The Combined Influences of Canopy Openness, Browsing Protection, and Low Intensity Fire on the Natural Regeneration of Oak in Southern Sweden

Benjamin Miles

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Supervisor:	**Magnus Löf, Swedish University of Agricultural Sciences, Southern Swedish Forest Research Centre**
Examiner:	Adam Felton, SLU, Southern Swedish Forest Research Centre

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Abstract

Whilst oak was historically prevalent in the landscape of temperate Europe, changes in the disturbance regime of forests have led to limited regeneration across its distribution. In this study, the fire oak hypothesis is tested to assess the tolerance of *Quercus robur* and *Quercus petraea* recruits (seedlings and saplings) to a low intensity burn, and how this response may differ depending on the presence of browsing and canopy openness. In five oak dominated forests, the use of a replicated field experiment, with a randomized block design revealed distinct differences in the conditions that favour the regeneration of oak. After the initially raised mortality of recruits in a burning treatment in the first two years, low levels of mortality were observed across treatments. For unburned recruits, growth was largely absent with lower light conditions, whilst under a canopy gap, a dramatic increase in growth was observed, heavily favouring the larger recruits. Most recruits survived a burning treatment by resprouting, after the above ground portion of the tree was killed (top-kill). However, the largest recruits measured (≈25 mm diameter) were found to survive without top-kill, but only in conjunction with a canopy gap. For burned recruits, growth was dramatically higher under a canopy gap, however, the elevated levels of browsing with this treatment point to benefits from fencing recruits. The results of this experiment highlight the importance of different treatment conditions on the successful regeneration of oak and suggest low intensity burns may allow the successful natural regeneration of oak, if complemented with browsing protection, and improved light conditions.

Keywords: Burn, Browsing, Disturbance, Fire, Light, Oak, Q.robur, Q.petraea, Ungulates

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Contents

List of Tables

List of Figures

1. Introduction

1.1 Oak in Northern Europe

Throughout the temperate zone of Europe the two oak species *Quercus robur* and *Quercus petraea* are present in many forests and parklands, their distribution ranging from the Iberian Peninsula to the south of Norway and Sweden (Caudullo et al. 2017). Whilst taxonomists agree that *Q.robur* and *Q.petraea* should be treated as different species, there is greater intraspecific genetic variation than interspecific (Gömöry et al. 2001). The species share a similar range, and environmental tolerance, as well as naturally hybridizing (Jensen et al. 2009). Consequently, for this study the species will not be distinguished between and are collectively referred to as 'oaks'.

Oaks are amongst the longest lived trees in Europe, known to reach over 1000 years of age, and attain diameters of up to three to four meters (Eaton et al. 2016). The great age and size that oaks can reach, coupled with physiological features such as rough bark, and large cavities, begin to explain the large number of associated species (Paltto et al. 2011). There are over 2300 species associated with oak, including 450 'red listed' species, and 326 with an obligate association (Mitchell et al. 2019b). This reflects the irrefutable importance of oak to conservation, and its irreplaceability in ecological value (Mitchell et al. 2019a).

In addition to its ecological value, oak has a rich cultural history, and an array of applications past and present, from the use of its acorns for animal feed, to its use in tanning leather (Eaton et al. 2016), as well as its high value timber (Löf et al. 2016), making oak one of the most economically important deciduous trees in Europe (Eaton et al. 2016).

1.2 The Decline of Oak and Changing Disturbances

Whilst abundant, and at points dominant across northern temperate Europe since the Pleistocene epoch (Godwin & Tallantire 1951; Vera 2000), oak has declined over recent centuries, and exists now only as an artefact of historic forest disturbances across more mesic sites (Vera 2000; Lindbladh & Foster 2010; Petersson 2019). Across northern temperate Europe the natural regeneration of oak is very limited both in forests used for production, and in reserves (Emborg et al. 2000; Vera 2000; Bobiec et al. 2011; Annighöfer et al. 2015).

Historically the development of Nothern European forests was thought to follow classical succession, where the climatic conditions are those which dictate the climax community of a forest. On mesic sites this would typically conclude with shade tolerant species, such as European beech (Fagus sylvatica), Norway spruce (Picea abies), and lime (Tillia chordata) (Clements 1916). However, even with periods of elevated temperature and a drier climate (Ellenberg 1988; Antonsson 2006; Olsson et al. 2010), the historic abundance of oak, as a light demanding species, stands in conflict with the assumption that traditional succession can adequately explain the mechanisms which controlled historic species assemblages. This led to a pivotal and extensive hypothesis developed by Vera (2000), which suggested that the primary control of vegetation dynamics across temperate Europe was not the climatic conditions, but instead assemblages were dictated by the top-down control of herbivores. Early in the Holocene these herbivores were wild grazers and browsers, whilst later livestock played a key role, with less distinct boundaries between the forest and agricultural land than in the present day. This in turn has been supported by field studies (Bakker et al. 2016). However, due to the absence of key herbivores in areas still exhibiting an abundance of light demanding species (Mitchell 2005), other authors have in many instances contested this hypothesis, reaching alternative conclusions (Svenning 2002; Birks 2005; Demeter et al. 2021).

Another such hypothesis offering explanation as to the historic abundance of oak is the occurrence of fires across temperate Europe, which are now largely supressed. Although better known as an agent of disturbance in the Mediterranean region, evidence for both human induced, and naturally occurring fires has been found in central Europe (Adámek et al. 2015), Sweden (Niklasson et al. 2002; Lindbladh et al. 2003; Olsson et al. 2010), Great Britain (Mason 2000), and Denmark (Hannon et al. 2000).

Whilst the role of fire in supporting oak regeneration, and maintenance in the canopy has been dismissed by some authors (Bennett et al. 1990; Vera 2000), others have highlighted as a likely explanatory component of the historic abundance of oak in Europe (Hannon et al. 2000; Mason 2000; Svenning 2002). Support and research are much stronger for the establishment of oak species in the United States (Abrams 1992; Brose et al. 2001, 2013; Shumway et al. 2001; Dey et al. 2019), where fire is actively used in the regeneration of oak, and regeneration methods with fire continue to develop (Loftis et al. 1993; Arthur et al. 2012). The physiological adaptations of oak species to fire in the US have, in part, also been found in *Q. robur* and *Q. petraea* (Petersson 2019).

1.3 The Ecology & Adaptive Traits of Oak

It is widely known that oak is favoured in drier environments (Ellenberg 1988; Kunz et al. 2018), but less attention is given to the fire adapted traits of oak, which can be found throughout its lifecycle. These begin with the provision of a thin litter layer for germination (Loftis et al. 1993; Greenberg et al. 2012), and heat tolerant acorns (Reyes & Casal 2006). The large allocation of biomass to roots, and the strong resprouting capacity (Valladares et al. 2002; Kabeya & Sakai 2005; Bobiec et al. 2018), enable oak to survive fire through resprouting after top kill (the loss of the above ground part of the seedling/sapling), with greater success for larger individuals (Dey & Hartman 2005; Petersson et al. 2020). The shade tolerant competitors of oak typically exhibit poorer resprouting capacity, and lower levels of survival (Ziobro et al. 2016; Petersson et al. 2020). Later in oak's life cycle, its thick bark relative to other species, most notably the shade tolerant species (Račko & Cunderlík 2007), allows for negligible loss of foliage, branches, or bark failures with low intensity fires (Conedera et al. 2010). Meanwhile, the poor tolerance of other, competing species would lead to the creation of canopy gaps and increased light levels in a mixed forest.

However, the effects of burning could be expected to differ depending on the availability of light to a recruit. Light is a key factor influencing the survival and growth of oaks, and it begins at the point of germination. Utilizing resources from the endosperm of the acorn, seedlings can reach the stage of a one-year-old sapling without the requirement of light, allowing some competition with the herb layer to be overcome (Jensen & Löf 2017; Bobiec et al. 2018; Johnson et al. 2019). However, whilst acorns have the capacity to germinate under low light conditions, once the reserves of the endosperm have been depleted seedlings will face mortality after 5-8 years, should adequate light levels not be reached (Vera 2000; Březina & Dobrovolný 2011). For maintained growth, oak seedlings require light levels exceeding 15% - 20% of full light (Löf et al. 2007), and growth is highly responsive to increasing light levels thereafter (Březina & Dobrovolný 2011; Modrow et al. 2020). With one of the greatest light requirements of the broadleaves in southern Sweden (Diekmann 1996), under low light conditions, oak exhibits poor growth and will be overtopped by its shade tolerant competitors, such as Norway spruce (Picea abies) and beech (Fagus sylvatica), leading to high levels of mortality, and at least growth suppression (Ligot et al. 2013; Jensen & Löf 2017). The light requirements of oak increase with size (Annighöfer et al. 2015), and even in high light environments, after around 30 years shade tolerant species such as beech can overtop young oak trees, becoming increasingly dominant over time (von Lüpke 1998).

As well as being poorly adapted to low light conditions, oak is amongst the most palatable species to browsers (Bergqvist et al. 2018). However, with a large allocation of biomass to roots (Valladares et al. 2002; Kabeya & Sakai 2005), and a strong ability to resprout (Ellenberg 1988; Mason 2000), oak can also be considered resilient, or tolerant, with regards to browsing (Bobiec et al. 2018). However, with high levels of browsing the growth of oak may be limited to the browse trap, whereby oak is unable to grow beyond a certain height until browsing pressure is reduced (Staver & Bond 2014; Churski et al. 2017; Bergqvist et al. 2018). A study by Bergquist et al. (2009) shows how the net growth of oak can almost be eliminated by browsing, unless protected. Notably, browsing does not typically induce mortality (Bideau et al. 2016), without the additional influence of competition (Jensen et al. 2020).

Whilst the effects of changes to light condition and browsing have been studied on oaks, and the effects of fire have been studied on oak species other than *Q. robur* and *Q. petraea*, what has been absent from the literature are studies combining the effects of changes to these conditions. Assessing the influence of different treatment combinations is essential for an understanding of how oak may respond in real life scenarios, as combining treatments reveal unforeseen, and more complex interactions between treatments.

2. Study Aim

The scope of this study is to assess the relative contributions and interactions of different biotic and abiotic effects, namely the effect of light intensity, browsing, and burning, on the growth of oak recruits, and how these effects may influence the capacity of oak recruits to successfully establish in the canopy. The study will primarily focus on responses over a five year period, but will draw additional conclusions from former research on the same experimental site (Petersson et al. 2020).

The study will assess:

1) The relative importance of canopy openness and browsing protection for the growth and survival of oak
    a. With a low intensity burning treatment
    b. In the absence of a burning treatment
2) The importance of oak recruit size prior to a low intensity burn on the
    a. Survival of oak without top-kill
    b. The growth of top killed recruits immediately following the burn, and 5 years later.
3) The combined influences of canopy openness, browsing protection, and a low intensity burn on the density of oak recruits and competing vegetation.

