To what extent does the presence of bramble (*Rubus fruticosus agg*) act as a facilitator of English oak (*Quercus robur*) regeneration at Knepp Wildland.

Presented by

Catherine King

as a Project

in part fulfilment of the requirements for the Bachelor's Degree in

BSc (Hons) Animal Science

at Plumpton College

2019.

Abstract

As high levels of ungulate browsing pressure can restrict natural oak regeneration, the presence of bramble may act as a nurse species, reducing the detection and vulnerability of oak saplings to herbivores. The extent to which the presence of bramble (*Rubus fruticosus agg*) acts as a facilitator of English oak (*Quercus robur*) regeneration was studied at a 20 acre area of the Southern Block at Knepp Wildland in West Sussex, England. In 2009 large free roaming herbivores were introduced to the Southern block, exposing the area to a natural grazing management system, with minimal human intervention. The reintroduction of ecosystem engineers, such as large herbivores is believed to have a profound impact on the biodiversity of habitats, through their grazing and disturbance techniques. One theory is that through browsing pressure, landscapes follow a cyclical process, which is composed of a shifting mosaic of open grassland, closed woodland and scrub. For this study the height of 711 oak saplings were recorded, alongside the presence or absence of bramble and degree of browsing damage. The results indicated that the presence of bramble was found to facilitate the regeneration of oak saplings, supporting the theory of associational resistance. This theory suggests that herbivory is reduced on one plant species when in the presence of a nurse plant species. Oak sapling growth was shown to be positively affected by the presence of bramble. Sapling height was significantly higher for saplings under the protection of bramble, and when browsing did occur, it was significantly lower for saplings which grew within a canopy of bramble.

TABLE OF CONTENTS

Introduction

Knepp Wildland is situated in West Sussex, England, a 3500 acre estate divided into the Northern block, Middle block and Southern block, figure 1. Prior to becoming a wilding project, it had been intensively farmed since the Second World War. In 2000, after many years of running at a loss, unable to compete with larger, industrialised farms, the decision was made to sell the livestock and farm machinery. After receiving Countryside Stewardship funding in 2002, the idea of turning Knepp into a wildland project was born. This funding allowed Knepp to reseed their land with native flowers and grasses (Tree, 2018).

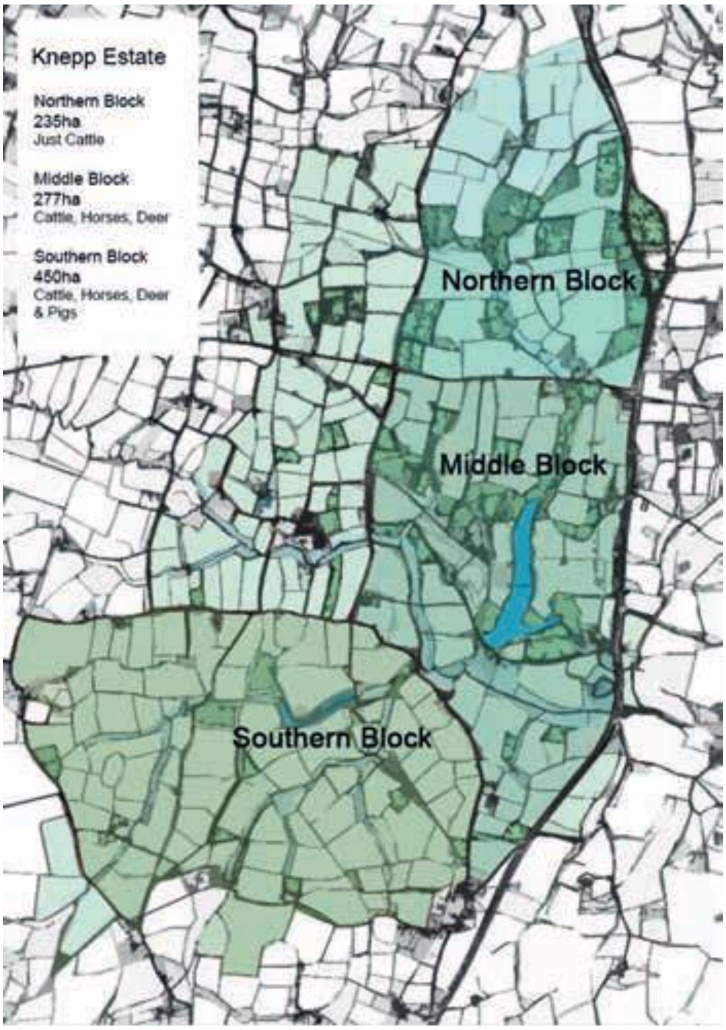


Figure 1. Knepp Castle Estate Wildland Project (Burrell 2018).
Showing the Northern block 580 acres, Middle block 684 acres and Southern block 1111 acres.

The basic concept of rewilding is to create more self-regulating biodiverse habitats by restoring, repairing and reinstating ecosystems that have been negatively impacted by human intervention, for example through urban expansion, deforestation and agriculture. Often this involves the reintroduction of keystone species, such as apex predators and large herbivores (Vera, 2002). Rewilding is a controversial issue, with fierce debate and disagreement amongst its critics and advocates. There is conflict and anxiety regarding the conservation goals it is attempting to achieve and division over the exact meaning of the word rewilding (Nogués-Bravo et al, 2016). Initially rewilding meant the reintroduction of apex predators to instigate top-down ecological control, whereas more recently, especially in England, with the absence of apex predators, it has been used to describe more naturalised grazing by large herbivores to influence and develop landscapes (Bressette, Beck and Beauchamp, 2012). One side of the debate claims that nature needs to be constrained and cannot thrive without human intervention, and that the reintroduction of plants and wild animals can have a profound influence on the environment with unpredictable consequences, for example the establishment of invasive species (Derham et al, 2018). The other view is that natural processes should be allowed to flourish through the provision of ecological corridors and connectivity, with the minimum of management, therefore creating self-regulating ecosystems (Hodder and Bullock, 2009). The 1995 reintroduction of grey wolves (*Canis lupus*) to Yellowstone National Park in the United States of America, is oft cited as a rewilding success story. The addition of the wolves created a trophic cascade. Through the wolves predating on the elk, there was a reduction of intense predation by elk (*Cervus canadensis*) on plant species, such as willow (*Salix spp*) (Ripple and Beschta, 2011).

The prefix ‘re’ in rewilding evokes a vision of returning to the distant past, but this has been declared an impossibility due to the loss of habitat, the extinction and extirpation of certain species, and the irreversibility of climate change (Carver, 2016). Knepp prefer the word wilding, without the problematic prefix. Their idea was not to return to the past but to use the past to help shape the future, by allowing the natural environmental processes to unfurl with minimum human intervention and no specific goals or targets (Tree, 2018). Grazing animals are ecosystem engineers (Müller et al, 2017), through the consumption of plant species, they can be hugely influential on the structure, function, composition and heterogeneity of landscapes, which in turn modifies and impacts the habitats of other animals (Gordon, Hester and Festa-Bianchet, 2004, Putman, Apollonio and Andersen, 2011). At Knepp the rewilding notion is to evaluate the effects these animals have on the regeneration of land that has previously been intensively farmed (Van Uytvanck and Hoffmann, 2009). Knepp reintroduced the free ranging herbivores, fallow deer (*Dama dama*), red deer (*Cervus elaphus*), Exmoor ponies (*Equus ferus caballus*) and English Longhorn cattle (*Bos primigenius*) (Burrell and Greenaway, 2011). Some of these were introduced to act as ecological proxies for their ancient ancestors, such as aurochs (*Bos primigenius*) and tarpans (*Equus ferus ferus)*, animals which were grazing in species rich environments long before humans instigated agriculture (Vermeulen, 2015).

As habitats become more fragmented, for example through urbanisation (Weisberg and Bugmann, 2003), herbivory becomes more vital for the spatial distribution of nutrients and seeds (Doughty, 2017). Large herbivores are drivers of biodiversity, through their different grazing and disturbance techniques they can influence plant species composition and populations (Olff and Ritchie, 1998, Bakker et al, 2006). In order to co-exist large herbivores have developed different feeding strategies. These are divided into three groups, browsers, grazers and intermediate feeders, figure 2. Each of these have their own unique environmental niche and therefore a different impact on vegetation. Browsers feed on the leaves, shoots, twigs and bark of woody plants and shrubs, grazers feed on grass and flowering plants, and intermediate feeders both graze and browse (Hoffman, 1989). These groups are determined by the composition of the food plants consumed and the digestive anatomy of the animal (Gordon, 2003). Red deer are classified as intermediate feeders, although they prefer to browse more than graze. Fallow deer are grazers, although they will browse in autumn and winter when grass nutrition is low (Hester et al, 2000). Longhorn cattle graze on longer grasses, as ruminants they can digest the harder cellulose, unlike the Exmoor ponies who predominantly graze on shorter grasses, where the cellulose is less developed. The ponies benefit from the regrowth where the cattle have previously grazed. Ponies may also browse from trees and shrubs (Vermeulen, 2015). Knepp also reintroduced Tamworth pigs (*Sus scrofa domesticus*) as proxies for wild boar (*Sus scrofa*). They are omnivores not herbivores, in the wild they are opportunistic foragers, feeding on leaves, roots, fruits, flowers, insects and small mammals (Pedrazzoli, 2017). Grazing and browsing will invariably include other methods of disturbance, for example the trampling of vegetation, including seedlings and saplings (Hester et al, 2006), pawing and scraping (Reimoser, Armstrong and Suchant, 1999) and bark stripping (Borkowski et al, 2017). Male deer also fray to remove the velvet from their newly grown antlers or for territorial scent marking, which can damage or kill trees (Gill, 1992). Browsing may not always be detrimental to trees, if browsing is of the leader shoots this can restrict growth but browsing of the lateral shoots can act as a form of pruning and result in accelerated growth (Konopka and Pajtik, 2015). Rooting by pigs is a prime example of both positive and negative disturbance, this involves searching for food items, such as bulbs or roots, then excavating the soil surface to obtain the item. Rooting exposes the soil, which may have been covered with dense vegetation, so can aid the germination of seeds. Rooting also increases the turnover of nutrients and minerals for improved plant growth and acceleration of the decomposition process (Sondej and Kwiatkowska-Falińska, 2017). The negative aspect is that the pigs will predate on seeds and roots, whilst also damaging saplings and understory vegetation, and severe rooting can cause soil erosion (Wirthner et al, 2012).

