth forest in Europe. The strictly protected part of the forest on the Polish side, the Białowieża National Park, situated just north of the village of Białowieża, is an area of relatively undisturbed primeval forest resting on the border between temperate and boreal climatic zones. It is "relatively" undisturbed in that while there has been hunting and game management in the forest during its time as a royal hunting reserve and extensive culling during the WO-I and WO-II, it has not been subjected to clear-cutting. The forest has been under strict protection against logging since 1541 and has been protected from all disturbances since its designation as a national park in 1921. The BNP consists of an un-managed strict reserve area of $47km^2$ in which research related activity and guided tourism is permitted (Area 1 on map 1), and an area subject to limited management in which the removal of dead *Picea abies* and *Pinus sylvestris* is permitted (Area 2 on map 1). The two forest areas are otherwise similarly protected. During the 19th century under tsarist Russia a grid based organisational unit was introduced for use in the forest. Each c. 1 km^2 compartment was numbered from west to east and north to south, and these compartments were further divided into four c. $500m^2$ sections.

Map 1 *– The study area and transects*



The forest is home to a great diversity of vegetation and, being on the border between temperate and boreal zones, is also made up of diverse deciduous, coniferous and mixed forest types. A list of major tree species in the forest would include *Picea abies*, *Pinus sylvestris*, *Carpinus betulus*, *Tilia cordata*, *Alnus glutinosa*, *Quercus robur*, *Acer platanoides*, *Fraxinus excelsior*, *Betula pubescens* and *Populus tremula,* though this is by no means a complete list of plant species in the area. Comprehensive surveys of the vegetation have been performed, yielding a list of some 632 vascular plants, 254 lichen species, 80 liverworts and over 3000 species of fungi (Falinski 1986). Another distinguishing feature of the forest is the presence of a variety of large mammals, most famously the

European bison, but also red and roe deer, wild boar, wolves and lynx. There are a total of 54 mammalian species, 232 bird species and 8,500 known insect species.

Data Collection

Transect lines were laid down during a previous study (van Eerbeek, Blanckaert et al. 2009) on a north to south line through the centre of 47 1-km^2 forest compartments described above (See map 1). Data collection was done in two distinct stages using these transects.

Firstly large scale characteristics of the forest were used from van Eerbeek & Blanckaert 2009 which were assessed by setting up plots at 50 metre intervals along the transects. The dominant tree species was recorded and overall forest type was classed as deciduous, coniferous or mixed. Soil moisture was categorized into four classes: 1) Dry, 2) mesic, 3) wet and 4) Bog. Canopy cover was estimated visually and grouped into seven percentage classes: 1) closed 0%, 2) 1-20%, 3) 20-40%, 4) 40-60%, 5) 60-80%, 6)80-90% and 7) 100%. Number of visible mature oak over 12 metres in height was recorded. This data was available for use from a previous study in the area (van Eerbeek, Blanckaert et al. 2009)

Using the same transects we collected data on characteristics of oak sapling regeneration sites at a finer scale. The transects were walked again and 1m^2 plots were set up when a *Quercus robur* sapling (less than 3m in height) was detected within 1 metre of the transect line. In the case of single saplings, plots were placed with the sapling base as the centre of the plot. In the case of multiple saplings within 1 metre of each other the plot boundary was placed to include them all. For each sapling plot a control plot was sampled. Control plots were placed 50 metres to the east of their paired sapling plots. To assess forest type in the local area the species and diameter of the nearest four mature trees to the centre of each plot was recorded. The distance of these four trees from the plot centre was also recorded as a rough guide to forest density at each plot location. The mean distance and diameter of these four trees was noted. Cover of herbs, shrubs, moss and leaf litter were noted down as a measure on the Londo scale (Londo 1970), and later converted to median percentage values for the analysis. Level of protection was assessed by measuring the height and distance away from the plot centre of dense shrubs or solid objects and noting down by how many degrees they surrounded the plot. Degrees of protection was ranked as 0, 90, 180, 270 or 360 degrees. In the case of multiple protective structures surrounding a plot, their mean height and distance away were used. Light availability was measured by taking a photograph directly upwards at a 1m height above the plot centre. These photographs were later analysed to determine the percentage of cover of tree canopy and open sky visible in the image using MATLAB v7.9.