3. Methods

3.1 Site Locations and Descriptions

Five experimental sites were established in 2016 and were situated within oak dominated forests in southern Sweden. On all sites, natural oak regeneration was occurring. The five sites were located between 45–95 m above sea level, and latitudes between 56.0 and 57.0 decimal degrees.

The sites were representative of many oak forests in southern Sweden, forming part of a mosaic landscape composed of mixed agricultural land, production forests of *Picea abies* and *Pinus sylvestris,* and a small amount of mixed broadleaf forest. Sites one, two and three had a slightly higher proportion of forest within the landscape, whilst sites four and five had a slightly higher proportion of surrounding farmland.

Figure 1. The five site locations across southern Sweden, (1) Abbetorp; (2) Barnebo; (3) Hornsö; (4) Sösdala; and, (5) Sperlingsholm.

3.2 Original Treatment Methodology and Site Setup

The experimental sites were structured as a randomized block design, with a canopy gap created for the experiment, adjacent to an area of closed canopy. Beneath both the gap and closed canopy area, an unfenced and fenced area was established, which in-turn contained an unburned and burned treatment plot (Figure 2.)

Paired unburned/burned treatments with the same fence/canopy conditions were situated immediately next to each other along the long edge of the treatment plot, without a buffer zone. Fenced/unfenced treatments within a canopy treatment were located 7–42 meters from each other, favouring plots with a similar size of oak regeneration. Canopy treatments were between 25–188 meters from each other at each site. Each treatment plot was 7.5 m by 3.5 m in length and width.

The canopy gap creation occurred in April 2016. The size of the gap created at each site was approximately 400m^2 (0.04ha). In these gaps all trees that formed the canopy were removed, but all seedlings and saplings remained. Within the canopy treatments, two areas were selected, one for a fenced and one for an unfenced treatment. The fences erected were 2 meters tall, and of steel wire. The fence mesh size permitted free access to rodents but prevented access by any larger mammals (Mesh size 5 × 5 cm from 0–0.8 m, 16 × 20 cm from 0.8–2.0 m).

Within each fenced/unfenced area, the plot was subdivided into an area for a burn treatment, and an area to leave unburned. Burning was undertaken at each site between the 29th of September and 7th of October 2016 and followed a particularly warm summer. A propane blow torch (1211960L Kemper) facilitated the simulation of a low intensity surface fire, that burned herbaceous vegetation and the top of the fine litter layer, and charred larger shrubs and pieces of litter. Flame heights reached approximately 40 cm, and all plots at each site were treated on the same day.

In 2016, within each treatment plot, all seedlings, saplings, and sprouts within browsing height (≤ 300 cm) were marked with a unique aluminium tag. In plots where the number of recruits was in excess of 100, a random subset of at least 50 were selected for measurement, by selecting every second, third or fourth recruit.

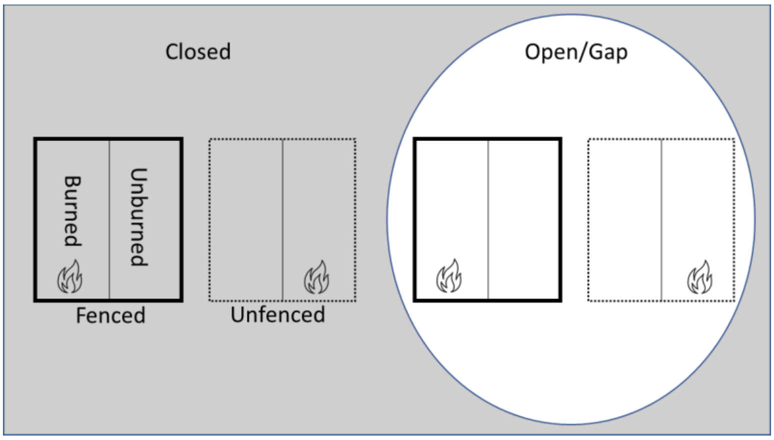

Figure 2. The 8 treatment combinations used in the experimental design; all treatment combinations occurred at each of the 5 experimental sites.

3.3 Measurements

The height and diameter of all tagged seedlings was recorded at the beginning of the experiment in April of 2016. Thereafter measurements were taken in late August of 2016, 2017, and 2018. In this study (2021), height (±1 cm), and diameter (±1 mm) measurements were taken in mid-September. Height was recorded from the base of the oak recruit to the top of the tallest shoot. The shoot was stretched along the length of the ruler for the measurement, giving the maximum length from ground to shoot. In instances where the oak had multiple stems, it was the height and basal diameter of the tallest stem that was recorded. Additionally, it was recorded whether the recruit was an original stem or a shoot from a dead/living stem. Where there were multiple stems, the number of stems was also recorded.

Recent browsing damage (the removal of a terminal or lateral shoot) to oak recruits was recorded in April and August between 2016 and 2018, and in mid-September in 2021. Browsing damage was not further classified into ungulate species.

In August of each year between 2016 and 2018, the woody vegetation present (≤300 cm) was assessed within four 2m^2 circular subplots in each treatment plot. In 2021 this measurement was taken in mid-September. In each subplot, height, basal diameter, stem type, and damage were recorded for non-oak species, and the number of oak individuals was counted.

In late June of each year between 2016 and 2018, and in mid-September 2021, light availability at 160cm above ground level was estimated using hemispherical imagery. The camera lens was positioned perpendicular to the forest floor, and the direction of magnetic north was marked within the photograph. Prior to 2021, light conditions were measured at each sampling plot, in 2021 measurements were recorded at a central position for each canopy treatment. The photos were analysed using GLA software (Frazer et al. 1999). In Table 1, the values of percentage transmittance prior to 2021 are means from across the gap, whilst in 2021 the values represent the central position between the fenced and unfenced areas in a canopy treatment. The lower values for the canopy gap transmittance on sites 1 and 2 can be attributed to the advanced regeneration reaching heights of above 160 cm.

Table 1. The amount of transmitted solar radiation, as a percentage of the total available radiation at each site. C denotes a closed canopy treatment; G denotes a canopy gap.

		Transmitted solar radiation (%)			
Site	Canopy Treatment	Year			
		2016	2017	2018	2021
	G	31.36	37.27	36.46	25.01
1	C	19.48	22.88	23.72	21.07
	G	40.41	38.25	37.49	25.75
2	C	18.50	22.51	26.70	21.15
	G	36.16	35.84	40.61	37.41
3	C	17.67	20.52	23.15	17.40
	G	41.59	39.96	35.26	40.33
4	C	22.95	16.89	17.30	17.42
	G	46.71	46.44	41.26	41.76
5	C	18.43	20.58	18.35	16.89

3.4 Statistical Analysis and Calculations

All statistical analysis was undertaken in RStudio Version 1.3.1073, modelling was undertaken using the R package 'lme4' (Bates et al. 2015). Models were chosen based on minimising the AIC value, whilst assessing the models graphically to check for normal distribution of residuals, and homogeneity of variance.

The probability of oak surviving a burning event without being top killed was analysed with a logistic regression, using data from site 4. The diameter in August 2016 was used as a predictor, and whether or not the recruit was top killed was a binary response. The model was fitted with a Poisson error distribution. Only recruits under an open canopy were included in the model.

Initial recruit recovery after burning was modelled with a linear mixed effect model, using the height of recruits before the burning treatment (August 2016), and the heights of recruits one year following (August 2017). Only individuals that were top killed, and in the burning treatment plots, were included in this analysis. The factors (treatments) canopy condition, and browsing protection were included as fixed effects, and to account for the nesting design of the experiment, random effects (site:canopy), were included in the model. To assess the percentage recovery of an individual, the percentage of the height of a recruit was calculated relative to its height prior to burning (August 2016). Visual inspection of the data suggested a nonlinear relationship between height in 2016 and percentage recovery, including height squared improved the model fit. The model was otherwise constructed as with height after burn.

The incidence of mortality was modelled with a generalised linear mixed effect model, the low incidence of mortality followed a Poisson distribution, and hence this was applied to the model. The fixed effects included were browsing protection and burning treatment. Canopy condition was excluded as it had no significance as a predictor and did not improve model fit based upon AIC testing. Random effects were included to account for nesting (site:canopy:fence). The large number of tags missing from recruits made it challenging to deduce which recruits were dead, and which the tags had fallen from, with a detection rate of 52% across sites. The number of individuals identified as dead was very small (n = 29) and all dead individuals were from a small number of treatment plots (13/40), hence these results are treated with caution.

Due to a fieldwork error, the height of recruits over 300 cm was recorded categorically as ‘over 3 meters’ rather than with their specific heights. Hence, the inclusion or exclusion of these 55 individuals in a height growth model would distort the estimation of effects. This led to modelling growth for three distinct groups – those that were top killed in burning treatments (all below 300 cm), those which were not in a burning treatment, and those which were not top killed in a burning treatment. In all instances, only individuals that were measured in 2021 were included in the analysis. For the top killed recruits, height in 2021 (which reflects the growth since top kill in 2016) was modelled with a linear mixed effect model with height prior to burning (August 2016). Browsing protection, and canopy condition were included as fixed effects, and the random effects as for the recruit recovery. For the unburned recruits, diameter was used for the growth metric, with the fixed effects of canopy condition, height in August 2016, and as a small number (2 recruits) had been top killed, this was also included as a categorical fixed effect. Browsing protection was an insignificant predictor and did not aid model fit based upon AIC testing, so was excluded. In most instances, recruits that were not killed during burning were rare, but on one site, a considerable number survived. These recruits were all under a canopy gap, and the growth of these individuals was modelled with a linear regression, with diameter growth predicted by height squared in August 2016 (prior to burning).

The log of the height of competing vegetation was used to normally distribute data, and was then modelled with a linear mixed effect model, with the fixed effects of canopy condition, browsing protection, and burning. Random effects were included in the form of the nesting of the experiment (site:canopy:fence:burn). In this instance, the 19 recruits (≈10%) that exceeded 300 cm were coded as 300 cm, as a greater variation could be expected in stem diameter of different species. As the measure was of height rather than of growth, the order of the data would not change.

The change in density of oak recruits, and of competing recruits (number of recruits in 2021 – number of recruits in 2016) followed a normal distribution, and hence were modelled with a linear mixed effect model, with canopy condition, browsing protection, and burning as fixed effects, and the nested random effects of the design (site:canopy:fence). For the change in conifer density, instances where there were no conifers present were excluded from the analysis, to reduce zero inflation.

The instances of browsing observed were relatively low, and followed a Poisson distribution, and hence were modelled as such. The fixed effects included were canopy condition, browsing protection, and burning, with the nested random effects (site:canopy:fence).

4. Results

For all models, a full table of model results is included in Appendix 1.