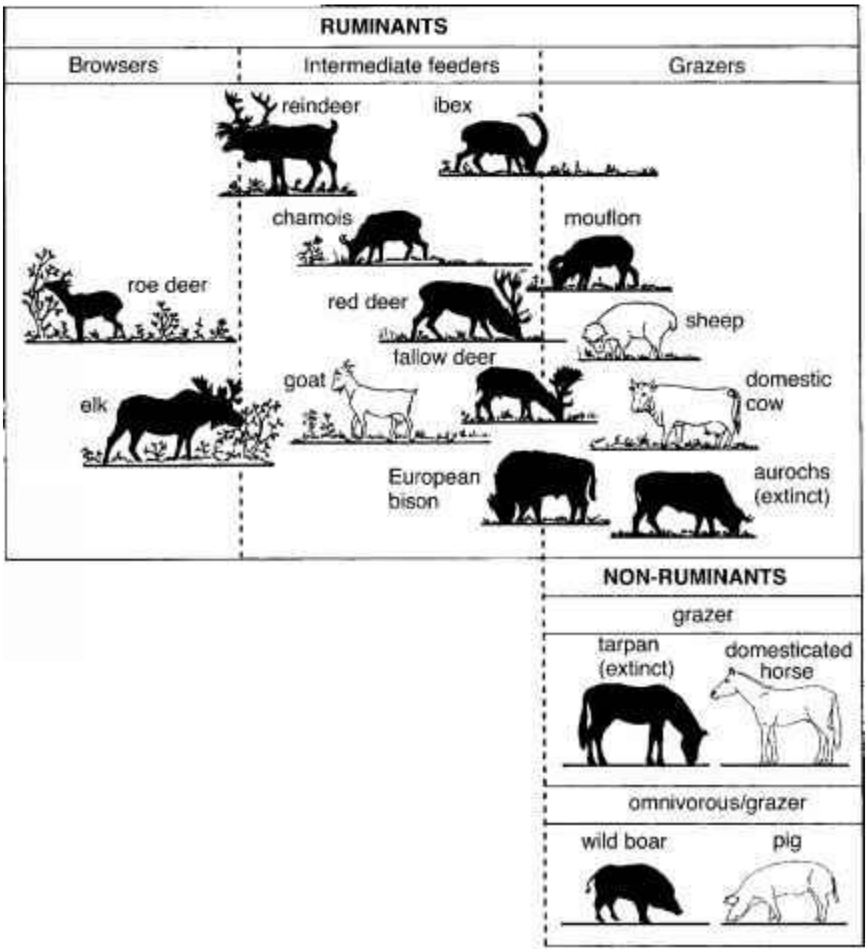


Figure 2. Large herbivores of Europe together with the omnivorous wild boar, classified according to their feeding strategy (Ecology Center, 2018).

For the past few decades there has been some concern that wood pastures are becoming threatened ecosystems through the lack of natural regeneration of trees (Humphrey and Swaine, 1997), triggering research into whether herbivory can drive vegetation succession (Convery et al, 2016). Vera (2000) hypothesised that through their disturbance, large herbivores can affect natural regeneration and have a fundamental impact on the diversity of landscapes. Vera challenged the previous opinion that before human intervention European landscapes were closed canopy forests. Instead he suggests that landscapes were more open and park-like. He argues that certain light-demanding species, such as oak (*Quercus*) and hazel (*Corylus*) would not have been able to regenerate in closed canopies, unable to compete with more shade tolerant trees, such as beech (*Fagus).* Yet their presence is persistent and well represented in historical pollen records, which questions the validity of the closed canopy theory. Vera's theory suggests that the park-like landscapes follow a cyclical process, driven by the high pressure of herbivore browsing. Vera states that without grazing the closed canopy woodland would have been maintained and therefore oak and hazel would be missing from the pollen data (Cornelissen, 2017). The cyclical process, figure 3, is composed of a shifting mosaic of open grassland, closed woodland and scrub, which would have been maintained by the presence of large herbivores.

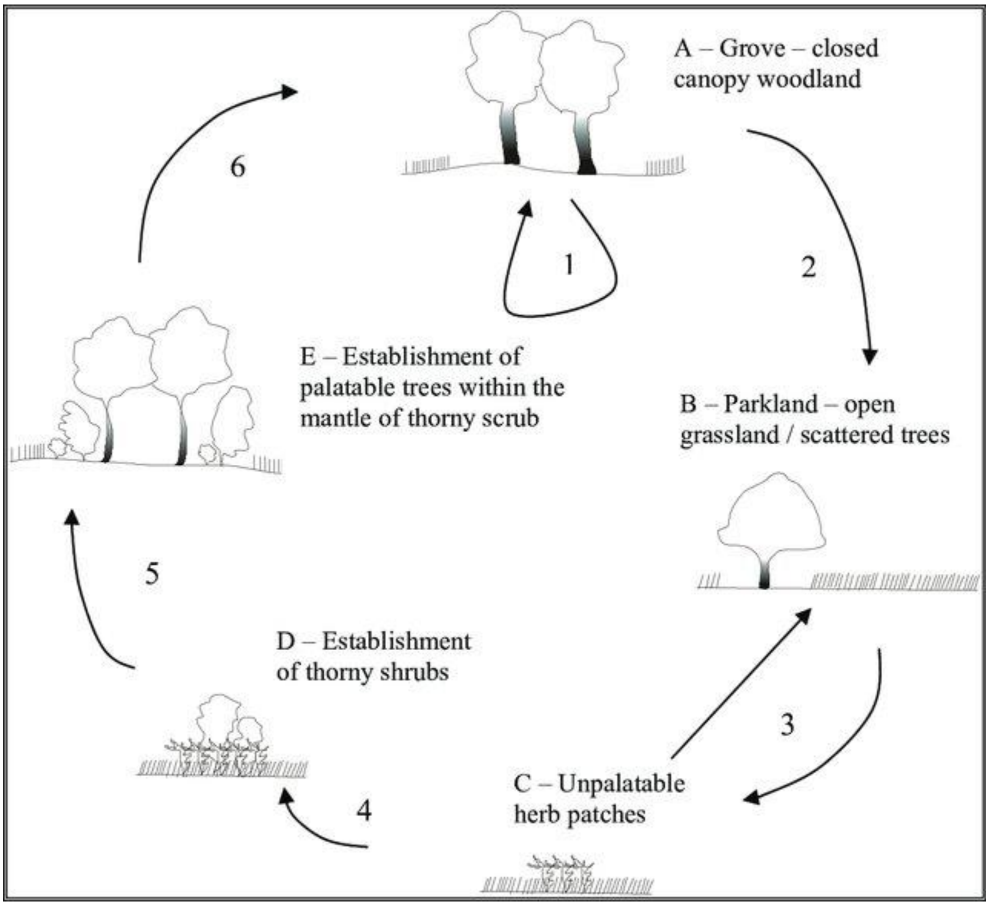


Figure 3. Cyclic succession in temperate woodlands (Hodder et al, 2005). Regeneration is prevented by grazing and trampling within the closed canopy grove. Light-demanding trees fail to regenerate because of the shade (A). Eventually, the trees in the closed canopy grove die and the canopy opens out. Grasses establish, attracting grazing animals and preventing the establishment of shrubs and trees (B). Disturbance by animals lead to establishment of non-palatable herbaceous species (C). Thorny shrubs develop under the protection of the scrub patches and in turn the shrubs offer protection to tree seedlings from grazers (D). The trees will then shade out the scrub creating a grove (E), which eventually develops into closed canopy woodland completing the cycle.

Historically this would have been predominantly aurochs and to a lesser extent, tarpans, as well as bison (*Bison bonasus*), elk (*Alces alces*) and deer (Hodder et al, 2005). Herbivory would prevent tree regeneration, therefore leading to the degeneration of the woodland pasture, allowing the transition to open grassland, which through grazing would subsequently enable the regeneration of trees and shrubs (Newton et al, 2013). Over time the trees would eventually die, and the cycle would be repeated (Newton et al, 2012). Vera is not without his critics, for example Bradshaw et al (2003) argue that fire, not herbivory, would have been the major influence on the opening of landscapes, and Bradshaw and Mitchell (1999) claim there is insufficient data to ascertain exact herbivore population densities and therefore, their impact on vegetation cannot be quantified. Largely, Vera's theory has been well supported and is significant in the evaluation of conservation management processes and principles (Lorimer and Driessen, 2014). Several rewilding projects have used the idea of these historical landscapes as models for their conservation and biodiversity projects, for example Oostvaardersplassen in Holland, the New Forest in England and Bialowieza Forest in Poland (Taylor, 2005). The transformation process of Knepp into wildland has also been heavily influenced by Vera's grazing ecology theory. Since becoming a wildland, Knepp has become a breeding site for numerous critically endangered birds, such as nightingales (*Luscinia megarhynchos*), turtle doves (*Streptopelia turtur*) and red kites (*Milvus milvus*), and has seen the reappearance of many small mammals, such as stoats (*Mustela erminea*), polecats (*Mustela putorius*) and harvest mice *(Micromys minutus*). Knepp is also home to all five UK species of owls, thirteen species of bats, over six hundred species of invertebrates and many rare plants, such as water violet (*Hottonia palustris*) and marsh speedwell (*Veronica scutellata*) (Tree, 2018).

Due to a lack of funding Knepp was initially unable to reseed or introduce the large herbivores to their Southern block. This area was left to its own devices. During this time Knepp noticed that thorny scrub had established, in which English oak (*Quercus robur*) saplings were growing. When additional funding was received in 2009, this enabled Knepp to dismantle internal fencing, ring fence the boundaries and introduce free roaming large herbivores to the southern block (Tree, 2018). As seedlings and saplings are less likely to survive in open grassland without some protection from the pressure of herbivory, it has been proposed that the regeneration of oak trees can only occur in the presence or vicinity of thorny or spiny shrubs, when grazing animals are present. An example is shown in figure 4. Open grassland would contain relatively unpalatable species, such as bramble (*Rubus fruticosus*), which could act as protection from herbivory (Kirby, 2004). This is known as the associational resistance theory and is a vital component in the cyclical process, where less palatable plant species reduce herbivory on more palatable species and aid their regeneration (Hambäck, Ågren and Ericson, 2000). Many plant species have evolved physical or chemical defences in response to herbivory, for example the thorns of bramble (Zangerl, 2003) or bracken (*Pteridium aquilinum*), which produces hydrogen cyanide when its fronds are damaged, making them ideal nurse species (Cooper Driver, 1990). The height and density of the nurse species can also be a protective feature, aiding concealment, making the sapling less open to detection by predators (Bazely et al., 1991, Barbosa et al, 2009). For example, blackthorn (*Prunus spinosa*) follows a divaricate growth pattern, producing a dense canopy, which is difficult for large predators to penetrate, allowing the sapling to establish and grow. This growth pattern is believed to be an evolutionary adaptation in response to browsing by large herbivores (Bakker et al, 2004). In order to complete the cyclical process, the saplings will outgrow and out-shade the original nurse species which helped facilitate their survival (Smit et al, 2005). The role of bramble as a protector needs to be balanced with its degree of palatability (Harmer et al, 2018). Although its thorny defences may be repellent to some predators, its young shoots and leaves can be a food source for several species of deer (Van Uytvanck et al, 2008). Bramble could also be a potential inhibitor of oak growth with regards to light availability (Gomez et al, 2001), and a competitor for water and nutrients (Linhart and Whelan, 1980, Vera, Bakker and Olff, 2009). Although many farmers consider thorny scrub as a nuisance and view it as a sign of neglected land, historically it was valued. In the 17th century forestry officers were instructed to throw acorns into thorny shrub, so the oak saplings could grow within shelter. In the 18th century there was a statute which imposed a punishment on anyone seen to be damaging thorn bushes, also in the 18th century, agricultural writer Arthur Standish wrote that, "'The thorn is the mother of the oak" (Tree, 2018).