All oak saplings (less than or equal to 3 meters in height) were counted and their heights were measured. Saplings were also examined to determine browsing intensity. This was done by counting how many of the saplings branches had been browsed and then expressing this as a percentage of the total number of branches.

Whilst sampling, the coordinates of all plots were recorded using a handheld GPS (Garmin C60Sx). This allowed us to combine the location of saplings and their associated data with the large scale measurements that were taken every 50 metres. The large scale plot closest to each sapling plot was given a value of 1 for sapling presence and all other large scale plots received a 0 representing sapling absence.

Data analysis

Data analysis was performed using SPSS v16.0 and R v2.10. The mean values of protection height, protection distance, moss cover, herb cover, leaf litter cover, light availability, average tree diameter and average tree distance for sapling plots and control plots were compared using a t-test. The significance of differences in the categorical variables degrees of protection and mature oak presence for sapling and control plots were tested using Pearson's chi square test. These results are displayed in table 1.

A Pearson's Chi square test was performed to determine whether management had a significant effect on presence of protective structures. Effects of the above variables on sapling presence were also analysed together on both large and small scales using binomial logistic regression models. A correlation matrix of all the predictor variables was first made to remove highly correlated predictor variables. In the case of highly correlated predictor variables the one with the lowest significance value from the previous t-test was removed. We then began with testing a full model including all variables and their interactions. Model selection was applied to come up with the most parsimonious model. Beginning with the variable with the highest p value variables were excluded from the model. If their exclusion improved the model fit, by reducing AIC value by >4, then they were left out of the model. Binomial regression models were also run with the data separated into area 1 (un-managed) and area 2 (managed), for both the large and small scales. The same model selection procedures were applied to these models.

A multiple regression model was made to determine the best combination of predictor variables to explain trends in sapling height on the small scale. The first round of model selection was performed by making a correlation matrix of all the predictor variables and sapling height. Variables whose correlation with sapling height was not significant (Sig. > 0.05) were excluded. In the case of two strongly correlating predictor variables the less significant of the two was removed. All possible combinations of the remaining predictors were run in the model and the run with the highest R^2 value was selected as the final model.

Level of browsing was plotted against degrees of protection for all saplings and then for saplings above and below 50cm in height.

Data on the dominant tree species and locations of saplings on both scales was used to calculate Jacob's selectivity indices for all the dominant tree species. The index estimates the likelihood of a sapling being located in an area where a particular tree species is dominant by taking into account the proportion of total saplings found associated with a particular tree species relative to the abundance of that tree species across all the plots. The results of this analysis are shown in figures 5 and 6. The calculation is shown below:

Jacob's Index = (r-p)/(r+p-2r*p)

p = number of plots with species x dominant / total number of plots

r = number of plots with species x dominant and sapling presence / number of plots with sapling presence

Results

A total of 161 saplings were found in 147 plots. The discrepancy between number of plots and number of saplings is due to 14 plots having 2 saplings within the $1m^2$. Of all 294 plots sampled (147 sapling plots and 147 control plots) 159 were sheltered by protective structures in some way. 138 of these structures were debris of dead spruce in the form of logs or piles of branches. Average height of saplings in the un-managed area was 61cm and in the managed area it was 33cm.

The major factors affecting sapling presence (Table 1) are height of protection and surrounding degrees of protection. Average distance of the four nearest trees to the plot centre is also significant, i.e. saplings are more likely to be found in less dense forest areas. Light availability is not a significant factor in determining sapling presence at this scale.

Table 1 *– Mean values of plot characteristics for plots where saplings are present and plots where saplings are absent.*

Variable	Mean (presence)	Mean (absence)	Significance
Protection height (cm)	**0.52**±0.5	**0.28**±0.41	**0.000**[2]
Protection degrees (°)	**113.5**±114.52	**56.3**±87.53	**0.000**[1]
Light availability (%)	**39.7**±15.58	**37.54**±17.18	**0.280**[2]
Herb cover (%)	**31**±28.63	**24.74**±26.43	**0.049**[2]
Moss cover (%)	**38**±35.7	**27.95**±33.89	**0.01**[2]
Leaf litter cover (%)	**51.7**±36.77	**59.76**±37.5	**0.061**[2]
Tree diameter (cm)	**22.19**±8.47	**22**±9.62	**0.595**[2]
Tree distance (metres)	**3.9**±1.27	**3.36**±1.49	**0.001**[2]
Oak presence	**n/a**	**n/a**	**0.292**[3]