4.1 Early Responses of Oak to Burning

4.1.1 Survival

Whilst generally there was a small number of recruits exceeding 20 mm diameter, a large number existed at site 4. The size distribution of recruits across sites is included in appendix 2. A logistic regression for recruits surviving a burn at site 4 revealed that with an increase in recruit diameter, the chance of surviving a burn without being top killed increased to nearly 100% at the largest diameters measured ($\beta_{\text{(Odds Ratio)}}$=1.27, 95% CI [1.14 - 1.45], p = < 0.001), (Figure 33).

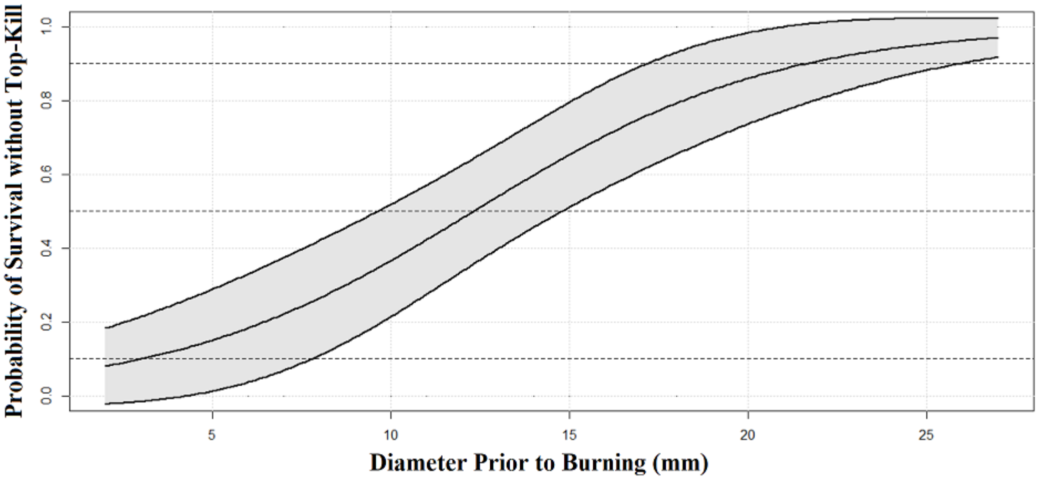

Figure 3. The predicted odds of survival from a logistic regression of how diameter of a recruit in 2016 effected the probability of surviving a burning treatment without being top killed until 2017.The model includes only site 4 of the experiment. A probability of 0 indicates 0% chance of survival, whilst a probability of 1 indicates 100% chance of survival. The ribbon represents the 95% confidence interval.

4.1.2 Recruit Recovery after Burning (August 2016 to September 2017)

The height of a recruit prior to burning significantly predicted the height of a recruit a year after burning (Figure 4), where height increased by 0.19 cm for every 1 cm larger in height a recruit was prior to burning ($t_{(830)}$ = 19.84, ß = 0.19, 95% CI [0.17 – 0.21] p = <0.001). The height of a recruit a year after burning was also near significantly increased by a canopy gap, which increased recruit height by 4.28 cm ($t_{(17)}$ = 1.92, ß = 4.28, 95% CI [-0.09 – 8.66], p = 0.055). Browsing protection did not significantly increase height, yet the coefficient was positive, and the confidence intervals narrowly intercepted zero ($t_{(17)}$ = 1.37, ß = 3.04, 95% CI [-1.33 – 7.41], p = 0.17). The model explained 36% of the variance (Marginal R^2 = 0.35), with the random effects increasing explanation of the variance (Conditional R^2 = 0.47).

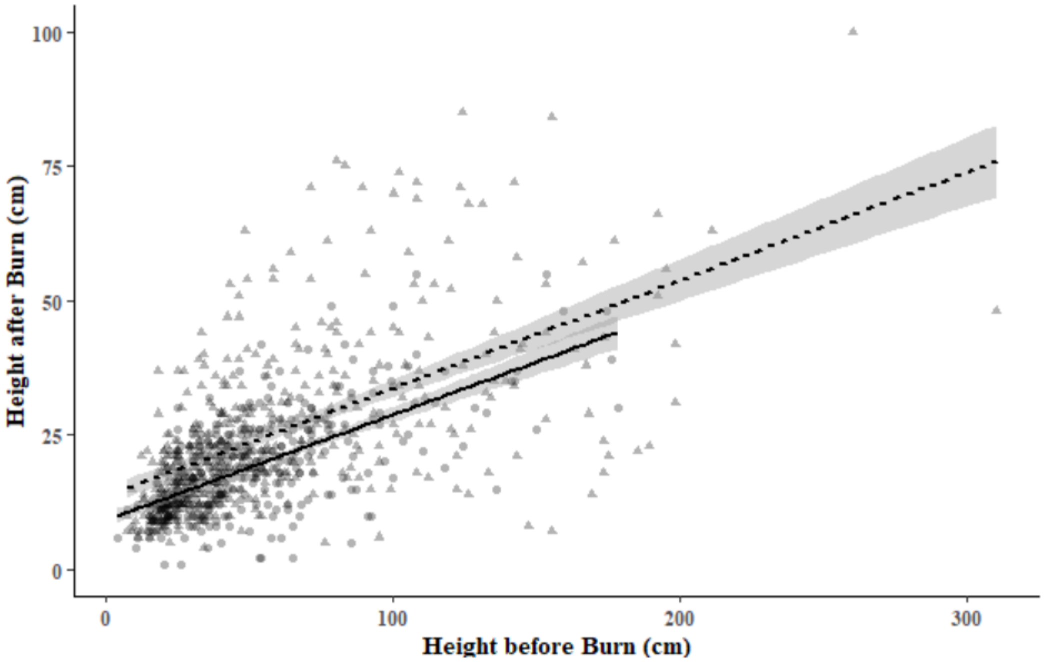

Figure 4. The fixed effect of height prior to burn on height after burn, with data points displayed for all sites with all top killed individuals in burned plots. Shaded circles indicate recruits in a closed canopy, whilst shaded triangles in an open canopy. A solid line follows the estimation for a closed canopy, and broken line for a canopy gap. The shaded area represents the 95% confidence intervals for the effect.

Whilst a linear relationship was observed between the height of a recruit a year after burning, and the height prior to burning, with canopy condition and browsing protection held constant, the height a recruit attained relative to its height prior to burning decreased with increasing height (Figure 5). The smallest surviving recruits (10 cm height) could be expected to recover 83% of their height (95% CI [76.65 - 90.20]), intermediate recruits (60 cm height) recovered 48% of their height (95% CI [44.12 – 52.81]), and larger recruits (160 cm) reached 24% of their height (95% CI [17.43 – 32.12]), (Marginal $R^2 = 0.455$, Conditional $R^2 = 0.525$).

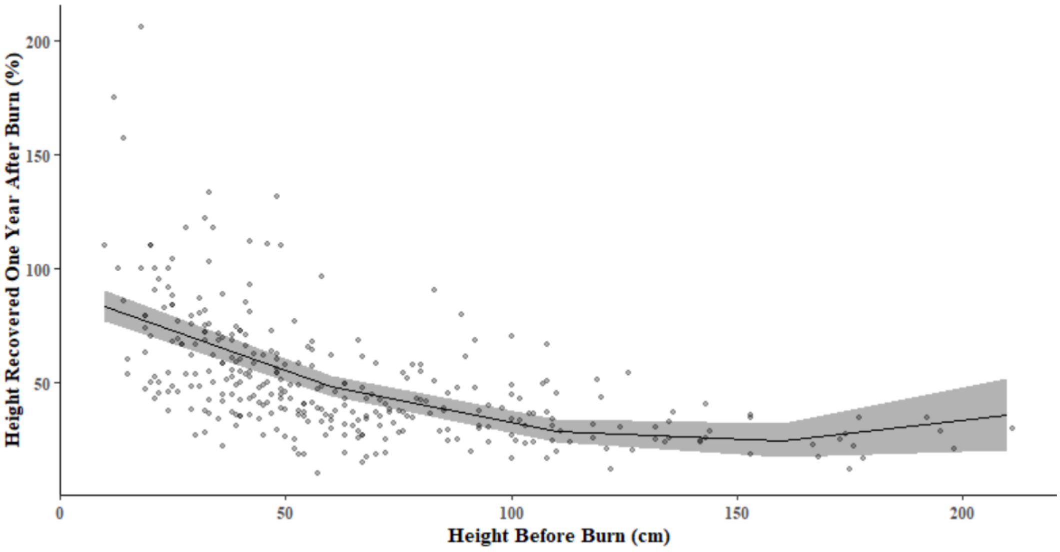

Figure 5. The effect of recruit height prior to burning on the percentage height that a recruit had recovered one year after burning. Plotted data is all recruits that were top killed in a plot with a burning treatment.

4.2 Results from 2021

4.2.1 Recruit Mortality

Between 2018 and 2021, the incidence of recruit mortality was significantly increased in plots that were not burned (z = 3.57, Incidence rate ratio = 9.02, 95% CI [2.70 – 30.16], p = <0.001), browsing protection may have increased the incidence of mortality, but the effect size was not significant (z = -1.48, Incidence rate ratio = 0.40, 95% CI [0.12 – 1.35], p = 0.14). A considerable amount of the variance was explained (Marginal $R^2 = 0.41$, Conditional $R^2 = 0.65$).

4.2.2 Growth - Burning Treatment, Top Killed

The importance of height prior to a burn for top killed individuals was maintained in 2021, with an increase in height of 0.54 cm for every 1 cm larger the recruit was prior to burning ($t_{(308)} = 11.89$, ß = 0.54, 95% CI [0.45 – 0.63], p = <0.001). The canopy condition also had a large effect on the growth of a recruit, with a 51.79 cm increase for those under a canopy gap ($t_{(17)} = 2.91$, ß = 51.79, 95% CI [16.85 – 86.73], p = 0.004). Although not significantly significant, there was an indication that height may be lost without browsing protection, with an interaction between a canopy gap and the absence of fencing ($t_{(17)} = -1.48$, $ß_{Gap} = -38.92$, 95% CI [-90.59 – 12.75], p = 0.139). Browsing protection alone had no significant effect on the growth of recruits ($t_{(17)} = -0.13$, ß = -2.43 95% CI [-40.23 – 35.37], p = 0.899). The fixed effects explained 38% of the variance (Marginal $R^2 = 0.38$), whilst the random effects considerably increased the variance explained (Conditional $R^2 = 0.66$), indicating a large influence of site on the growth of top killed recruits.