Figure 4. An oak sapling at Knepp surrounded by bramble (King, 2018). Although this sapling has outgrown the height of the bramble, it is still protected by the wide diameter of the bramble canopy.

With the release of the herbivores, Knepp were keen to observe the battle between vegetation succession and herbivore disturbance, instigating this study to determine to what extent does the presence of bramble facilitate the growth of English oak saplings by reducing large herbivore browsing damage.

Another point to consider is that for the oak saplings to benefit from associational resistance, their acorns need to establish in the vicinity of bramble, and it is believed that Eurasian jays (*Garrulus glandarius*) play an important role in the dispersal of acorns. Jays collect and cache acorns, carrying up to six in their throat or gullet. In a four-week study, 65 jays had dispersed approximately 500,000 acorns (Vera, 1997). They have a preference of caching the acorns at the fringes of hedges, thorny scrub and at the base of shrubs (Kuiters and Slim, 2003). Although the jays feed on the acorns, this is coincidently reduced during the period when the oak seedlings begin to emerge. When the jays do return to the acorn, they lift the seedling to reveal the acorn, which is removed and eaten, usually leaving the seedling unharmed. This is a mutualistic symbiotic relationship, in which the jays benefit from the diet of the acorns and the oak benefits from the acorn being planted in protective thorny scrub, where, if not eaten by the jays, the seedlings can thrive (Birch et al, 2016). Acorns are also distributed throughout landscapes by rodents, such as wood mice (*Apodemus sylvaticus*), and by barochoric seed fall, but it is believed that the method in which jays hammer the acorn into the earth provides more adequate protection from predation and a more tenable establishment (Bobiec, Reif and Öllerer, 2018), also decreasing depredation by other species (Haas and Heske, 2005).

This study hypothesises that bramble acts as a safe site for the survival and growth of oak saplings by the means of associational resistance, thereby contributing to the conservation of habitat biodiversity through the theory of cyclical vegetation turnover.

Methods and Materials

Study Site

Knepp Wilding Estate is situated in the south east of England, in the county of West Sussex. The survey site is the 20 acre New Barn Two area of the Southern Block, figure 5. The land is characterised by heavy low Weald clay over a bedrock of limestone. The area is unfenced and there is no vegetation control. The area was arable land from the 1980s to 2004 and left fallow in 2005 (Tree, 2018). Annual precipitation is 389.2mm and the mean temperature is 3 °C and 21 °C in January and July, respectively (Met Office, 2019a). The site is open scrub, composed of grassland, bramble and shrub thickets and saplings and trees, the most abundant are bramble (*Rubus fruticosus agg)*, blackthorn (*Prunus spinosa),* hawthorn (*Crataegus monogyna),* English oak (*Quercus robur)* and sallow (*Salix cinereal*).

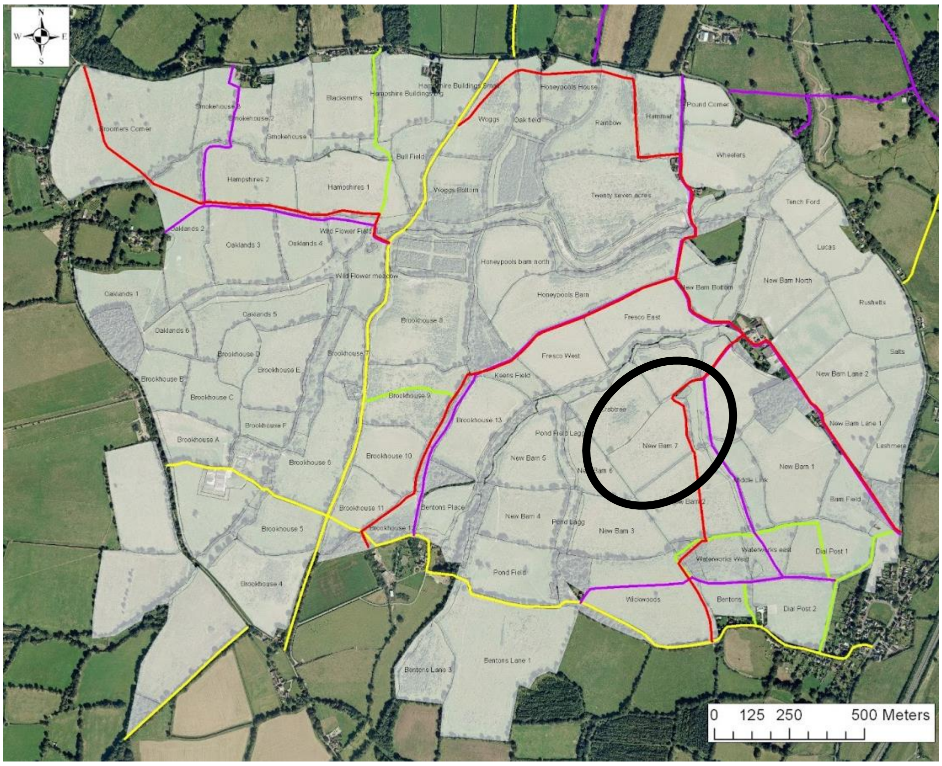


Figure 5. The 20 acre New Barn Two area circled in black (Knepp, 2018).

Data Collection

With the permission and assistance of Knepp Estate's ecologist, data was collected by a group of volunteers for five consecutive days during December 2018. New Barn Two is clearly divided by two paths, creating four sections. Volunteers walked parallel continuous transects, recording saplings along the whole length of the transect line, over the course of the five days until all four sections were exhaustively completed. The transect perimeters were defined by wooden canes, so there was no crossover. Data was recorded onto data sheets, under the heading columns (1) Ten digit grid reference, (2) Sapling species, (3) Sapling height (cm), (4) Bramble measurement (cm), (5) Browsing incidence and (6) Bramble presence and species. Grid references were obtained using handheld GPS devices or the mobile phone app Grid Reference Free OS. Sapling species were identified using a photographic key. All sapling species within the area were recorded but only English oak were used in this study. Sapling height was measured using wooden canes marked with 10cm intervals. Saplings with height <20cm were not recorded. If tree height exceeded the measuring cane, a visual estimation of height was recorded. The depth of the bramble was measured as the closest point to the sapling that could be achieved without encroaching into the bramble, using wooden canes marked with 10cm intervals. Where access was not possible to measure with the cane, a visual estimation of depth was recorded. Browsing incidence was recorded by visual assessment and classified as heavy >50% sapling damage, light <50% damage or none. An example of heavy browsing is shown in figure 6. Bramble presence was recorded as yes or no. Species of all bramble present were recorded but only *Rubus fruticosus* was used in this study. Saplings that had been recorded were identified by being tied with biodegradable string, to avoid repetition. The data was transferred from the data sheets into Microsoft Excel. Data from a similar but not identical, study in 2009, where 577 oak saplings were recorded, was available from Knepp via the file sharing website Dropbox. Grid references from 2009 were compared to 2018 to ascertain survival and mortality rates during the eight years.

Figure 6. An example of heavy browsing on an oak sapling at Knepp (King, 2018).
A large proportion of the bark has been browsed.

Livestock

Knepp livestock are free ranging and as there is no provision of supplementary feeding, grazing levels are high and constant. The density and species composition are estimated annually by walking transect surveys. Livestock species composition stored on the file sharing website Dropbox, can be seen in table 1. Figures for 2017 were used in the study as data for 2018 was not yet available.

Table 1. Quantity of Livestock for 2009 and 2017		
Species	**2009**	**2017**
Fallow deer, *Dama dama*	30	165
Red deer, *Cervus elaphus*	0	14
Tamworth pigs, *Sus scrofa domesticus*	35	7
Longhorn cattle, *Bos primigenius*	77	94
Exmoor ponies, *Equus ferus caballus*	11	10
Total	**153**	**290**

Data Analysis

The study sample was 711 saplings in 2018 and 577 saplings in 2009. The significance threshold was set at P=<0.05.

Genstat Undergraduate Release 18.1 was used to perform a Chi-square test of association (X^2) to determine whether there was an association between the survey year and the severity of browsing damage, in categories heavy, light or none. The Chi-square value was then used in calculating Cramer's V coefficient to quantify the strength of the association.

JASP version 0.9 was used to perform a two-way analysis of variance (ANOVA). Bramble presence and browsing damage were entered as the independent variables, with sapling height as the dependent variable. The test was used to understand if there was an interaction between the two independent variables on the dependent variable.

Results

Data for 711 oak saplings were recorded.

Data from 2009 and 2018 was cross referenced, but no grid references were found to tally.

Survey year and browsing damage

The Chi-square test of association showed there was a statistically significant association between the survey year and severity of browsing ($X^2_{(2)}$ =35.02, p<0.001). Table 2 and figure 7 summarise the observed frequencies for the severity of browsing in the categories heavy, light and none in 2009 and 2018, with table 2 also displaying the divergence of the observed data from the expected values.

Table 2. Summary of the level of browsing damage with regards to survey year. Expected frequencies are shown in brackets.

		Level of browsing damage			
		Heavy	**Light**	**None**	**Total**
Year	2009	339	156	82	**577**
		(357.04)	(116.03)	(103.93)	
	2018	458	103	150	**711**
		(439.96)	(142.97)	(128.07)	
	Total	**797**	**259**	**232**	**1288**

The probability of a sapling being heavily browsed in 2009 was 58.75%, compared to 64.41% in 2018, and the probability of no browsing was 14.21% in 2009 compared to 21.10% in 2018.