[1] = Kruskall – Wallis test

[2] = T – test

[3] = Pearson's chi square test

Presence and absence of saplings

In the small scale binomial logistic regression model (table 2) degrees of protection is the most significant promoter of sapling presence that was measured having a p value < 0.01. Its positive coefficient tells us that it encourages sapling presence. Protection height has a p value below 0.05, and so is also significant. Distance of protection is shown to be significant, but its negative coefficient implies that the further away the protection, the less likely a sapling is to be present. Distance of mature trees, light, moss and mature oak presence are also flagged for having p values smaller than 0.1 do not explain a significant part of the variation.

Table 2 *- Binomial logistic regression: Small scale*

Variable	**Coefficient**	**Std. error**	**z value**	**Pr>(z)**
Intercept	-1.095249	0.699076	-1.567	0.11718
herb	0.006373	0.005272	1.209	0.22673
leaf litter	-0.004326	0.005719	-0.756	0.44941
distance	0.205737	0.117287	1.754	0.07941
diameter	0.001097	0.015510	0.071	0.94363
Oak (y)	0.537944	0.277794	1.936	0.05281
light	-0.018587	0.009608	-1.934	0.05306
moss	0.011704	0.005982	1.957	0.05041
prot degrees	0.005445	0.001960	2.779	0.00545**
prot height	1.071104	0.461228	2.322	0.02022*
prot dist.	-0.519657	0.219561	-2.367	0.01794*

The large scale binomial logistic regression model results shown in table 3 reveal a strong influence of tree type on oak sapling presence. oak saplings have a lower abundance in deciduous and mixed forest types as can be seen from the very low p-values ($p < 0.001$) and negative coefficients of these categories. Moistness and canopy cover are evidently also hindrances to sapling growth as they have low p-values (Moistness: $p < 0.01$, canopy cover: $p < 0.05$) and negative coefficients. Presence of mature oaks was removed before running the final version as its removal resulted in a significant drop in AIC value of the model, indicating that presence of mature oak was not a good predictor of sapling presence.

Table 3 *- Binomial logistic regression: Large scale*

Variable	**Coefficient**	**Std. error**	**z value**	**Pr>(z)**
Intercept	1.10460	0.61784	1.788	0.07380
Tree type (dec)	-1.73940	0.23585	-7.375	1.64e-13***
Tree type (mixed)	-0.99905	0.24358	-4.101	4.11e-05***
Moistness	-0.58917	0.22076	-2.669	0.00761**
Canopy cover	-0.17910	0.08662	-2.068	0.03867*

*= $p < 0.05$

**= $p < 0.01$

***= $p < 0.001$

Sapling height

From the results of the correlation matrix moss cover, herb cover, light availability, protection degrees and protection height were selected for testing in the multiple regression. Protection height was excluded because of high correlation with protection degrees. Of all the possible combinations of the remaining predictor variables the highest r^2 was obtained when light availability and protection degrees were included. The r^2 of this model was 0.312 (31.2% of variation in sapling height is explained). From the standardised beta coefficients given by the model we can see that an increase in both variables has a positive impact on sapling height. Protection degrees has a considerably greater effect than light availability according to the standardised beta values. The results of the multiple regression are shown in table 4

Table 4 *- Multiple Regression Output Table*

Variable	Standardised beta	Sig.
Protection degrees	0.465	0.000
Light availability	0.198	0.005

$r^2 = 0.312$

Figures 1 and 2 show the number of saplings in each protection category for saplings > 50cm and saplings < 50cm respectively. These figures show that larger saplings tend to be found in more protected plots whereas smaller ones are more abundant in the less protected plots.