4.2.3 Growth - Unburned Treatment

For oak recruits in plots that were not burned, the intercept for diameter growth was very low ($t_{(33)} = 0.51$, , ß = 0.34, 95% CI [-0.97 – 1.65]), diameter growth may have been increased by a canopy gap, but the positive effect was not significant ($t_{(39)} = 1.29$, ß =1.04, 95% CI [-0.54 – 2.62], p = 0.198). The inclusion of browsing protection did not improve the model fit. The diameter growth of a recruit may have been dependent on height under a closed canopy, but the predictor was not significant ($t_{(529)} = 1.35$, ß = 0.007, 95% CI [-0.003 – 0.017], p = 0.179). Further, there was an interaction between the height in 2016, and a gap in the canopy, indicating that growth under the canopy gap significantly increased with increasing height at the start of the measurement period ($t_{(529)} = 3.90$, ß = 0.024, 95% CI [0.012 – 0.037], p = < 0.001). A large amount of variance remained unexplained (marginal $R^2 = 0.35$), whilst the random effects explained a small amount of additional variance (conditional $R^2 = 0.45$).

4.2.4 Growth - Burning Treatment, not Top Killed

From the recruits that survived a burning treatment on site 4, the height of a recruit prior to the burning treatment significantly predicted the growth ($F_{(1,28)}$ = 72.41, p = < 0.001). There was an exponential relationship between the height of a recruit and the subsequent diameter growth, where height squared predicted a large amount of the variance in the growth in diameter (R^2 = 0.721, β = 2.761e^{-04}, t = 8.509, p = <0.001).

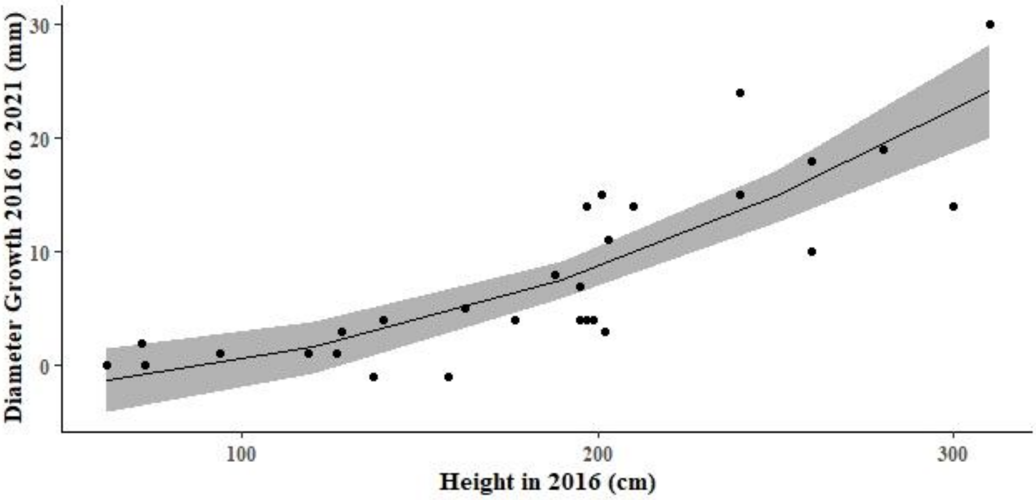

Figure 6. The diameter growth between 2016 and 2021 of recruits that survived a low intensity burn under a canopy gap on site four without being top killed. The line represents the model prediction, whilst the shaded area indicates 95% confidence intervals.

4.2.5 Competing Vegetation

There was no significant difference between any of the treatment factors and the relative density of (non-oak) broadleaved vegetation. The number of coniferous species detected across sites and treatments was very low in both 2016 and 2021. A burning treatment significantly reduced the density of conifers (β = -1470.59, 95% CI [-2765.67 - -175.50]), with almost no conifers remaining in burning plots in 2021.

The height of competing vegetation was significantly increased by the presence of a canopy gap (ß = 0.60, 95% CI [0.17 – 1.03], p = 0.006), however, there was an interaction effect between a canopy gap and the absence of browsing protection, reducing the height of competing vegetation (ß = -0.81, 95% CI [-1.51 – -0.11], p =

0.023). The unburned plots had a near significant increase in the height of competing vegetation compared to the unburned plots (ß = 0.30, 95% CI [-0.02 – 0.62], p = 0.068), and whilst the inclusion of browsing protection alone improved model fit, the effect was not significant (ß (unfenced) = -0.19, 95% CI [-0.76 – 0.39], p = 0.525). Overall, the amount of variance explained by the model was low (marginal R^2 = 0.272), with the random effects slightly increasing the explained variance (conditional R^2 = 0.375).

4.2.6 Density of Oak Recruits

There were two significant effects altering the density of oak recruits, where burning significantly reduced the number of recruits (($t_{(18)}$ = -2.85, ß = -15375, 95% CI [-26335 – -4414], p = 0.007), but not in conjunction with browsing protection, where the number of recruits was found to increase (($t_{(18)}$ = 3.04, ß = 23125, 95% CI [7623 – 38626], p = 0.005). Browsing protection was not found to significantly affect oak density ($t_{(27)}$ = -0.869, ß = -6875, 95% CI [-22964 – 9214], p=0.391), and nor was the creation of a canopy gap ($t_{(17)}$ = 1.09, ß = 7562, 95% CI [-6536 – 21661], p = 0.283). Whilst the effects of burning and the interaction between burning and browsing protection were significant, the fixed effects explained a very small amount of the variance, whilst the random effects explained a large amount of the variance (Marginal R^2 = 0.16, Conditional R^2 = 0.61)

4.2.7 Browsing

In September 2021 the only observed instances of browsing were by ungulates. The incidence of browsing was lower in burned plots with a closed canopy (z = -3.68, ß = 0.11 95% CI [0.03 – 0.36]), and also in a canopy gap without a burning treatment (z = -3.44, ß = 0.24, 95% CI [0.11 – 0.54]). The largest effect was an interaction between a burning treatment and a canopy gap, where the incidence of browsing increased (z = 2.88, ß = 9.62, 95% CI [2.06 – 44.85]), the amount of variance explained by the fixed effects was small (marginal R^2 = 0.214, conditional R^2 = 0.694).

5. Discussion

The results found here highlight a size dependent treatment effect, with oak surviving a burning treatment through top kill for smaller recruits, or complete survival for larger recruits. Growth was improved across treatments by creating a canopy gap, but there was some indication that this improved growth may be reduced if the recruits are not protected from browsing. Furthermore, it was found that when oak recruits are protected from browsing, a burning treatment will lead to a significant gain in the number of oak recruits after a five-year period. However, without browsing protection a burning treatment leads to a considerable reduction in recruit density.

5.1 The Effect of Size on Tolerance and Survival of Burning

Whilst oak recruits typically survive a low intensity burn through resprouting following top kill (Petersson et al. 2020), here it found that survival without top kill can differ across the diameter distribution observed, with the largest diameter recruits often surviving with their stem intact. Notably, the larger diameter recruits were only observed on a single site, and the observation of a single site is not adequate for extrapolation, hence further studies would be required with larger recruits subject to a burn.

Survival without top kill is atypical for recruits of this diameter based upon the findings of other studies in the US (Barnes & Van Lear 1998; Dey & Hartman 2005). However, it is still important to investigate how survival at these small diameters differs across species native to northern Europe. In this instance, the largest surviving recruits had a height advantage of over 280 cm when compared to the largest reshoots, conferring an advantage of many growing seasons. In addition, supressing the growth of smaller recruits which were top killed, and reducing competition from the lower density of surviving recruits. Survival without top-kill was not possible to test for competing vegetation here, but if oak recruits do exhibit a higher incidence of survival (without top kill) with low intensity fire, young oak trees could be liberated from shade tolerant competitors, which can begin to overtop oak regeneration even in light environments (von Lüpke 1998). This could in turn adjust the management implications for the utilisation of fire, where incidence of mortality would be sufficiently low at higher diameters that successive burns could be applied to control other woody species, whilst not negatively impacting the growth of oak. It is also important to consider the impact of variable fire intensities with different environmental conditions, which could lead to structural differences within the treatment area, depending on whether mortality, top kill, or survival without top kill dominate. However, on a larger scale, fire intensity would be more heterogenous across the site, limiting the capacity to influence the outcome (Penman et al. 2007).

The height of an oak recruit prior to burning was an important predictor of a recruit's height one year following. Whilst proportional height recovery of larger recruits was lower after one year, their size prior to burn was still reflected in their height 5 years later. At the end of the 5-year period, this equated to a 75 cm difference between the smallest and largest recruit heights prior to burning. This indicates that the extent of the rooting system and below ground resources is important not only for survival but is also reflected in the rate of growth. Similar observations were found by an old study of species of oaks in the US, where the size of resprouts was dependent on the size of advanced regeneration following a clear cut (Sander 1971). The results here do not allow for comments on the survival or size related growth of other species, but it is known that oak allocates a large amount of resources to its roots (Valladares et al. 2002; Kabeya & Sakai 2005), whilst competing species are typically less conservative with resource storage (Barbaroux & Bréda 2002; Genet et al. 2010). Hence, the relatively larger storage of resources, alongside the advantages of a greater root system could confer oak an early advantage, irrespective of survival of other species. The percentage of height regained was initially much smaller for the larger recruits, but the fact that the recruits retained their position within the regeneration pool five years following may be reason enough to consider a second burn after the initial advantages have been realized. This could confer oak a cumulative advantage over competing species which have lower reserves, or low incidence of resprouting.

It is particularly interesting that across sites, even the smallest oak recruits present in 2016 survived the burning treatment through top kill, and these were found to be able to recover much of their lost height after one year. In areas of relatively dense but small oak regeneration, if oak was found to have higher incidence of survival than other seedlings of this size, this finding could support successive burns as a management tool for increasing the relative abundance of oak in the regeneration pool, as posited by (Ziobro et al. 2016), especially in instances where dispersal of other species into the site is limited.

5.2 Survival and Density Changes of Oak and Competing Vegetation

Petersson et al. (2020) found that the levels of mortality of recruits two years after a low intensity fire was significantly greater in burned plots (≈25%), which were further increased by a closed canopy (≈40%), with only a small increase in mortality with a closed canopy alone. Whilst the observed incidence of mortality was low 2-5 years following the burn, recruit mortality was significantly increased in the absence of a burning treatment and was likely increased with browsing protection. First, this finding indicates that the impacts of a burning treatment are largely realized in the first few years, with vitality of recruits not being compromised thereafter. Additionally, this observation suggests that in the unburned plots, mortality is now driven by competition, and the observation that competition is a greater determinant of recruit survival than browsing is consistent with the observations of Jensen et al. (2020). Burning will offset this competition by reducing recruit size and density, whilst the reduced recruit density and increased vigour of surviving (not top-killed) recruits may allow recruits to reach a larger size prior to mortality induced by competition.