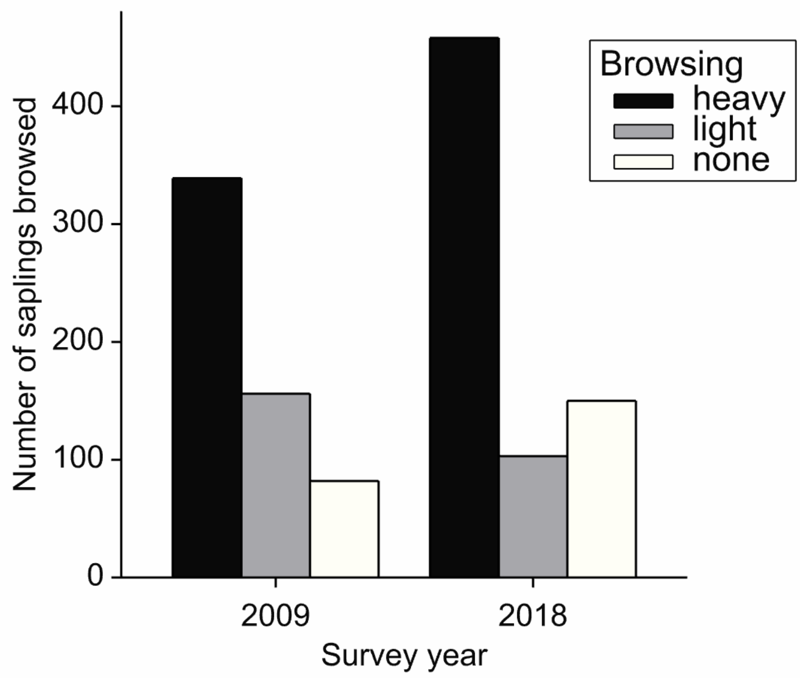


Figure 7. Frequency distribution of heavy, light and no browsing for oak sapling surveys conducted in 2009 and 2018. The graph shows that heavy and no browsing follow a similar trend across both years, with less proportion of light browsing for 2018.

Despite a statistically significant association between the survey year and severity of browsing, Cramer's coefficient (V) was calculated as 0.165, indicating that the association was low.

The effect of bramble presence and browsing damage on oak sapling height

The Levene's test for equality of variances was statistically significant, ($F_{(5, 705)}$=71.65, P=<0.001). This was due to the variances of the groups being unequal, therefore the assumption of homogeneity of variance was violated. A QQ-plot of the residuals was made, visual assessment showed that they were normally distributed. As the sample size was relatively large and ANOVA is considered robust enough to cope with violation of homogeneity, a two-way

ANOVA was conducted. This test examined the effect of bramble presence and browsing damage on oak sapling height, for which there was a statistically significant interaction ($F_{(2, 705)}$=8.62, P=<0.001). The mean height for a sapling with bramble present and heavy browsing was 106.93cm (s.d.=62.90cm, n=70) compared to 65.57cm (s.d=37.26cm, n=388) for a sapling with no bramble and heavy browsing, showing that the presence of bramble and heavy browsing gives a mean increase in height of 41.36cm. For bramble presence and light browsing, there was a mean increase of 46.03cm, with a mean height of 169.60cm (s.d=109.94cm, n=75) compared to light browsing and no bramble, with a mean of 123.57cm (s.d=114.47cm, n=28). For bramble presence and no browsing, the mean height was 316.76cm (s.d=119.84cm, n=136) compared to no bramble and no browsing, with a mean of 176.43cm (s.d=151.43cm, n=14), showing that the presence of bramble gives a mean height increase of 140.33cm. These results are represented visually in figure 8.

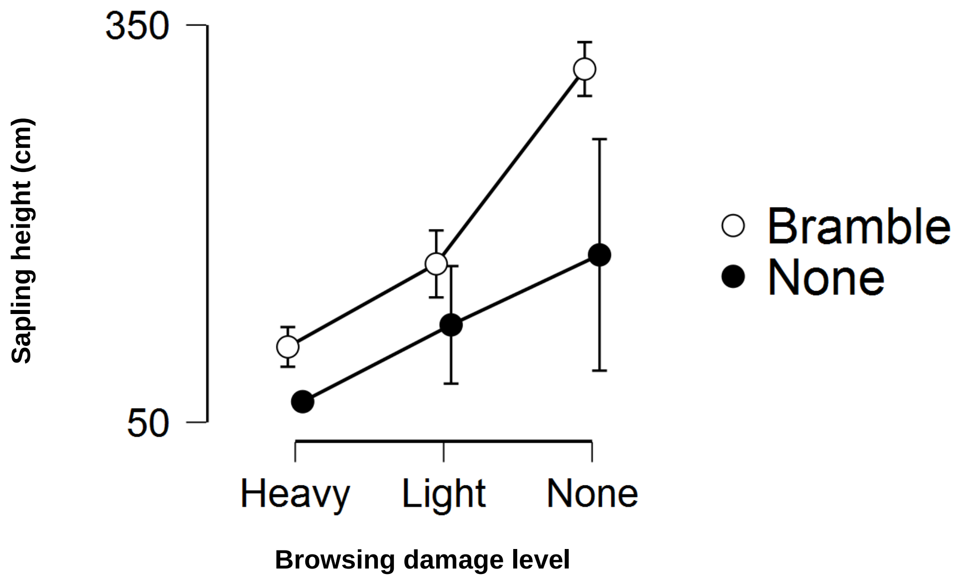


Figure 8. Displaying the interaction effect of the presence of bramble and the level of browsing damage on oak sapling height (cm).
Showing 95% confidence interval levels. This graph shows that sapling height increases when in the presence of bramble and subjected to low or no browsing damage. At the two extremes, a sapling in the presence of bramble and with no browsing had a mean height of 316.76cm (s.d.=119.84cm, n=136), compared to a mean height of 65.57cm (s.d.=37.26cm, n=388) for a sapling with no bramble and subjected to heavy browsing, showing an increase of 251.19cm for bramble presence and no browsing.

The ANOVA showed that there was a statistical significant effect on the presence of bramble and sapling height ($F_{(1, 705)}$=58.82, P=<0.001), without the consideration of the level of browsing damage. The association with bramble positively influenced oak seedling height growth, with bramble present the mean sapling height was 225.20cm (s.d.= 139.60cm, n=281), compared to without bramble presence, where the mean was 72.96cm (s.d.=57.78cm, n=430), showing that the presence of bramble gives a mean increase in height of 152.24cm.

There was also shown to be a significant effect of the level of browsing ($F_{(2, 705)}$=93.60, P=<0.001) with regards to sapling height, without the consideration of the presence of bramble. When subjected to heavy browsing the mean sapling height was 71.90cm (s.d.=44.67cm, n=458), for light browsing the mean height was 157.10cm (s.d.=112.50cm, n=103) and for no browsing the mean height was 303.70cm (s.d.=129.20cm, n=150), showing that no browsing gave a mean increase in height of 146.60cm compared to light browsing, and a mean increase of 231.80cm compared to heavy browsing.

Simple main effects analysis showed that bramble had a significant effect on all three browsing categories, heavy ($P=<0.001$), light ($P=0.008$) and none ($P=<0.001$). Without the protection of bramble 54.57% of saplings were heavily browsed, compared to 9.85% in the presence of bramble.

Discussion

This study examined the effect of bramble presence and browsing damage on oak sapling height, for which there was a statistically significant interaction. The results suggest that bramble acts as a facilitator for oak saplings at Knepp Wildland, helping to promote sapling growth and reduce the likelihood of browsing damage. The data provides evidence that the oak saplings experienced reduced herbivory damage by growing in close proximity to bramble, and that the saplings benefitted from associational resistance with regards to an increase in height. The results indicate the importance of facilitation and the crucial role that bramble plays in the successful establishment, growth and survival of oak saplings. The results agree with the concept of associational resistance and concur with other studies which also highlight the protective quality of shrubs when surrounding saplings. In a similar study Rousset and Lepart (1999) found that downy oak (*Quercus humilis*) is more heavily damaged by herbivory when growing in open spaces, and the density of saplings was higher amongst shrubs. Gomez et al (2001) found that herbivory on Scots pine (*Pinus sylvestris*) was reduced when completely surrounded by shrubs. They suggested this was due to the concealment of the sapling, making them less prone to discovery by herbivores and more difficult to access. Saplings with only 50% coverage were more heavily damaged by herbivory than those with 100% coverage. Garcia et al (2000) reported a reduction of herbivory for European yew (*Taxus baccata*) when concealed by shrubs. Although pine and yew are less palatable than oak, making them less susceptible to herbivory, this concealment theory has also been reported by Callaway (1992) for blue oak (*Quercus douglasii*) and valley oak (*Quercus lobate*). Additionally Harmer and Morgan (2007) reported that 80% of oak saplings survived when protected with >25% bramble cover. A study by Jensen, Gotmark and Lof (2012) also suggested concealment as a factor of bramble protection, alongside the dilution effect, which reduces the risk of herbivory to an individual sapling when it is surrounded by a higher density of neighbouring plants, rather than being isolated (Valdes and Ehrlen, 2019). Similar to the dilution effect, Castagneyrol et al (2013) proposed that nurse species may decrease the apparency of oak saplings, reducing the probability of detection through interference of visual cues. The notion being that the combined foliage mix of both plant species would make the sapling less apparent to a predator. In support of the concealment theory, Hester et al (2006) and Harmer, Boswell and Robertson (2005) reported that browsing frequency and intensity increased when the sapling reached a height where it was visible above the bramble and more likely to be detected by herbivores. Jensen, Löf and Witzell (2012) also reported that as oak saplings outgrew the bramble the risk of browsing damage was increased, although the bramble could still sustain some degree of deterrence. Unfortunately, bramble height was not recorded in this study, so it was not possible to ascertain if the Knepp saplings would become vulnerable to browsing damage once they had reached a certain height, and to determine at what height the protective qualities of the bramble become invalid. It would be beneficial for the evaluation of management processes to determine if there was a relationship between increased sapling height and increased browsing.

Sapling height in this study was also influenced by the level of browsing damage, with a 322% increase in height for saplings not subjected to browsing damage versus heavy browsing. It was found that there was a 44% increase in browsing for unprotected saplings. In a 25 year study Kelly (2002) found a 38% increase in browsing on sessile oak (*Quercus petraea*) saplings which did not have the protection of surrounding vegetation. In a study of the Norway spruce (*Picea abies*) by Smit, Den Ouden and Muller-Scharer (2006) browsing damage was found to be the major cause of death for saplings and sapling survival was found to be significantly higher in the presence of unpalatable plants, such as dwarf thistle (*Cirsium acaule*), and browsing intensity was significantly lower. This was also found by Van Uytvanck et al (2008) in a study on oak and willow in the presence of bramble and blackthorn, where the shrubs formed large, dense, impenetrable thickets, enabling the saplings to grow taller, therefore increasing their chances of survival. They found that 90% of saplings died from herbivory within the first year. If they survived, they became stronger and less susceptible to browsing, illustrating the importance of shrubs as a facilitator for tree regeneration. Their research found that bramble was particularly effective due to its fast growth, which enables it to function as a formidable defence against herbivory in the sapling's vital first year. This was also supported by Castro et al (2004), who reasoned that during their research shrubs acted as safe sites for saplings.