Figure 1 *– Number of saplings > 50 cm in each protection category*

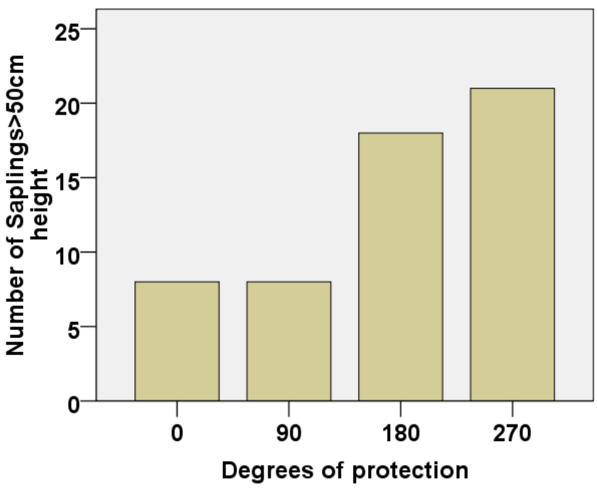
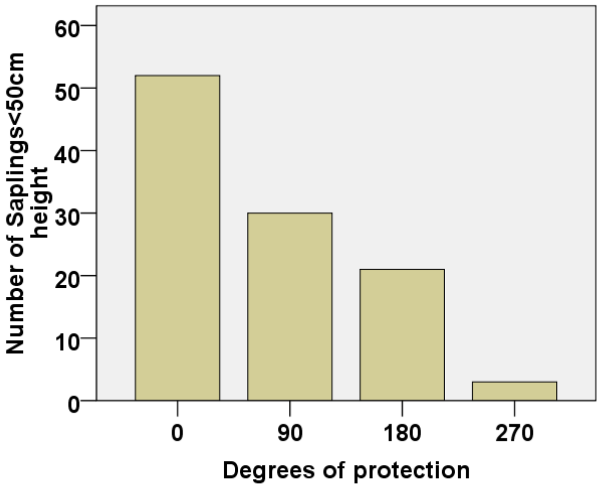


Figure 2 *– Number of saplings < 50 cm in each protection category*



Figures 3 and 4 show the effect of protection on browsing level of saplings > 50cm and saplings < 50cm respectively. For larger saplings there is a clear trend of decreasing browsing level for more protected saplings. The trend is not present for smaller saplings.

Figure 3 *– Effect of protection on browsing level of saplings > 50cm*

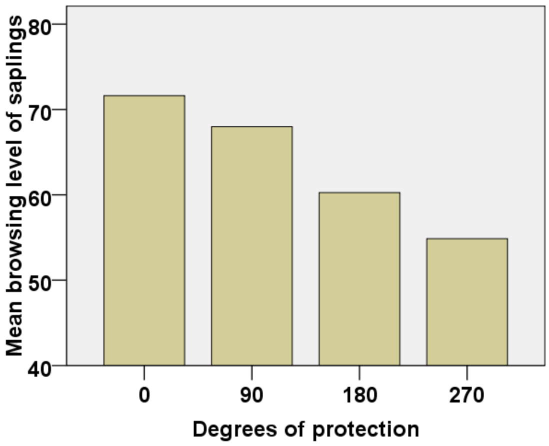
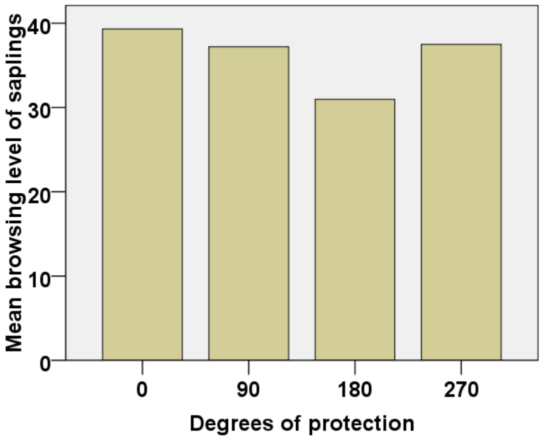


Figure 4 *– Effect of protection on browsing level of saplings < 50cm*



Management effects

Our Pearson's Chi square test showed that the relationship between management and presence of protection was highly significant ($p < 0.001$). This effect is also visible in Figure 8 which shows that a much greater proportion of plots are protected in the un-managed area.