Whilst burning mortality was low after the losses exhibited in the first two years, oak recruit density was found to increase in burned plots that were fenced. The initial losses of recruit density to burning (25% to 40%), show that any increase in oak density must be from the establishment of seedlings. The favourable seedbed that burning confers acorns may explain the increased density of recruits (Loftis et al. 1993; Greenberg et al. 2012), whilst in the absence of browsing protection, it is likely that boar and ungulates inhibited regeneration through the consumption of acorns (Lambert et al. 2005). Light conditions may have negligible influence due to the light conditions exceeding that for oak seedlings across treatments, and the high initial tolerance of oak recruits to low light conditions (Johnson et al. 2019). However, the variance explained by the treatment conditions was very low, whilst the variance explained by the random effects was much higher, therefore site related factors such as local climate, the incidence of mast years and other non-treatment factors such as the prevalence of rodents play critical roles in recruitment.

The insignificant influence of any treatment on the density of competing vegetation may be in part attributed to the low prevalence of the mesophytic shade tolerant broadleaf tree species posited to be most impacted by the application of a burning treatment (Appendix 2, Figure 8), with many of these species towards the limit of their native range (San-Miguel-Ayanz et al. 2016). The species which were prevalent at these sites were aspen (*Populus tremula*), birch (*Betula* spp.), alder buckthorn (*Rhamnus frangula*) (short lived, light demanding species), and rowan (*Sorbus aucuparia*). None of these species have been found to prevent the regeneration of oak, but to impede it (Götmark & Kiffer 2014; Modrow et al. 2020), and perhaps their rapid dispersal countered their losses to burning. As with the oak regeneration, the growth of these species was increased with an open canopy, but without browsing protection, there was a large reduction in height with a canopy gap, as these species are also favoured forage for browsers (Van Hees et al. 1996; Månsson et al. 2007; Myking et al. 2011).

The small number of coniferous species, which were primarily Norway spruce (*Picea abies*), a mesophytic shade tolerant species, were eliminated from the regeneration pool at the burned sites, which links to the finding that the historic suppression of fire coincides with the greater abundance of Norway spruce (Niklasson et al. 2002; Spinu et al. 2020).

5.3 The Conditions Important for the Growth of Burned Oak

The growth of top killed recruits was greater under a canopy gap, but if the recruits were not protected from browsing, this increased growth was largely lost. Under a closed canopy, browsing protection had no significant impact. The top killed recruits experienced reduced levels of competition, due to the mortality from burning, and the reduced size from top kill, yet notably some competition remained from the larger survivors on some sites. The higher light conditions under the canopy gap, which were around 40% transmittance allowed for greater rates of growth as oak, is highly responsive to increased light levels (Březina & Dobrovolný 2011; Modrow et al. 2020).

However, as the burning treatment reduced the height of recruits through top kill, much of the vegetation in the burned plots was within the browse height of all ungulates present (Nichols et al. 2015). As there is a high prevalence of browsers in southern Sweden (Milner et al. 2006), which preferentially browse on oak, especially in patches of high density (Kuijper et al. 2009; van Beest et al. 2010; Bergqvist et al. 2018), it appeared that a component of the increased growth may be lost without browsing protection. The effect size was insignificant at alpha level, however there is evidence for site-dependent browsing frequency, in the large random effects of observed browsing incidence. Hence, whilst the effects of an open canopy are important for the competitive advantage of oak, and its early survival in a burning treatment, it may often be necessary to fence burned recruits, depending on the prevalence of browsers at the specific site.

For the large number of recruits which had survived without top-kill on site 4, the effects of competition were already apparent, where recruits under 150 cm had near zero growth in diameter. Some of this difference in growth may be attributed to shaded recruits favouring growth in height over growth in diameter (Sevillano et al. 2016), whilst otherwise could be attributed to a lower net photosynthesis, with decreasing light availability down the vertical gradient of the plot. Whilst the top-killed recruits may still grow in the shaded conditions until their carbon balance reaches near zero (Kneeshaw et al. 2006), the benefits to oak of burning this stand are better placed with the larger recruits that survived without top-kill. Hence, a low intensity burn can have variable effects depending on the size of recruits, and form of survival (top kill vs complete survival), which will alter the structure and representation within size classes. Notably, all of the larger individuals surviving at this site were under a canopy gap, highlighting that light becomes more important as a recruit ages, and that light aids the resistance to disturbance (Annighöfer et al. 2015; Petersson et al. 2020). But additionally, this finding suggests that a low intensity burning treatment could be better utilized at other sites a longer period after a canopy gap is created, where the larger size of recruits may result in higher levels of survival without top kill, whilst reducing the level of competition from species with lower tolerance to burning.

5.4 The Conditions Important for Oak in the Absence of Burning

In the unburned plots, growth in diameter was near zero for recruits in under a closed canopy, irrespective of height in 2016, whilst under an open canopy growth was increased with increasing height in 2016. Browsing protection did not alter growth in diameter. Comparing the growth of recruits by diameter instead of height does come with some limitations, such as the smaller degree of precision relative to the degree of variance, the tendency of shaded recruits to favour growth in height over diameter (Sevillano et al. 2016), and whilst browsing can reduce growth in diameter through limiting net photosynthesis, it cannot reduce the diameter, perhaps contributing to the absent impact of browsing protection on the results.

Under the closed canopy it is plausible that the smallest recruits could have a rate of growth smaller than the precision of measurement, whilst for the larger recruits, increased allocation of energy to non-photosynthetic tissue may explain the limited growth (Kneeshaw et al. 2006). Nevertheless, this highlights the shade intolerance of oak, and indicates even with low levels of competing vegetation, growth will be small or absent without higher levels of light. Where shade tolerant competitors are present, they will outcompete oak regeneration. Hence it is essential to increase the light available to oak if it is to successfully regenerate. The increase in growth with increasing size is likely a similar effect to that described in the burned plots of site four, whereby the largest individuals are best able to assimilate the increased light, whilst smaller recruits receive only a fraction of the increased light.

The observation that growth in diameter was not affected by browsing protection in a canopy gap could be explained by the factors limiting growth which now exist in each of the plots. Browsing may be the limiting factor to growth outside of a fence, whilst instead competition may limit the growth of recruits inside the fence, encouraging height growth rather than diameter growth for shaded recruits. Other studies have found that a canopy gap increases the incidence of browsing, whilst browsing protection increases the rate of growth in height under an open canopy (Barrere et al. 2021), which corresponds to the observations for the burned recruits here, highlighting that the absent effect of browsing protection may be an artefact of the metric of growth, and it seems quite apparent in the photographs of sites (Appendix 3), that browsing protection under a canopy gap has favoured the growth of oak.

5.5 Limitations and Considerations

A key limitation of the methods applied here, is the linear relationship included within the model to account for initial size differences within the pool of recruits within each treatment. Assessing the growth across all sizes within a treatment plot is an inherently difficult task, due to the array of limits to growth acting upon the recruits of each size class, for example, under an open canopy with a fence intraspecific competition is a limiting factor to the growth of the smallest recruits, whilst in an unfenced burned plot, browsing may lead to a browse trap, limiting the growth across the population in a very different way. These size related differences are important when testing the hypothesis, as recruits of each size class do not have an equal probability of establishing in the canopy, it is the largest recruits which are of greatest importance. Future studies may benefit from either selecting the ten largest recruits of oaks and competing vegetation to minimise the effects of competition, or instead assess growth by measuring all recruits in a subplot and considering transition across size classes.

5.6 Conclusion

The results of this study highlight the great importance of higher light levels for successful natural regeneration of oak, with greater levels of growth across treatments. A controlled burn may favour the natural regeneration of oak, by increasing the establishment of seedlings and releasing larger recruits from competition, although it appears that fencing may be important, due to the high densities of browsers in present day Sweden.

Whilst the results of this study offer clues as to the response of competing vegetation, the low incidence of shade tolerant species across sites, and failure to detect instances of reshooting leaves gaps in the understanding of how other species may respond to the treatment. Hence there is a need for studies comparing the survival of competing vegetation to contextualise these findings for oak, as it is the tolerance of other species which discern the appropriateness of the management strategy. Furthermore, studies assessing the impact of successive burns would reveal how oak may compare to species where the extent of below ground resources become essential.

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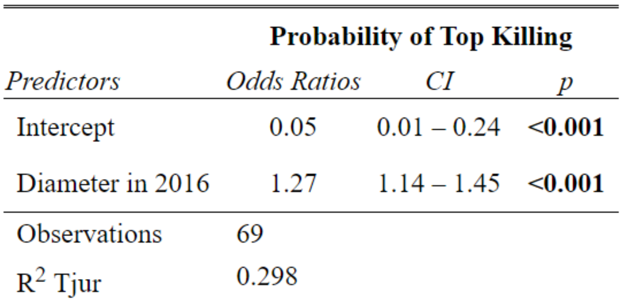
7. Appendices

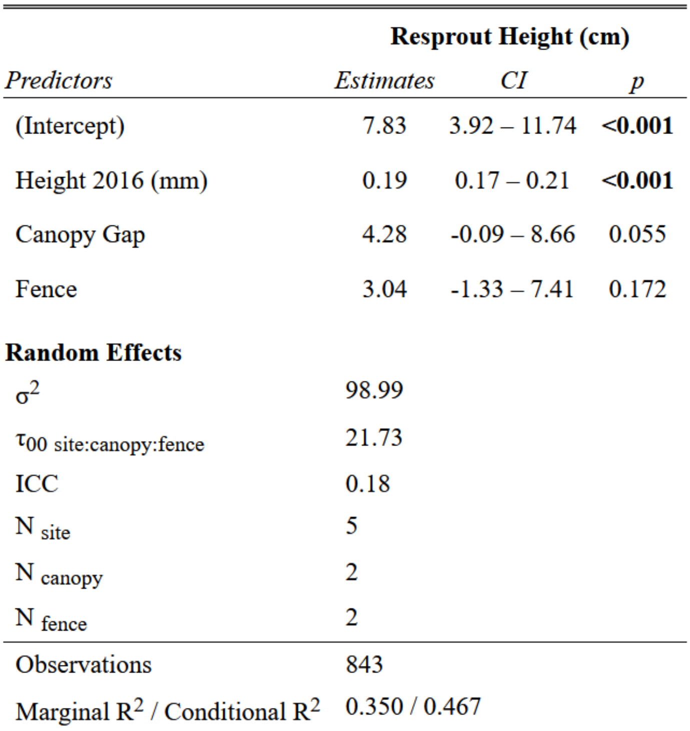
Appendix 1 – Tables of Model Results

Table 2. Results of a logistic regression of top killed vs not top killed recruits at site 4.



	Probability of Top Killing		
Predictors	*Odds Ratios*	*CI*	*p*
Intercept	0.05	0.01 – 0.24	**<0.001**
Diameter in 2016	1.27	1.14 – 1.45	**<0.001**
Observations	69		
R^2 Tjur	0.298		

Table 3. The model results from a mixed effect model determining the resprouting height of recruits 1 year following a burn.