This study found that the heights of the tallest oak saplings were positively related to the presence of bramble. With a 208% increase in height for saplings growing in the presence of bramble. Saplings growing within bramble were less exposed to herbivory and the severity of browsing was reduced, which enabled an increase in sapling height. This indicates that saplings will suffer less damage than if they were fully exposed. Kuiters and Slim (2002; 2003) and Rooney and Waller (2003) found that all oak saplings >100cm were associated with bramble, which led them to suggest that under their research conditions bramble was vital for the regeneration of oak trees. In this study 81% of saplings >100cm were associated with bramble.

Contrary to the findings of this study, Harmer, Boswell and Robertson (2005) found that the relationship between sapling height and shrub presence were inconsistent and that the effect of shrubs may be disadvantageous and detrimental to sapling growth. Although their study differed somewhat from the Knepp study as data was recorded annually over a four-year period and included 15 species of saplings and more than 30 species of ground vegetation, such as bramble, bracken, ivy (*Hedera helix*), herbs and grasses. An adverse effect of bramble on silver fir (*Abies alba*) was found by Schreiner, Bauer and Kollmann (2000) which they reported as being due to competitive and unfavourable growth conditions, such as insufficient light and water. Research by Kelly (2002) also concluded that bramble had an unfavourable effect on oak sapling growth due to its heavy shade. According to Annighöfer et al (2015) oak tree regeneration is dependent on light availability and competition with shrubs for water and nutrients. Harmer et al (2018) found that the role of facilitator varied amongst different sapling species. Their study showed that bramble was positively related to sapling height for silver birch (*Betula pendula*) and willow (*Salix spp*) but had an adverse effect on oak growth. They suggested this was dependant on several factors, such as the timing of seedling establishment and the growth rate of each species. Although oak is considered a light demanding species, they can tolerate a certain degree of shade in the first few years by utilising the nutrients transferred from the acorn to their taproot, but if lack of light persists, they will die within three to five years (Harmer and Morgan, 2007). More detailed research may be required to determine whether the interaction between shrubs and saplings is facilitative or competitive. It may be that there is a balance between the two, with the relationship shifting over time. This study showed a positive relationship between bramble and oak saplings, but it should be considered that the observations were made at only a single point in time. During the observations it appeared that the saplings were dependent upon the bramble for survival, yet it could be that facilitation and competition were amalgamated, rather than occurring in isolation. This may be especially evident when there is variance in environmental conditions and competition for resources either intensify or abate (Wright, Schnitzer and Reich, 2014). For the sapling it may be that protection from herbivory is more important than the affliction of abiotic stress. Over time the sapling will outgrow the bramble, but not necessarily out compete it, as at this point, they may be occupying a different niche (Callaway and Walker, 1997). As previously mentioned, the continued growth of the sapling may be to its detriment as it may then become conspicuous to large predators. The topic of facilitation versus competition is a complex one, which requires further research. From the results of this study it is suggested that associational resistance is of key importance in the regeneration of oak trees. Although it has been proposed by other studies that shrubs can be in direct competition with saplings, this study suggests that instead of being a competitor, bramble has a positive effect on the saplings by reducing herbivory. Bramble may protect one sapling to the detriment of its neighbouring sapling, or a sapling may be protected just by its close but not encompassing proximity, where the herbivore is deterred as it is unable to avoid the bramble whilst attempting to browse the sapling (Kruess and Tscharntke, 2002).

It is interesting to note that not all browsing damage or disturbance leads to tree mortality. 64% of saplings in this study were subjected to heavy browsing and considered alive. Again though, it must be considered that this study was only at a single point in time and subsequent studies may report high mortality levels for the recorded saplings. It must also be considered that the classification of browsing damage as heavy, light or none may have been too simplified and generic, making it open to observer subjectivity. Some of the reported heavy incidences may not be substantial enough to be detrimental to sapling survival. Although the presence of shrubs significantly reduces the level of browsing, associational resistance is dependent on predator size and is considered ineffective against smaller predators, such as lagomorphs, rodents or invertebrates (Manson, Ostfeld and Canham, 2001). Although the shrub canopy provides an effective barrier against larger herbivores, it has the inverse effect for smaller ones, providing them with a safe habitat (Olff et al, 1999), in which they can consume saplings and seeds (Norrdahl et al, 2002). Van Uytvanck et al (2008) reported that grazing of the European rabbit (*Oryctolagus cuniculus*) in their study was the main cause of oak sapling mortality. Both Oosterveld (1983) and Bakker and Olff (2003) found that high densities of rabbits were able to prevent tree regeneration and Bakker et al (2004) concluded that bramble offered no protection against rabbit predation. Small mammals will also feed on the young shoots of bramble, as reported by Crawley and Long (1995) and Hodder et al (2005). Van Uytvanck et al (2008) suggested that an acorn which had not yet transitioned into a seedling whilst under a canopy of established bramble is unlikely to survive predation by smaller herbivores. Oak tree regeneration may also be reduced by the consumption of acorns, not only by smaller predators but also by cattle, pigs, ponies and deer (Sweitzer and Van Vuren, 2002). In field experiments Sun, Gao and Chen (2004) found that 86% of acorns were lost to predation.

This study found a statistically significant association between the survey year and severity of browsing, showing that a trend exists and is not random, despite this Cramer’s coefficient (V) indicated that the association was low. Figure 7 shows a smaller proportion of light browsing in 2018 compared to 2009. This is also the classification with the largest differences in expected values for both years, table 2, with both years suggested to be at ~20%. This may be explained by the fluctuation in livestock population densities between the years, table 1. In 2018 there was an 89% increase of livestock overall, which may account for the higher than expected incidences of heavy browsing. Also, in 2009 the lower than expected incidences of no browsing may be due to the livestock not utilising the entire area available to them.

Another factor which may have had an influence on the results are that the method of browsing classification differed between the two years. In 2009 browsing was classified as heavy, medium, light and none. In the comparative study against 2018, data classified as medium was transferred into the heavy classification, which could have skewed results. Also, data in 2009 was collected in May, versus data collection in December for 2018. Variation in season can affect browsing frequency and intensity due to food availability, during spring and summer a larger proportion of the livestock's diet would be grasses (Gill, 1992). Another aspect which may have contributed to the difference is the variation in precipitation. Precipitation levels may affect the growing conditions for vegetation and consequently grazing strategies (Bat-Oyun et al, 2016). In May 2009 southern England received less than 75% of the average May rainfall, compared to December 2018 when rainfall was above average (Met Office, 2019b).

As the grid references between the years did not correspond, the survival and mortality rates of the saplings from 2009 could not be determined, therefore the longevity of the saplings from 2009 is unknown. The ten-digit grid reference equates to 1m precision (Geograph, 2018), so further analysis may be able to determine if any of the data from the survey years corresponds. The average growth of an oak sapling is 50cm per year (Woodlands Trust, 2019), as the tallest sapling in 2009 was 200cm, it may be feasible to assume that the saplings recorded >650cm in 2018 are the ones also recorded in 2009.

Although this study provides no statistical data for jays, they are considered one of the most important accumulators and dispersers of acorns. Their method of caching the acorns through burial in the ground is more effective than other species which either consume the acorns or disperse in manner not conducive with establishment (Den Ouden, Jansen and Smit, 2005). Jays use spatial memory when retrieving cached acorns, which may account for why they do not cache in open spaces, preferring instead thorny scrub and shrubs, using these as landmarks (Pesendorfer et al, 2016). Through a genetic analysis study, Worrell, Rosique and Ennos (2014) found acorns that had been transported up to 1.5km away from the parent tree. They believe that the jay is the only disperser capable of carrying acorns for that distance. During their observations, they reported an average of 25 jays per hour flying through the woodland, with decreased activity when the supply of acorns started to diminish. In a review of nut dispersal, Vander Wall (2001) highlighted the importance of the mutualistic relationship between the oak and the jay. With the jay removing the acorns away from the parent tree, which is an area of high predation, to areas that generally favour establishment of the seedling. Pesendorfer, Sillett and Morrison (2017) reported that the jays' dispersal is non-random and that their selection for scrub can aid acorn establishment and therefore oak regeneration. Jays may be considered as providing an important ecosystem service by restoring degraded wood pastures (Sonesson, 1994), and driving biodiversity through the recovery of fragmented landscapes (McConkey et al, 2012).

There have been numerous studies which support the theory of grazing ecology, which is essentially the ensuing conflict between herbivore disturbance and vegetation succession. In site comparison studies, Bakker et al (2004) proposed that grazing by large herbivores leads to a shifting mosaic of open grassland, closed woodland and scrub, as outlined in Vera's theory. In a review of the cyclical vegetation theory Olff et al (1999) concluded that large grazing herbivores instigate and maintain plant diversity. Both Vera (2009) and Sutherland (2002) reported on Oostvaardersplassen in the Netherlands, a rewilding experiment, that used historical vertebrate and pollen data to recreate the open landscapes of pre-agricultural Europe. The experiment introduced Konik ponies (*Equus ferus caballus*) and Heck cattle (*Bos Taurus*) to represent extinct tarpans and aurochs, as well as red and roe (*Capreolus capreolus*) deer. The open landscape has been maintained by their grazing, alongside 60,000 Greylag geese (*Anser anser*), who made an unexpected appearance. The geese have driven vegetation succession by turning the closed reedbeds into open water, which has benefitted and attracted other plant and animal species, in particular rare breeding birds, such as the spoonbill (*Platalea leucorodia*) and the marsh harrier (*Circus aeruginosus*). The different feeding strategies of the herbivores ensure that no individual type of vegetation can dominate. For example, the grass eaters, such as cattle will stimulate the establishment of trees and shrubs, whilst the deer will slow down the regeneration through browsing damage (Vera, 2002).

Using palaeoecological studies Johnson (2009) suggests that ancient landscapes would have been species rich open landscapes and that the extinction of many large herbivores led to a change in vegetation culminating in closed canopy forests. Like Vera (2000) he maintains that oaks would not have been able to regenerate either in the shade of closed canopies or under the heavy browsing pressure of open landscapes without the protection of nurse species.

Many studies support the concept of large herbivores being drivers of biodiversity. Analysing data from 252 large herbivore studies Koerner, Smith and

Zelikova (2018) suggested that large herbivores are crucially important for maintaining plant biodiversity, through the suppression of dominant species. In similar studies, Kohyani et al (2008) investigated the introduction of large herbivores as a conservation tool, their findings indicated a positive effect on plant diversity. Bullock et al (2001) found seven new species of grass during a 12 year grazing experiment; Liu et al (2015) found a significant increase in plant diversity during a two year cattle and sheep grazing study; and in a 40 year study Mountford and Peterken (2003) found that open transects with grazing herbivores were more species rich in comparison to closed transects with no herbivores. Similarly, in a grassland study Bakker and Olff (2003) recognised the crucial role of herbivores in species richness. They also included rabbits in their study, who through burrowing create bare patches in which plants can regenerate. Millett and Edmondson (2013) also conducted grazing experiments for smaller mammals over 36 years, reporting that they have an impact on the composition of ecosystems through their disturbance techniques, which are often more intense, such as rabbit burrowing, than large herbivores. Although this study did not include data for small herbivores, their level of disturbance and its effect on vegetation composition at Knepp should not be underestimated. Interestingly, Pryke, Roets and Samways (2016) found that the presence of wild grazers increased insect diversity; Vera, Bakker and Olff (2009) claim that 80% of European butterfly species live in grassland and scrub habitats; and Brändle and Brandl (2001) reported that the oak tree is associated with the highest number of insect species compared to other European trees.