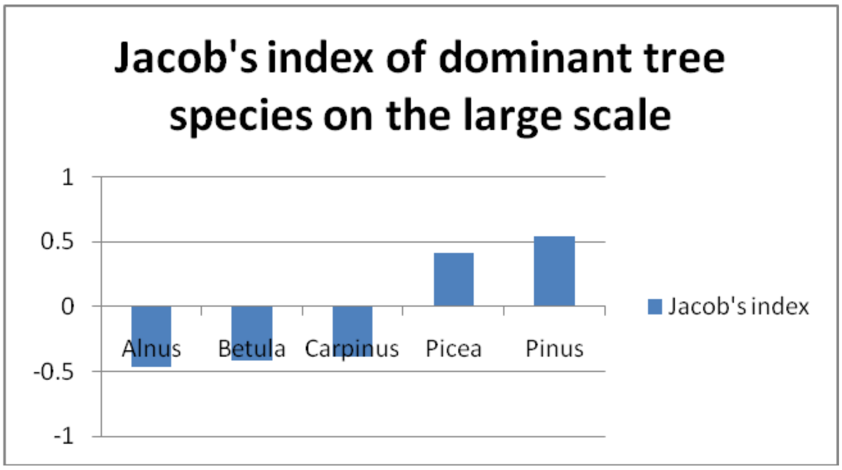
Binomial logistic regression models were run on the small scale data after separating it into managed and un-managed data sets. The run for the un-managed data set gave results similar to that of the whole data set, but with slightly lower significance values for protection. The managed data set however produced a model output in which none of the small scale variables had significance values below 0.05. Given the number of protective structures found that were formed from dead spruce (138 out of 159) this result from the managed area data is unsurprising. The removal of dead spruce by foresters means that protective structures are scarce in the managed area and so the protection variables that were significant in the overall model lost their importance in the managed model. As a result variation of sapling presence in the managed model is not well explained by the predictor variables (the data is close to over-dispersion).

Binomial logistic regression models were also run on the large scale data after separating the data set into managed and un-managed areas. This had a similar effect as with the small scale data, with previously strongly significant variables decreasing in significance in the managed area. In particular saplings did not avoid deciduous and mixed forests as strongly when only the managed area was analysed. This indicates that without the dead spruce debris that is abundant in the un-managed forest coniferous areas are not as good an environment for oak saplings.

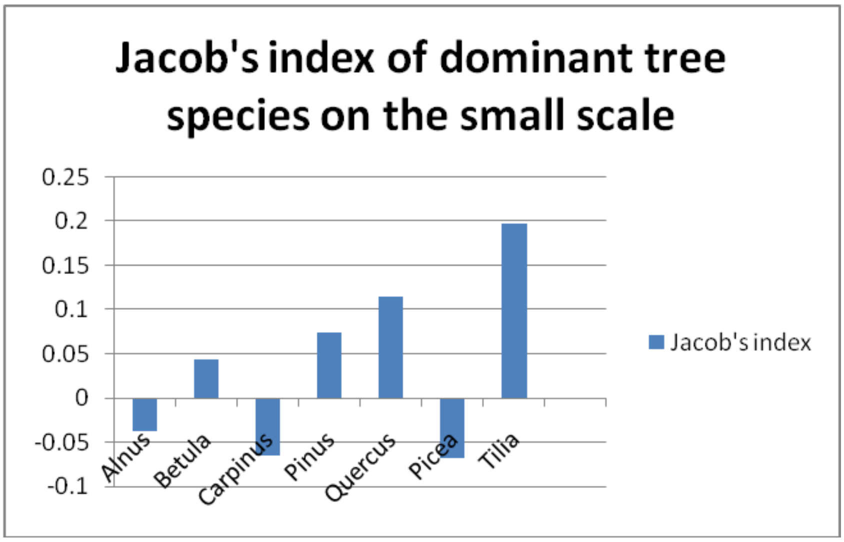
Mature tree effects

The Jacob's indices for the large scale data (Figure 5) are positive for *Picea abies* and *Pinus sylvestris* indicating that saplings are more likely to be found growing in coniferous forest types. The dominant deciduous tree species of the forest have negative indices, implying that oak saplings are less likely to be found when these species are dominant.