	Resprout Height (cm)		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	7.83	3.92 – 11.74	**<0.001**
Height 2016 (mm)	0.19	0.17 – 0.21	**<0.001**
Canopy Gap	4.28	-0.09 – 8.66	0.055
Fence	3.04	-1.33 – 7.41	0.172
Random Effects			
σ^2	98.99		
$\tau_{00\ \text{site:canopy:fence}}$	21.73		
ICC	0.18		
N_{site}	5		
N_{canopy}	2		
N_{fence}	2		
Observations	843		
Marginal R^2 / Conditional R^2	0.350 / 0.467		

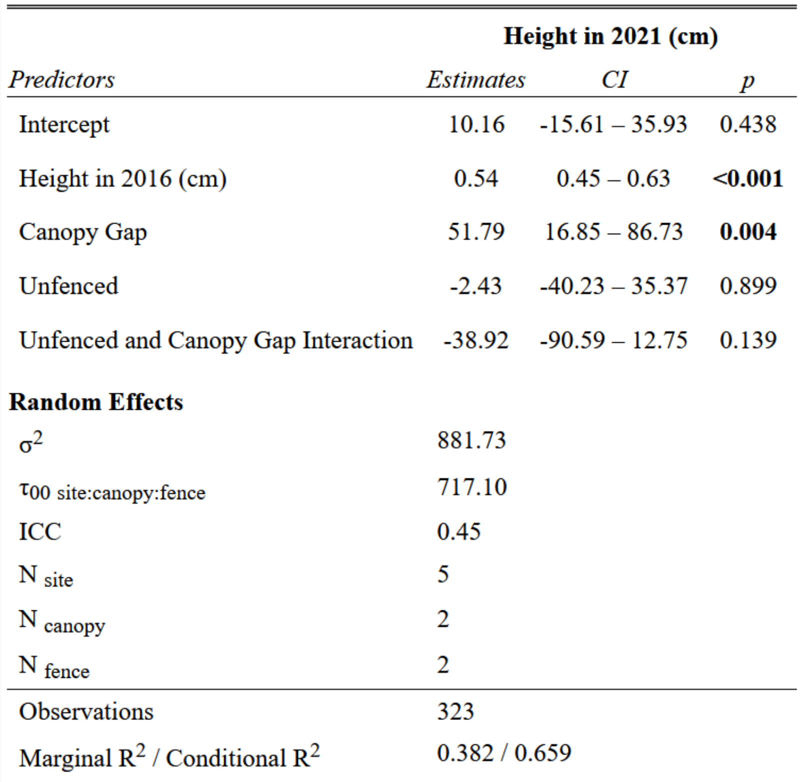
Table 4. The model results from a mixed effect model describing how height prior to burning effects the percentage height recovery 1 year later.

	Percentage Recovery (%)		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	77.71	66.87 – 88.56	**<0.001**
Height before burn	-0.91	-1.11 – -0.72	**<0.001**
Height before burn squared	0.00	0.00 – 0.00	**<0.001**
Canopy Gap	14.77	6.57 – 22.96	**<0.001**
Fenced	9.45	1.22 – 17.67	**0.025**
Random Effects			
σ^2	350.58		
τ_{00} site:canopy:fence	51.94		
ICC	0.13		
N_{site}	5		
N_{canopy}	2		
N_{fence}	2		
Observations	317		
Marginal R^2 / Conditional R^2	0.455 / 0.525		

Table 5.The results of a generalized mixed model showing the predictors of mortality across sites.

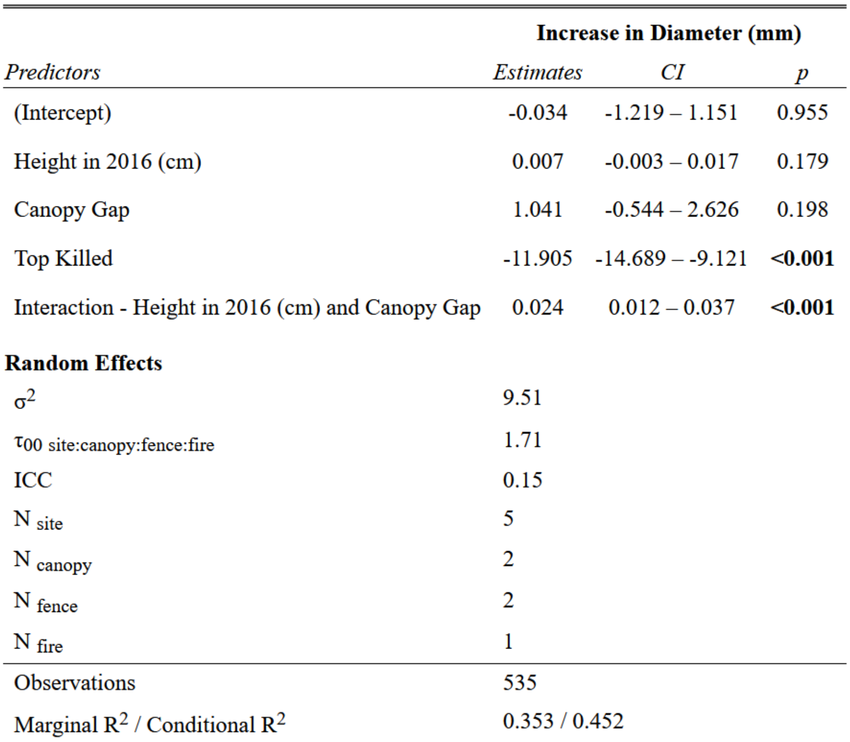
	Incidence of Mortality		
Predictors	*Incidence Rate Ratios*	*CI*	*p*
(Intercept)	0.14	0.03 – 0.56	**0.006**
Unburned	9.02	2.70 – 30.16	**<0.001**
Unfenced	0.40	0.12 – 1.35	0.140
Random Effects			
σ^2	1.22		
τ_{00} site:canopy:fence	0.84		
ICC	0.41		
N_{site}	5		
N_{canopy}	2		
N_{fence}	2		
Observations	40		
Marginal R^2 / Conditional R^2	0.414 / 0.653		

Table 6.Results of a mixed effects model of how treatments effect height in 2021, for recruits that were top killed.



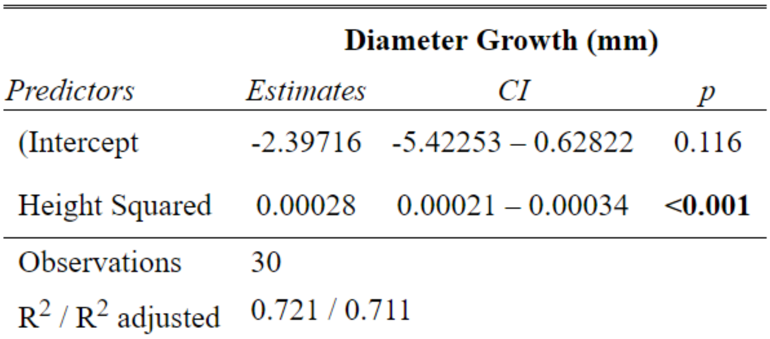
	Height in 2021 (cm)		
Predictors	*Estimates*	*CI*	*p*
Intercept	10.16	-15.61 – 35.93	0.438
Height in 2016 (cm)	0.54	0.45 – 0.63	**<0.001**
Canopy Gap	51.79	16.85 – 86.73	**0.004**
Unfenced	-2.43	-40.23 – 35.37	0.899
Unfenced and Canopy Gap Interaction	-38.92	-90.59 – 12.75	0.139
Random Effects			
σ^2	881.73		
τ_{00} site:canopy:fence	717.10		
ICC	0.45		
N_{site}	5		
N_{canopy}	2		
N_{fence}	2		
Observations	323		
Marginal R^2 / Conditional R^2	0.382 / 0.659		

Table 7. Results for a mixed effect model indicating how treatments effected diameter increase for recruits that in an unburned treatment.



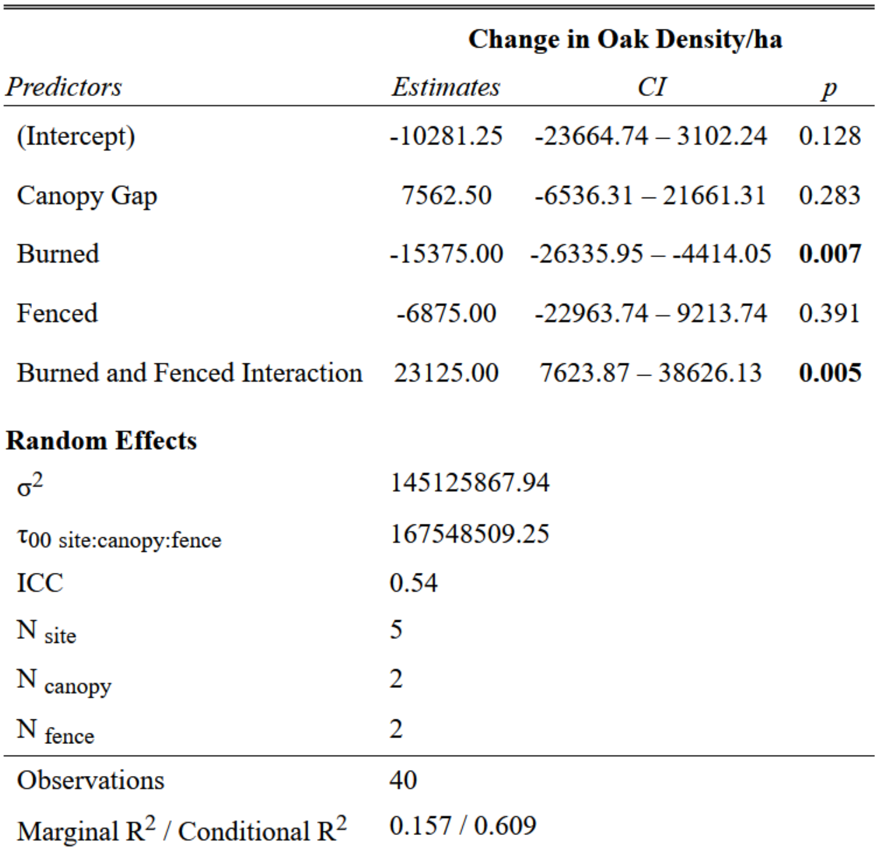
	Increase in Diameter (mm)		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	-0.034	-1.219 – 1.151	0.955
Height in 2016 (cm)	0.007	-0.003 – 0.017	0.179
Canopy Gap	1.041	-0.544 – 2.626	0.198
Top Killed	-11.905	-14.689 – -9.121	**<0.001**
Interaction - Height in 2016 (cm) and Canopy Gap	0.024	0.012 – 0.037	**<0.001**
Random Effects			
σ^2	9.51		
τ_{00} site:canopy:fence:fire	1.71		
ICC	0.15		
N_{site}	5		
N_{canopy}	2		
N_{fence}	2		
N_{fire}	1		
Observations	535		
Marginal R^2 / Conditional R^2	0.353 / 0.452		

Table 8. The results from a linear regression indicating the effects of height on diameter growth of recruits which were not top killed in site 4.