In their study Rey Benayas and Bullock (2012) found the natural regeneration of trees is almost as effective as the active planting of trees. They claim that rewilding projects are essential for the prevention of biodiversity loss. Despite numerous examples of success, the use of herbivores as a tool for biodiversity remains controversial (Newton et al, 2013). Many conservationists and scientists have argued that maintaining diverse landscapes is only achievable through human intervention and manipulation, and that scientific evidence is lacking. Although the notion of rewilding is not always totally disputed, rather that there should be an element of caution (Nogués-Bravo et al, 2016). Navarro and Pereira (2012) reviewed 23 rewilding studies, finding that although 60 species of birds, 24 species of mammals and 26 species of invertebrates had benefitted, 101 species had been adversely affected. The wilding of Knepp is still in its infancy, which makes it difficult to determine the extent and significance of its contribution to the conservation of the natural landscape. Based on the thriving wildlife and high level of plant and animal species reintroduction reported by Knepp, the abandonment from agriculture seems to be a positive one. The results of this study indicate that oak regeneration will increase by the facilitation of both jays and bramble, in accordance with the theory of cyclical vegetation turnover through large herbivore grazing.

Conclusion

In conclusion the results of this study found that there was an interaction between the presence of bramble and the level of browsing damage on oak sapling height. It can be concluded that for this study the theory of associational resistance is supported, and to some degree the results support a contribution to the conservation of habitat biodiversity through the theories of grazing ecology and cyclical vegetation turnover. This study has highlighted that the previously farmed New Barn Two area at Knepp, had developed into open scrub, and through herbivore grazing pressure, oak regeneration was mostly restricted to bramble thickets. With time it is hoped that this area will evolve in to a self-regulating habitat of high biodiversity. From the outlined research it can be concluded that there needs to be a balance between herbivory and tree regeneration. Through their disturbance large herbivores have both a positive and negative effect on the landscape, and it would appear that these can occur concurrently.

Future experimental research would be especially informative with regards to conservation management decisions. In order to obtain more advantageous data, the following recommendations are proposed. As cross referencing of the grid references failed to show any correlation between the 2009 and 2018 saplings, it may have been beneficial to measure the sapling stem diameter to achieve a better understanding of age, which would have provided more substantial evidence and data for the survival and mortality rates from 2009 to 2018. In order to ascertain the association between bramble and the saplings, data could have been recorded on saplings with 100% bramble cover, <100% cover, saplings found in close proximity, but not within bramble, and saplings found in random open spaces. Upon comparison, this would have provided an indication on the strength of the association between sapling and bramble. Although other shrub and tree species were recorded during data collection, they were not used in this study. In further studies it would be interesting to record which shrub species are most prevalent as nurse species, and measure their efficacy through analysis of growth, survival and mortality rates. Also, whether there is an association between a particular species of tree and a particular species of shrub; and whether there is a significant difference in browsing intensity between shrub species, with regards to their physical or chemical defences in response to herbivory. Although not conducive with the rewilding concept of no intervention, artificial manipulation of the bramble canopy could provide valuable information on at which height and depth bramble is more effective; and also, whether and at which point it becomes invalid as a nurse species when the saplings outgrow it, becoming visible to large predators. One of the aims of this study was to identify whether bramble helps facilitate the regeneration of oak, therefore determining its value as a conservation tool. Bramble is a low-cost tool which requires zero human involvement, but as previously mentioned, associational resistance is believed to be ineffective against smaller predators, therefore it is necessary to differentiate between predators. To clarify more conclusively on the benefit of bramble, there are various methods which can be employed to determine which animal is responsible for the damage. Predators can be identified by the height of the damage, for example low browse lines would indicate smaller mammals, such as sheep. Also, the form of the damage, whether it is browsing, rubbing or trampling; the size of any teeth marks; identification of footprints; and faecal pellet transects (Forest Research, 2019). Faecal pellets can also be a good indication on the density of animals present (Kellner and Swihart, 2017). The use of camera traps could also provide more nuanced data. Identification would also provide data for the analysis of which predator is associated with the highest degree of damage. It is also worth considering that the expectations of the observers could have influenced the results. Finding a sapling amongst bramble may have been viewed as a success and observers may have been less inclined to classify it as being heavily browsed, unconsciously interpreting the level of damage to fit in with the goals of the study. As mentioned previously, browsing incidence was classified as heavy, light or none and could have been subject to misinterpretation, which may also have impacted the results. A limitation of this study is that the chronology of events from 2009 to 2018 could not be determined, therefore it is uncertain what implications this may have on the conclusions drawn. A failing of the methodology was the reliance that recording the grid references would provide insight and correlation between the survey years. If investigation of the saplings at Knepp is to continue, it would be recommended to perform more frequent surveys and perhaps tag the saplings for easier identification. Although the 2009 sapling data was entered into a Geographical Information System (GIS), it was beyond the scope of this study to use GIS for the 2018 data. GIS provides spatial data and GIS modelling can be used to estimate the density of saplings and patterns of establishment. GIS would give more detailed and precise data, giving a greater ability to monitor and measure the saplings (RSPB, 2019).

Rewilding may be considered unpredictable and still in its test phase, posing many challenges, not least from its adversaries, but it appears from the outlined research that it provides an opportunity to recover biodiversity. The wood pastures of Knepp and Oostvaardersplassen may be some of the closest representations of previous species rich environments available, allowing the valuable opportunity to study vegetation succession and regeneration, and to some extent test grazing theories, although this would be a very gradual process. Any lessons learnt so far may not be appropriate for all habitats, with regards to aspects, such as differing climates and soil properties; especially for land that had previously been used in agriculture, where the soil may be eroded or subjected to large amounts of artificial fertilisers. Although the concept of rewilding specifies there should be little or no human interference, initially some projects may require intervention to help restoration, for example previously intensely farmed areas may be lacking in nutrients and attract only invasive species (Cramer, Hobbs and Standish, 2008). It remains unclear what benefits may be reaped from complete non-intervention and how much biodiversity can be truly recovered in the long term (Kelly, 2001). With no specific goals and by allowing natural processes to take over, it could mean that the level of success cannot be measured. The danger may be that expected outcomes are based purely on aspirations. Although throughout history humans may have, to some extent, controlled and shaped nature, ultimately humans cannot change the laws of nature, nature is wild and wilful (Carver, 2014).

Word count: 8492

Acknowledgements

Firstly, I would like to thank my project supervisor, Dr Amber de Vere, for her great support, expertise and constructive guidance.

I would also like to express my appreciation to Knepp Ecologist Penny Green for providing me with the opportunity to conduct my research at Knepp estate, and also assisting in the data collection alongside the volunteers, Josh Brown, Sam Mould, Fiona Hailstone, Ted Green, Jill Butler, Josef Amin, Louise Morton and Izzy Taylor, who worked tirelessly for five days, and without whom it would not have been possible to collect such a large amount of data.

In addition, I would also like to acknowledge my friends, Alexandra Wheeler and Kathryn Clarke, for their proofreading, editorial advice and encouragement.

References

Annighöfer, P., Beckschäfer, P., Vor, T. and Ammer, C., 2015. Regeneration Patterns of European Oak Species (Quercus petraea (Matt.) Liebl., Quercus robur L.) in Dependence of Environment and Neighborhood. *PLoS One,* 10 (8).

Bakker, E.S. and Olff, H., 2003. The impact of different sized herbivores on recruitment for subordinate herbs in grassland. *Journal of Vegetation Science,* 14, pp. 465-474.

Bakker, E. S., Olff, H., Vandenberghe, C., De Maeyer, K., Smit, R., Gleichman, J. M. and Vera, F. W. M., 2004. Ecological anachronisms in the recruitment of temperate light-demanding tree species in wooded pastures. *Journal of Applied Ecology*, 41 (3), pp. 571-582.

Bakker, E.S., Ritchie, M.E., Olff, H., Milchunas, D.G. and Knops, J.M., 2006. Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. *Ecology Letters,* 9, pp. 780-788.

Barbosa, P., Hines, J., Kaplan, I., Martinson, H., Szczepaniec, A. and Szendrei, Z., 2009. Associational Resistance and Associational Susceptibility: Having Right or Wrong Neighbors. *Annual Review of Ecology, Evolution, and Systematics*, 40, pp. 1-20.

Bat-Oyun, T., Shinoda, M., Cheng, Y. and Purevdorj, Y., 2016. Effects of grazing and precipitation variability on vegetation dynamics in a Mongolian dry steppe. *Journal of Plant Ecology,* 9 (5), pp. 508-519.

Bazely, D.R., Myers, J.H. and Da Silva, K.B., 1991. The response of number of bramble prickles to herbivory and depressed ability. *Oikos*, 61, pp. 327–336.

Birch, J., Weston, P., Rinaudo, T. and Francis, R., 2016. Releasing the Underground Forest: Case Studies and Preconditions for Human Movements that Restore Land with the Farmer-Managed Natural Regeneration (FMNR) Method. *Land Restoration*, 2 (7), pp. 183-207.

Bobiec, A., Reif, A. and Öllerer, K., 2018. Seeing the oakscape beyond the forest: a landscape approach to the oak regeneration in Europe. *Landscape Ecology,* 33 (4), pp. 513-528.

Borkowski J., Dobrowolska, D., Dąbrowski, W., Banul, R. and Załuski, D., 2017. Young conifer stands form a deer browsing refuge for an oak admixture: silvicultural implications for forest regeneration under herbivore pressure. *European Journal of Forest Research,* 136 (5–6), pp. 787–800.

Bradshaw, R.H.W., Hannon, G.E. and Lister, A.M., 2003. A long-term perspective on ungulate–vegetation interactions. *Forest Ecology and Management,* 181, pp. 267-280.

Bradshaw, R.H.W. and Mitchell, F.J.G., 1999. The palaeoecological approach to reconstructing former grazing–vegetation interactions. *Forest Ecology and Management,* 120, pp. 3-12.

Brändle, M. and Brandl, R., 2001. Species richness of insects and mites on trees: expanding Southwood. *Journal of Animal Ecology,* 70 (3), pp. 491-504.

Bressette, J., Beck, H. and Beauchamp, V.B., 2012. Beyond the browse line: complex cascade effects mediated by white-tailed deer. *Oikos*, 121 (11), pp.1749-1760.