Figure 5 *– Jacob's indices indicating likelihood of sapling presence in forest types dominated by various tree species. (From the large scale data)*



The Jacob's indices for the small scale (Figure 6) are considerably smaller than those for the large scale indicating that sapling presence is driven by large scale forest type but not by proximity to individual trees on a local scale.



Discussion

This study showed that both protection from browsing and forest type are important factors in oak recruitment. There was a significant effect of protection on sapling presence and size and we have reason to believe this is due a direct impact of protection on browsing pressure. The effect of forest type on sapling success was also found to be strong, with most saplings appearing in coniferous forest types. This can be attributed to the fact that the majority of protective ground cover is made up of *Picea abies* debris, making forest types containing this species more favourable for sapling survival. In the managed areas where protective structures were removed, forest type still had an effect, but it was diminished. Average sapling height in the un-managed area was 61 cm, whereas in the managed area it was only 33 cm.

87% of protective structures recorded in the study were dead *Picea abies* logs or branches. This not only highlights the potential importance of spruce as a provider of protection, but also shows how the removal of dead spruce would leave the managed part of the forest with less protective cover.

Direct effects of protection

Our study demonstrated that protective structures, most notably the aforementioned spruce logs, facilitate the presence and growth of oak saplings and that this is most likely achieved through a browsing exclosure effect created when logs surround a sapling. Our binomial logistic regression models and our multiple regression models tell us that protection degrees was the most significant factor determining sapling presence and height. The height of protection was also significant, and protection was significantly less effective at greater distances from the plot centre.

Protection effects on browsing intensity

Exclosure experiments performed in the Białowieża Primeval Forest have shown that browsing becomes the main limiting factor once a sapling exceeds 50cm in height but that saplings smaller than this are relatively unaffected (Kuijper, Cromsigt et al. 2009) which matches our discovery that un-protected large saplings are browsed more than un-protected small saplings (Figures 3 and 4). Looking at saplings greater than 50cm in height from our study we see that there is a clear decrease of browsing at greater levels of protection (Figure 3) whereas the saplings smaller than 50cm do not show this decrease (Figure 4). This decrease in browsing pressure occurs despite the attractiveness to browsers of greater ground vegetation and cover from predators provided by tree-fall areas (Gotmark, Berglund et al. 2005). Presumably because of a combination of this decrease in browsing facilitated by protection and the vulnerability of larger saplings to browsing pressure we find most of the saplings > 50cm in height in protected plots. The number of smaller saplings decreases with increasing level of protection implying that protection actually has a negative effect on saplings at early stages of growth. Browsing level of small saplings is generally lower and does not decrease with increasing protection so their success must be limited by other factors. It is possible that higher protection also creates too much shade at levels below our measurement of light availability (1m) for smaller saplings to prosper and other studies have shown increased seed predation in areas of greater ground cover (Smit, den Ouden et al. 2009).

Given the seemingly negative effect of protection on smaller saplings the best scenario for oak would be to germinate in a healthy coniferous forest and spend the early stages of growth un-protected and only later, when it is large enough to be a target for browsers, for the surrounding conifers to be killed by bark beetles.

Light and protection

Quercus robur is considered to be a light demanding species (Čater and Batič 2006) and so it was surprising to see that light availability did not have a significant effect on sapling presence on a local scale. Light availability was shown to affect sapling height, but our multiple regression model results show that protection degrees is a considerably stronger predictor of sapling height. Due to the simultaneous occurrence of favourable light conditions and high levels of protection in tree-fall areas it is difficult to disentangle the effects of these two predictors and an experimental set-up with both variables controlled would be required to do so. Other research on protective effects of structures on saplings has generally shown the opposite. That is that protection, particularly from shrubs, tends to limit the amount of light reaching the protected sapling (Callaway 1992; Bakker, Olff et al. 2004). In this study we measured light at 1 metre from the forest floor so it is possible that ground cover below this height caused shading and was limiting for saplings in smaller size classes. This would also explain the tendency of areas with higher protection to have less saplings in smaller size classes that was discussed above. An alternative explanation for not finding an effect of light is the higher ungulate visitation and browsing frequency of trees growing in forest gaps when compared to closed forests (Kuijper et al. 2009).