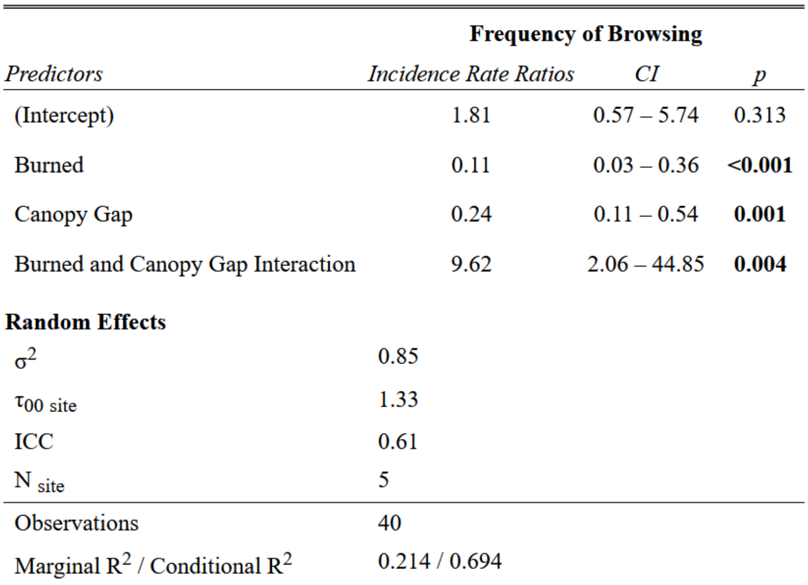
	Diameter Growth (mm)		
Predictors	*Estimates*	*CI*	*p*
(Intercept	-2.39716	-5.42253 – 0.62822	0.116
Height Squared	0.00028	0.00021 – 0.00034	**<0.001**
Observations	30		
R^2 / R^2 adjusted	0.721 / 0.711		

Table 9. The results of a mixed effects model indicating how the treatments effected the density of oak recruits on each site.



	Change in Oak Density/ha		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	-10281.25	-23664.74 – 3102.24	0.128
Canopy Gap	7562.50	-6536.31 – 21661.31	0.283
Burned	-15375.00	-26335.95 – -4414.05	**0.007**
Fenced	-6875.00	-22963.74 – 9213.74	0.391
Burned and Fenced Interaction	23125.00	7623.87 – 38626.13	**0.005**
Random Effects			
σ^2	145125867.94		
τ_{00} site:canopy:fence	167548509.25		
ICC	0.54		
N site	5		
N canopy	2		
N fence	2		
Observations	40		
Marginal R^2 / Conditional R^2	0.157 / 0.609		

Table 10. The results of a generalised mixed effect model indicating the effects of treatment on the frequency of browsing.



	Frequency of Browsing		
Predictors	*Incidence Rate Ratios*	*CI*	*p*
(Intercept)	1.81	0.57 – 5.74	0.313
Burned	0.11	0.03 – 0.36	**<0.001**
Canopy Gap	0.24	0.11 – 0.54	**0.001**
Burned and Canopy Gap Interaction	9.62	2.06 – 44.85	**0.004**
Random Effects			
σ^2	0.85		
τ_{00} site	1.33		
ICC	0.61		
N site	5		
Observations	40		
Marginal R^2 / Conditional R^2	0.214 / 0.694		

Table 11. The results of a mixed effect model indicating predictors of the change in density of coniferous species over the study period.

	Change in Conifer Density		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	-367.65	-1588.67 – 853.37	0.521
Burned	-1470.59	-2765.67 – -175.50	**0.030**
Fenced	698.53	-632.05 – 2029.10	0.272
Canopy Gap	-496.32	-1745.63 – 752.99	0.401
Random Effects			
σ^2	1307975.11		
$\tau_{00\ \mathrm{site:canopy:fence}}$	0.00		
N_{site}	3		
N_{canopy}	2		
N_{fence}	2		
Observations	17		
Marginal R^2 / Conditional R^2	0.332 / NA		

Appendix 2 – Complementary Graphs

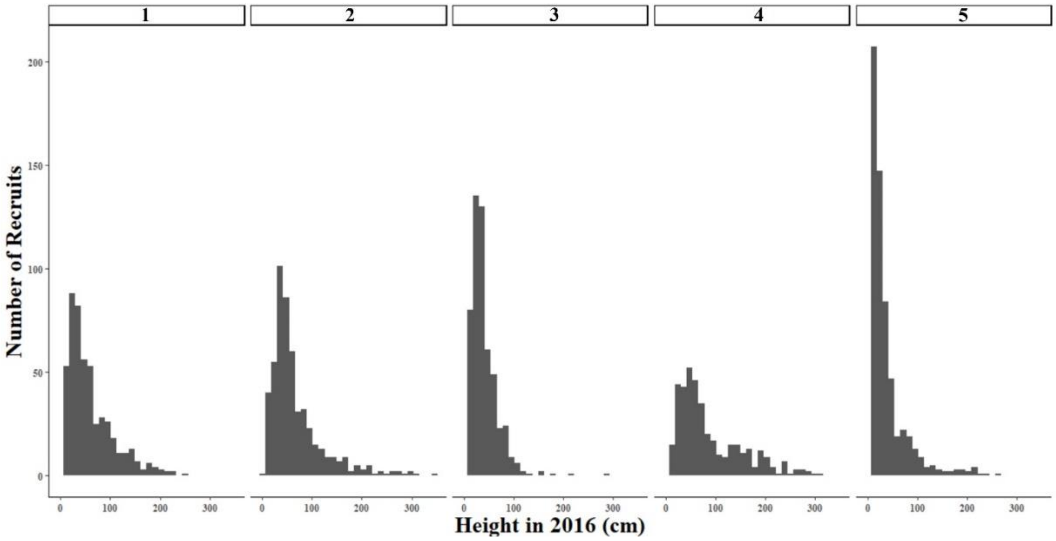


Figure 7. The number of recruits observed in each height class in August 2016, separated by site.

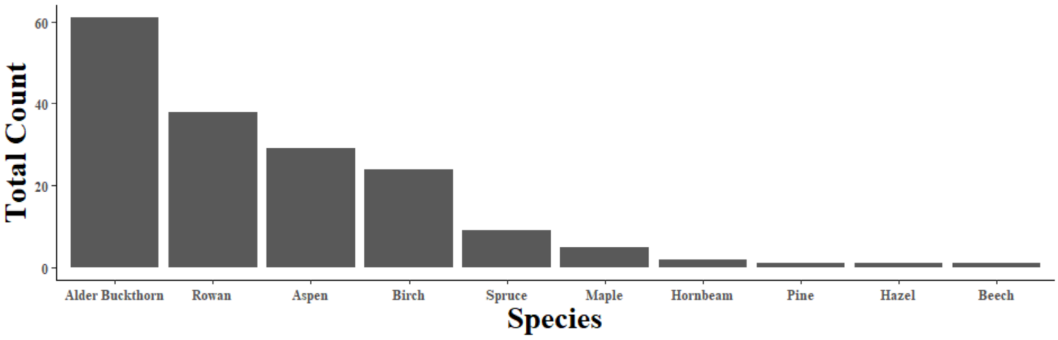
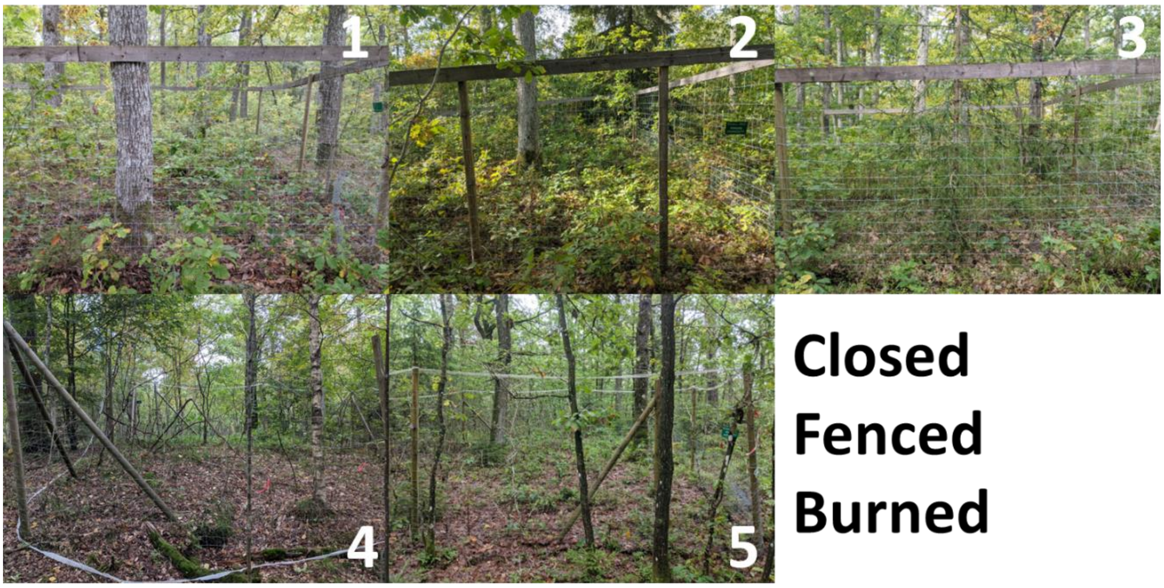
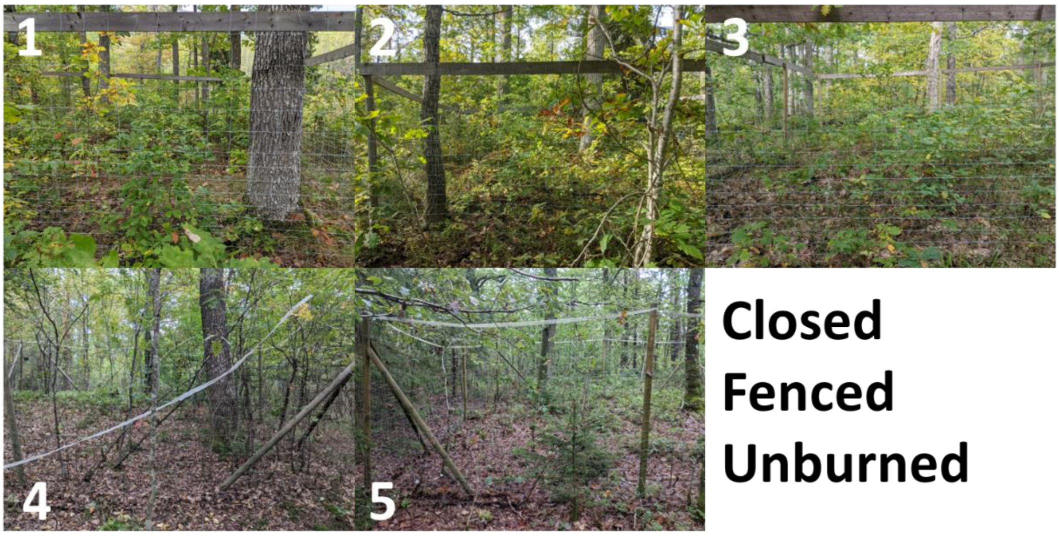