Bullock, J.M., Franklin, J., Stevenson, M.J., Silvertown, J., Coulson, S.J., Gregory, S.J. and Tofts, R., 2001. A plant trait analysis of responses to grazing in a long-term experiment. Journal of Applied Ecology, 38 (2), pp. 253-267.

Burrell, C., 2018. *Map of Knepp Estate*. [Image online]. Available at <https://static1.squarespace.com/static/595ca91bebbd1a1d0aaab285/t/5b1af97b1ae6cfcbab41befa/1528494463789/InPractice100_Jun2018_Knepp+%28003%29.pdf> [Accessed 25 November 2018].

Burrell, C. and Greenaway, T., 2011. Knepp Castle Wildland Project. *Landscape Archaeology and Ecology,* 9.

Callaway, R.M., 1992. Effect of shrubs on recruitment of Quercus douglasii and Quercus lobate in California. *Ecology*, 73, pp. 2118-2128.

Callaway, R.M. and Walker, L.R., 1997. Competition and Facilitation: A Synthetic Approach to Interactions in Plant Communities. *Ecology,* 78 (7), pp. 1958-1965.

Carver, S., 2014. Making real space for nature: a continuum approach to UK conservation. *ECOS,* 35 (314), pp. 5-17.

Carver, S., 2016. Rewilding. Conservation and Conflict. *ECOS,* 37 (2), pp. 3-10.

Castagneyrol, B., Giffard, B., Péré, C. and Jactel, H., 2013. Plant apparency, an overlooked driver of associational resistance to insect herbivory. *Journal of Ecology,* 101 (2), pp. 418-429.

Castro, J., Zamora, R., Hodar, J.A., Gomez, J.M., Gomez-Aparicio, L., 2004. Benefits using shrubs as nurse plants for reforestation in Mediterranean mountains: a 4-year study. *Restoration Ecology,* 12, pp. 352–358.

Convery, I., Davis, P., Stone, P.G. and Davis, P., 2016. *Changing Perceptions of Nature*. New York: Boydell and Brewer.

Cooper Driver, G.A., 1990. Defense Strategies in Bracken, Pteridium aquilinum (L.) Kuhn. · *Annals of the Missouri Botanical Garden,* 77 (2), pp.281.

Cornelissen, P., 2017. *Large herbivores as a driving force of woodland-grassland cycles: The mutual interactions between the population dynamics of large herbivores and vegetation development in a eutrophic wetland.* PhD. Wageningen University. Available at <http://edepot.wur.nl/396698>. [Accessed 26 February 2019].

Cramer, V.A., Hobbs, R.J. and Standish, R.J., 2008. What’s new about old fields? Land abandonment and ecosystem assembly. *Trends in Ecological Evolution*, 23, pp.104-112.

Crawley, M.J. and Long, C.R., 1995. Alternate bearing, predator satiation and seedling recruitment in Quercus robur. *Journal of Ecology*, 83, pp. 683-696.

Den Ouden, J., Jansen, P.A. and Smit, R., 2005. Jays, Mice and Oaks: Predation and Dispersal of Quercus robur and Q. petraea in North-western Europe. In: P.M. Forget, J.E. Lambert, P.E. Hulme, S.B. Vander Wall, eds. 2005. *Seed fate: predation, dispersal and seedling establishment*. Oxford: CAB International. Ch. 13.

Derham, T.T., Duncan, R.P., Johnson, C.N. and Jones, M.E., 2018. Hope and caution: rewilding to mitigate the impacts of biological invasions. *Philosophical Transactions B,* 373.

Doughty, C.E., 2017. Herbivores increase the global availability of nutrients over millions of years. *Nature Ecology and Evolution,* 1 (12), pp. 1820-1827.

Ecology Center, 2018. *Feeding Strategies.* [Image online]. Available at <https://www.ecologycenter.us/rain-forests/herbivorous-mammals-and-birds.html> [Accessed 20 December 2018].

Forest Research, 2019. *Recognising types of mammal damage to trees and woodland.* [Online]. Available at <https://www.forestresearch.gov.uk/research/recognising-types-of-mammal-damage-to-trees-and-woodland/> [Accessed 26 March 2019].

García, D., Zamora, R., Hódar, J.A., Gómez, J.M. and Castro, J., 2000. Yew (Taxus baccata) regeneration is facilitated by fleshy-fruited shrubs in Mediterranean environments. *Biological Conservation*, 95, pp.31–38.

Geograph, 2018. *Grid Reference Precision.* [Online]. Available at <https://www.geograph.org.uk/help/map_precision> [Accessed 10 December 2018].

Gill, R.M.A., 1992. A Review of Damage by Mammals in North Temperate Forests: 1. Deer. *Forestry,* 65 (2), pp. 145-169.

Gómez, J.M., Hódar, J.A., Zamora, R., Castro, J. and García, D., 2001. Ungulate damage on Scots pines in Mediterranean environments. *Canadian Journal of Botany*, 79 (6), pp. 739-746.

Gordon, I.J., 2003. Browsing and Grazing Ruminants: are they different beasts? *Forest Ecology and Management*, 181, pp. 13–21.

Gordon, I.J., Hester, A.J., Festa-Bianchet, M., 2004. The Management of Wild Herbivores to Meet Economic, Conservation and Environmental Objectives. *Journal of Applied Ecology,* 41, pp. 1021-1031.

Haas, J.P. and Heske, E.J., 2005. Experimental Study of the Effects of Mammalian Acorn Predators on Red Oak Acorn Survival and Germination. *Journal of Mammalogy*, 86 (5), pp.1015–1021.

Hambäck, P.A., Ågren, J. and Ericson, L., 2000. Associational Resistance: Insect Damage to Purple Loosestrife Reduced in Thickets of Sweet Gale. *Ecological Society of America*, 81 (7), pp. 1784-1794.

Harmer, R., Boswell, R. and Robertson, M., 2005. Survival and growth of tree seedlings in relation to changes in the ground flora during natural regeneration of an oak shelterwood. *Forestry*, 78 (1), pp. 21-32.

Harmer, R., Kiewitt, A., Morgan, G. and Gill, R., 2018. Does the development of bramble (Rubus fruticosus L. agg.) facilitate the growth and establishment of tree seedlings in woodlands by reducing deer browsing damage? *Forestry,* 83 (1), pp. 93-102.

Harmer, R. and Morgan, G., 2007. Development of Quercus robur advance regeneration following canopy reduction in an oak woodland. *Forestry: An International Journal of Forest Research*, 80 (2), pp. 137–149.

Hester, A.J., Bergman, M., Jason, G.R. and Moen, J., 2006. Impacts of Large Herbivores on Plant Community Structure and Dynamics. In: K. Danell, P. Duncan, R. Bergstrom and J. Pastor, eds. 2006. *Large Herbivore Ecology, Ecosystem Dynamics and Conservation*. Cambridge: Cambridge University Press. Ch. 4.

Hester, A.J., Edenius, L., Buttenschon, R.M. and Kuiters, A.T., 2000. Interactions between forests and herbivores: the role of controlled grazing experiments. *Forestry,* 73 (4).

Hodder, K.H. and Bullock, J.M., 2009. Really Wild? Naturalistic Grazing in Modern Landscapes. *British Wildlife,* 20, pp. 37-43.

Hodder, K.H., Bullock, J.M., Buckland, P.C. and Kirby, K.J., 2005. *Cyclic succession in temperate woodlands*. [Image online]. Available at <https://www.researchgate.net/publication/234038266_Large_herbivores_in_the_wildwood_and_modern_naturalistic_grazing_systems> [Accessed 10 April 2019}.

Hodder, K.H., Bullock, J.M., Buckland, P.C. and Kirby, K.J., 2005. Large herbivores in the wildwood and in modern naturalistic grazing systems. *English Nature Reserve Reports,* 648.

Hoffman, R.R., 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia*, 78, pp. 443-457.

Humphrey, J.W. and Swaine, M.D., 1997. Factors Affecting the Natural Regeneration of Quercus in Scottish Oakwoods. II. Insect Defoliation of Trees and Seedlings. *Journal of Applied Ecology*, 34 (3), pp. 585-593.

Jensen, A.M., Götmark, F. and Löf, M., 2012. Shrubs protect oak seedlings against ungulate browsing in temperate broadleaved forests of conservation interest: A field experiment. *Forest Ecology and Management*, 266, pp. 187–193.

Jensen, A.M., Löf, M. and Witzell, J., 2012. Effects of competition and indirect facilitation by shrubs on Quercus robur saplings. *Plant Ecology,* 213 (4), pp. 535-543.

Johnson, C.N., 2009. Ecological consequences of Late Quaternary extinctions of megafauna. *Proceedings of the Royal Society B: Biological Sciences*, 276.

Kellner, K.F. and Swihart, R.K., 2017. Herbivory on planted oak seedlings across a habitat edge created by timber harvest. *Plant Ecology,* 218, pp. 213-223.

Kelly, D.L., 2002. The regeneration of Quercus petraea (sessile oak) in southwest Ireland: a 25-year experimental study. *Forest Ecology and Management*, 166, pp. 207–226.

Kirby, K.J., 2004. A model of a natural wooded landscape in Britain as influenced by large herbivore activity. *Forestry,* 77 (5).

King, C., 2018. *Heavy browsing example on oak sapling at Knepp.* [Photograph]. (Catherine King's own private collection).

King, C., 2018. *Oak sapling in bramble at Knepp.* [Photograph]. (Catherine King's own private collection).

Knepp, 2018. *Southern Block*. [Image online]. Available at <http://www.kneppblog.co.uk/p/maps.html> [Accessed 25 November 2018].

Koerner, S.E., Smith, M.D. and Zelikova, T.J., 2018. Change in dominance determines herbivore effects on plant biodiversity. Nature Ecology and Evolution, 2, pp. 1925–1932.

Kohyani, P.T., Bossuyt, B., Bonte, D. and Hoffmann, M., 2008. Grazing as a management tool in dune grasslands: Evidence of soil and scale dependence of the effect of large herbivores on plant diversity. Biological Conservation, 141 (6), pp. 1687-1694.

Konopka, B. and Pajtik, J., 2015. Why was browsing by red deer more frequent but represented less consumed mass in young maple than in ash trees? *Journal of Forest Science,* 61 (10), pp. 431-438.

Kruess, A. and Tscharntke, T., 2002. Contrasting responses of plant and insect diversity to variation in grazing intensity. *Biological Conservation*, 106, pp. 293-302.

Kuiters, A.T. and Slim, P.A., 2002. Regeneration of mixed deciduous forest in a Dutch forest heathland, following a reduction of ungulate densities. *Biological Conservation*,105, pp. 65–74.

Kuiters, A.T. and Slim, P.A., 2003. Tree colonisation of abandoned arable land after 27 years of horse-grazing: the role of bramble as a facilitator of oak wood regeneration. *Forest Ecology and Management,* 181, pp. 239-251.