Management effects

We knew prior to the study that part of the forest was under limited management that allowed removal of dead *Picea abies* and therefore removal of potential protection for saplings. The lack of protection in the managed area was also clear in our results as was the importance of this protection to sapling success.

It was evident from the lack of a strong predictor variable in the managed part of the forest that there are more mechanisms driving oak regeneration than were investigated in this study. We assumed that both source and dispersal would not be limiting factors given the abundance of mature *Quercus robur* as a seed source and the forest's fame as a haven for bird and mammal species that could act as dispersers. However, there are undoubtedly patterns of source and dispersal that could limit oak regeneration in certain areas. Indeed, there have been accounts in the literature of preferential dispersal of acorns by Jays to areas of coniferous forest (Healy 2002; Kunstler, Curt et al. 2004).

Mature trees and forest type

The Jacob's indices for the large scale show a positive effect of coniferous tree dominance in the forest type on presence of saplings. The indices at the small scale are considerably smaller indicating that mature trees are an important factor in the context of large scale forest type but do not have such a significant effect as individuals at a local scale.

A relationship was found between forest type and protection. Forest types where *Picea abies* was present were more likely to contain large quantities of dead wood due to the vulnerability of this tree species to bark beetle attack that ultimately results in the death of the tree and its neighbours. This dead wood then provides protection for oak saplings. The large scale data shows us that saplings occurred in higher numbers in coniferous forest types. Results from the managed area of the study site show that this is mainly attributable to protective effects of spruce logs. In the managed area dead spruce logs are removed to prevent spread of the bark beetle throughout the forest and so close to no protection is available. Our study showed that in the managed area of the forest there is a lesser effect of forest type on sapling success illustrating that not forest type but protective structures are the main factor involved. Presumably this is because the protective effects of dead *Picea abies* debris, normally strongly associated with coniferous forest types, are absent due to the management activity. Despite this effect sapling presence was still affected by forest type in the managed area, but to a much lesser extent than in the un-managed forest. It is also worth noting that variation in sapling presence in the managed area was not strongly related to any of the predictor variables measured for both large and small scales.

Effects of moss cover

Moss cover was shown to be a moderately significant predictor of both sapling presence and sapling height, despite being strongly negatively correlated with protection degrees. We can attribute this relationship to a second set of conditions in which a small number of saplings were found. In some extremely boggy parts of the forest *Quercus robur* saplings were found growing on elevated mounds formed at the base of large trees or left by the decaying remains of large tree stumps. These mounds were covered by moss and surrounded by standing water. Although they were not, according to our results, protected from browsing it is interesting to note that the saplings growing in these conditions were also sometimes reliant on the debris of dead trees for survival. The presence and characteristics of these mounds in boggy forest types is described in the literature (Falinski 1986).

Relationship of Quercus robur and Picea abies

There are conflicting analyses of oak regeneration in Białowieża Primeval Forest in the literature. One study suggests an absence of oak regeneration throughout the forest and attributes this absence to a lack of certain large herbivore species in the forest (Vera 2000). Mechanisms are offered by which oak may regenerate in gaps maintained by large grazers, but it is stated that these mechanisms are not currently operating. Conversely it has been suggested that oak is regenerating in forest gaps created by die-back of diseased *Picea abies* trees. A cyclical mechanism is proposed whereby certain bird species use the ridges in mature oak bark to fix *Picea* cones in place during feeding, which results in patches of *Picea* growth in areas where there is or was mature oak. Once these *Picea* have matured they are then attacked by bark beetle and die back, creating gaps in which oak may regenerate (Bobiec 2002). In combination with dispersal habits of the jay mentioned above and the protective effects afforded by dead spruce we have some solid reasons for *Quercus robur* saplings to regenerate preferentially in coniferous forest.

Management implications

The findings in this study highlight the potential importance of sapling recruitment facilitation by protective structures in a forest with a full complement of herbivores. We have also seen that management practises employed to protect one tree species, namely the removal of dead *Picea abies* to prevent bark beetle spread, can have negative impact on the regeneration of another potentially desirable tree species. Other studies have shown hunting to be ineffective at controlling large deer populations (Milner, Bonenfant et al. 2006) and perhaps more success could be seen by leaving a certain degree of debris behind after logging if an area is to be re-planted.

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