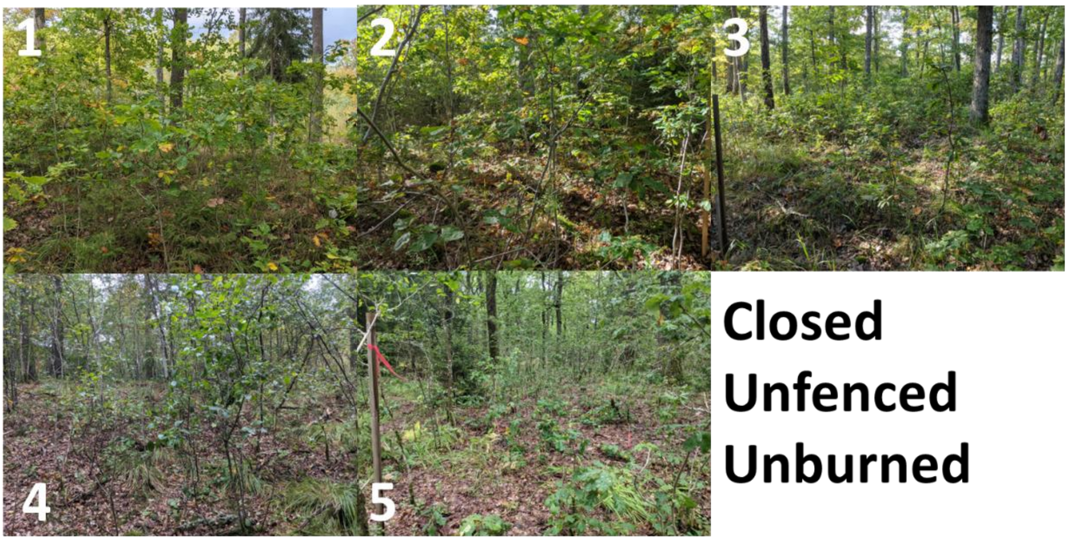
Figure 8. The total number of non-oak species included in the dataset across all sites and treatments in 2021.

Appendix 3 – Treatment Photos



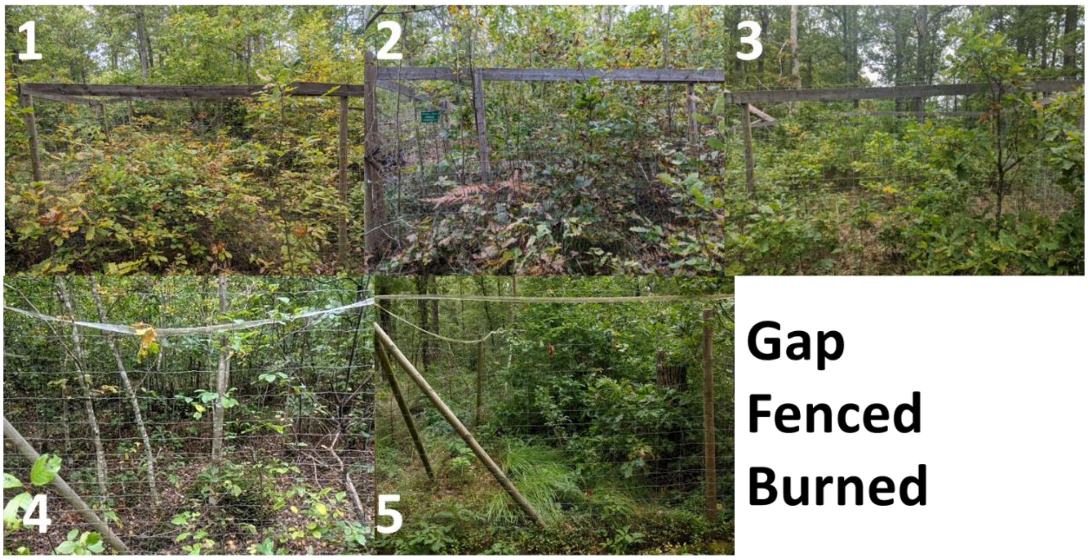


Closed
Fenced
Unburned



Closed
Unfenced
Unburned

Closed
Unfenced
Burned


1
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Gap
Fenced
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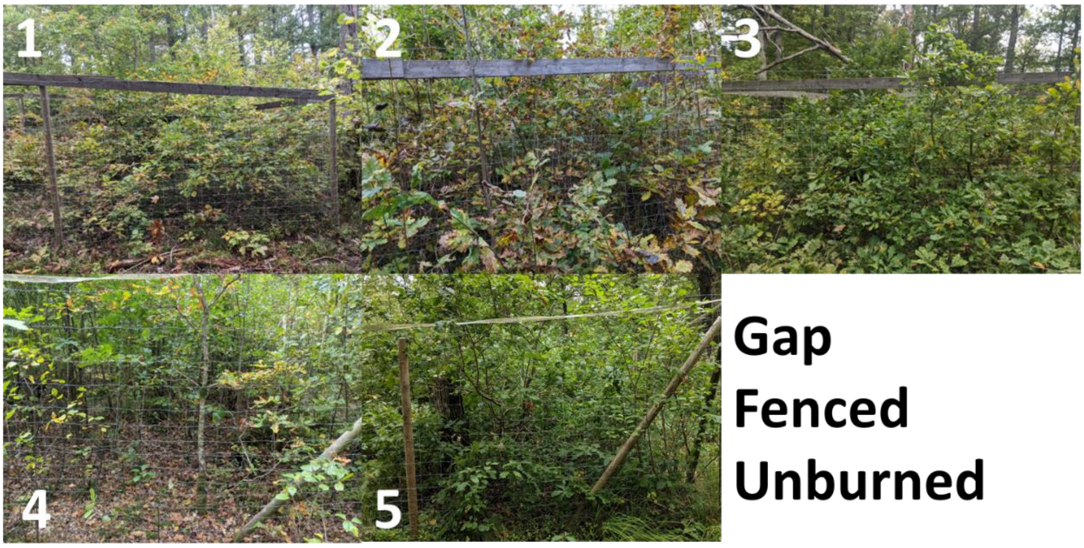
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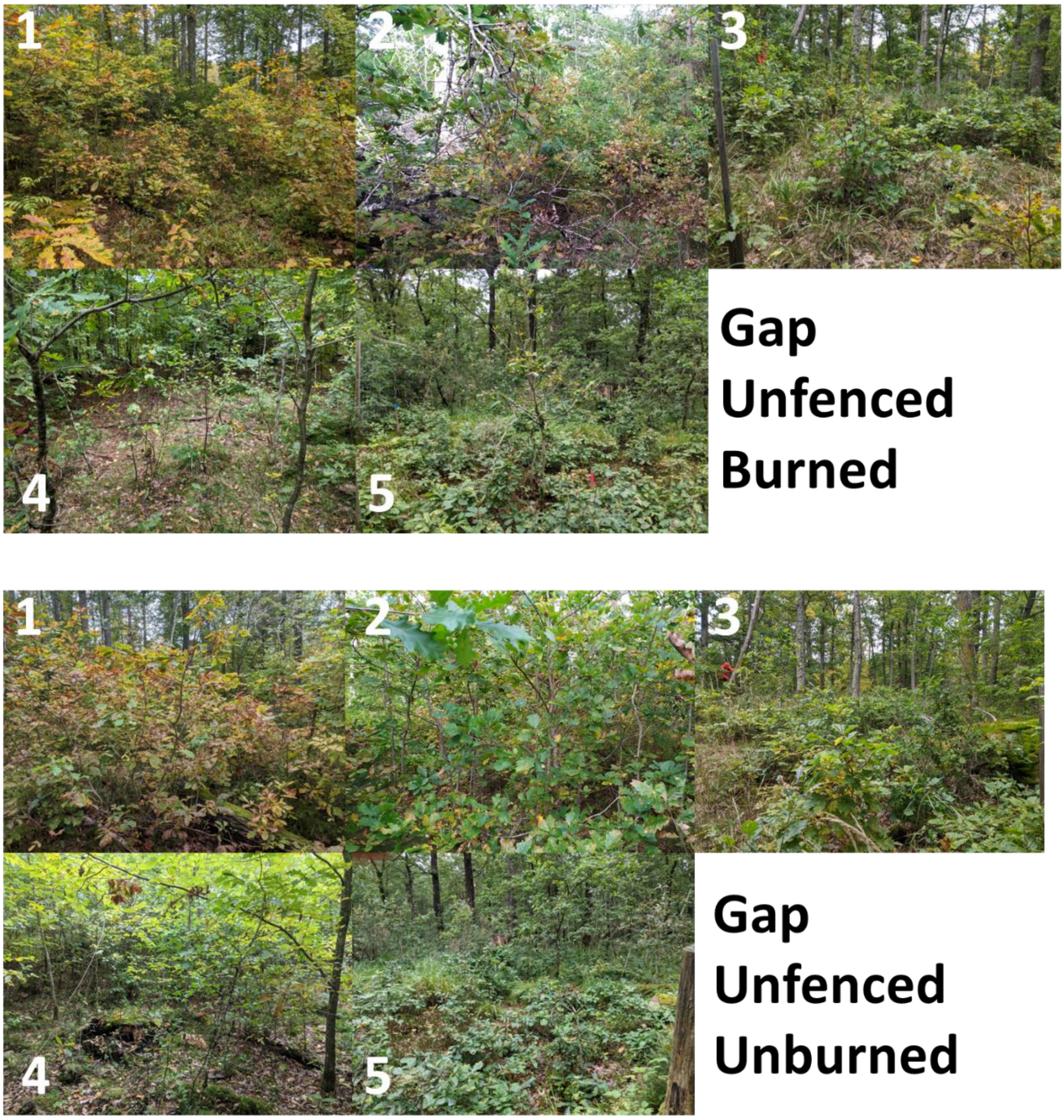

Figure 9. All photos above, of treatment plots, where numbers denote the sites.