Linhart, Y.B. and Whelan, R.J., 1980. Woodland regeneration in relation to grazing and fencing in Coed Gorswen, North Wales. *Journal of Applied Ecology*, 17, pp. 827-840.

Liu, J., Feng, C., Wang, D., Wang, L., Wilsey, B.J. and Zhong, Z., 2015. Impacts of grazing by different large herbivores in grassland depend on plant species diversity. Journal of Applied Ecology, 52 94), pp. 1053-1062.

Lorimer, J. and Driessen, C., 2014. Experiments with the wild at the Oostvaardersplassen. *ECOS,* 35 (314), pp. 45-51.

McConkey, K.R., Prasad, S., Corlett, R.T., Campos-Arceiz, A., Brodie, J.F., Rogers, H. and Santamaria, L., 2012. Seed dispersal in changing landscapes. Biological Conservation, 146 (1), pp. 1-13.

Manson, R.H., Ostfeld, R.S. and Canham, C.D., 2001. Long-term effects of rodent herbivores on tree invasion dynamics along forest–field edges. *Ecology*, 82, pp. 3320-3329.

Met Office, 2019a. *Southern England Climate.* [Online]. Available at <https://www.metoffice.gov.uk/climate/uk/regional-climates/so> [Accessed 25 March 2019].

Met Office 2019b. *Climate Summaries.* [Online]. Available at <https://www.metoffice.gov.uk/climate/uk/summaries> [Accessed 20 April 2019].

Millett, J. and Edmondson, S., 2013. The impact of 36 years of grazing management on vegetation dynamics in dune slacks. Journal of Applied Ecology, 50 (6), pp. 1367-1376.

Mountford, E.P. and Peterken, G.F., 2003. Long-term change and implications for the management of wood-pastures: experience over 40 years from Denny Wood, New Forest. *Forestry: An International Journal of Forest Research*, 76 (1), pp. 19–43.

Müller, A., Dahm, M., Bøcher, P.K., Root-Bernstein, M. and Svenning, J.C., 2017. Large herbivores in novel ecosystems - Habitat selection by red deer (Cervus elaphus) in a former brown-coal mining area. *PloS*, 12 (5).

Navarro, L.M. and Pereira, H.M., 2012. Rewilding Abandoned Landscapes in Europe. *Ecosystems,* 15 (6), pp. 900-912.

Newton, A.C., Cantarello, E., Lovegrove, A., Appiah, D. and Perrella, L., 2012. The influence of grazing animals on tree regeneration and woodland dynamics in the New Forest, England. *Trees, Forested Landscapes*, 12, pp. 159-175.

Newton, A.C., Cantarello, E., Tejedor, N. and Myers, G., 2013. Dynamics and Conservation Management of a Wooded Landscape under High Herbivore Pressure. *International Journal of Biodiversity,* 2013.

Nogués-Bravo, D., Simberloff, D., Rahbek, C. and Sanders, N.J., 2016. Rewilding is the new Pandora's box in conservation. *Current Biology,* 26 (3), pp. 87-91.

Norrdahl, K., Klemola, T., Korpimaki, E. and Koivula, M., 2002. Strong seasonality may attenuate trophic cascades: vertebrate predator exclusion in boreal grassland. *Oikos,* 99, pp. 419-430.

Olff, H. and Ritchie, M.E., 1998. Effects of Herbivores on Grassland Plant Diversity. *Tree,* 13, pp. 261-265.

Olff, H., Vera, F.W.M., Bokdam, J., Bakker, E.S., Gleichman, J.M., Maeyer, K.D. and Smit, R., 1999. Shifting Mosaics in Grazed Woodlands Driven by the Alternation of Plant Facilitation and Competition. *Plant Biology,* 1 (2), pp. 127-137.

Oosterveld, P.,1983. Eight years of monitoring of rabbits and vegetation development on abandoned arable fields grazed by ponies. *Acta Zoologica Fennica,* 174, pp. 71-74.

Pedrazzoli, M., Dal Bosco, A., Castellini, C., Ranucci, D., Mattioli, S., Pauselli, M. and Roscini, V., 2017. Effect of age and feeding area on meat quality of wild boars. *Italian Journal of Animal Science,* 16 (3), pp. 353-32.

Pesendorfer, M.B., Sillett, T.S., Koenig, W.D. and Morrison, S.A., 2016. Scatter-hoarding corvids as seed dispersers for oaks and pines: A review of a widely distributed mutualism and its utility to habitat restoration. The Condor, 118 (2), pp. 215-237.

Pesendorfer, M.B., Sillett, T.S. and Morrison, S.A., 2017. Spatially biased dispersal of acorns by a scatter-hoarding corvid may accelerate passive restoration of oak habitat on California's largest island. Current Zoology, 63 (4), pp. 363–367.

Pryke, J.S., Roets, F. and Samways, M.J., 2016. Wild Herbivore Grazing Enhances Insect Diversity over Livestock Grazing in an African Grassland System. PLoS One, 10.

Putman, R., Apollonio, M. and Andersen, R., 2011. *Ungulate Management in Europe: Problems and Practices*. Cambridge: Cambridge University Press.

Reimoser, F., Armstrong, H.M. and Suchant, R., 1999. Measuring forest damage of ungulates: What should be considered. *Forest Ecology and Management*, 120 (1), pp. 47-58.

Rey Benayas, J.M. and Bullock, J.M., 2012. Restoration of Biodiversity and Ecosystem Services on Agricultural Land. *Ecosystems,* 15 (6), pp. 883-889.

Ripple, W.J. and Beschta, R.L., 2011. Trophic cascades in Yellowstone: The first 15 years after wolf reintroduction. *Biological Conservation,* 145 (1), pp. 205-213.

Rooney, T.P. and Waller, D.M., 2003. Direct and Indirect Effects of White-tailed Deer in Forest Ecosystems. *Forest Ecology and Management*, 181, pp. 165–176.

Rousset, O. and Lepart, J., 1999. Shrub facilitation of Quercus humilis regeneration in succession on calcareous grasslands. *Journal of Vegetation Science*, 10, pp. 493–502.

Royal Society for the Protection of Birds (RSPB), 2019. *Mapping and GIS.* [Online]. Available at <https://www.rspb.org.uk/our-work/conservation/conservation-and-sustainability/mapping-and-gis/> [Accessed 20 April 2019].

Schreiner, M., Bauer, E.M. and Kollmann, J., 2000. Reducing predation of conifer seeds by clear-cutting Rubus fruticosus agg. in two montane forest stands. *Forest Ecology Managemen*t, 126, pp. 281 –290.

Smit, C., Béguin, D., Buttler, A. and Müller-Schärer, H., 2005. Safe sites for tree regeneration in wooded pastures: A case of associational resistance? *Journal of Vegetation Science,* 16, pp. 209-214.

Smit, C., Den Ouden, J. and Muller-Scharer, H., 2006. Unpalatable plants facilitate tree sapling survival in wooded pastures. *Journal of Applied Ecology* 43, pp. 305–312.

Sondej, I. and Kwiatkowska-Falińska, A.J., 2017. Effects of Wild Boar Sus scrofa L Rooting on Seedling Emergence in Białowieża Forest. *Polish Journal of Ecology*, 65 (4).

Sonesson, L.K., 1994. Growth and survival after cotyledon removal in Quercus robur seedlings, grown in different natural soil types. Oikos, 69, pp. 65–70.

Sun, S., Gao, X. and Chen, L., 2004. High Acorn Predation Prevents the Regeneration of Quercus liaotungensis in the Dongling Mountain Region of North China. *Restoration Ecology,* 12 (3), pp. 335-342.

Sutherland, W.J., 2002. Openness in Management. *Nature,* 418, pp. 834-835.

Sweitzer, R.A. and Van Vuren, D.H., 2002. Rooting and Foraging Effects of Wild Pigs on Tree Regeneration and Acorn Survival in California's Oak Woodland Ecosystems. *USDA Forest Service General Technical Reports,* 184.

Taylor, P., 2005. *Beyond Conservation.* London: Earthscan Publications Limited.

Tree, I., 2018. *Wilding.* London: Picador.

Valdes, A. and Ehrlen, J., 2019. Resource overlap and dilution effects shape host plant use in a myrmecophilous butterfly. *Journal of Animal Ecology,* 88 (4), pp. 649-658.

Van Uytvanck, J. and Hoffmann, M., 2009. Impact of grazing management with large herbivores on forest ground flora and bramble understorey. *Acta Oecologica*, 35, pp. 523–532.

Van Uytvanck, J., Maes, D., Vandenhaute, D. and Hoffmann, M., 2008. Restoration of wood pasture on former agricultural land: The importance of safe sites and time gaps before grazing for tree seedlings. *Biological Conservation*, 141, pp. 78-88.

Vera, F.W.M., 1997. *Metaphors for the Wilderness: Oak, Hazel, Cattle and Horse*. PhD. Wageningen University. Available at http://www.google.com/url?sa=t&rct=j&q=&esrc=s&source=web&cd=12&ved=2ahUKEwiKzNO-quvgAhXjVBUIHSQ_DJYQFjALegQIAhAC&url=http%3A%2F%2Fedepot.wur.nl%2F212241&usg=AOvVaw0GHYLlYBVVlQ7KPzFswow8> [Accessed 05 March 2019].

Vera, F.V.M., 2000. *Grazing, Ecology and Forest History.* Oxon: CABI Publishing.

Vera, F.V.M., 2002. The Dynamic European Forest. *Arboricultural Journal,* 26, pp. 179-211.

Vera, F.V.M., 2009. Large-scale nature development – the Oostvaardersplasse. *British Wildlife*, 6, pp. 28-36.

Vera, F.V.M., Bakker, E.S. and Olff, H., 2009. *Large Herbivore Ecology, Ecosystem Dynamics and Conservation.* Cambridge: Cambridge University Press.

Vermeulen, R., 2015. *Natural Grazing. Practices in the rewilding of cattle and horses*. Nijmegen: Free Nature.

Weisberg, P.J. and Bugmann, H., 2003. Forest Dynamics and Ungulate Herbivory: from Leaf to Landscape. *Forest Ecology and Management,* 181, pp. 1-12.

Wirthner, S., Schütz, M., Page-Dumroese, D.S., Busse, M.D., Kirchner, J.W. and Risch, A.C., 2012. Do changes in soil properties after rooting by wild boars (Sus scrofa) affect understory vegetation in Swiss hardwood forests? *Canadian Journal for Forestry Research*, 42, pp. 585–592.

Woodlands Trust, 2019. *English Oak.* [Online]. Available at <https://shop.woodlandtrust.org.uk/english-oak> [Accessed 12 January 2019].

Worrell, R., Rosique, C. and Ennos, R., 2014. Long-distance colonisation of oak dispersed by jays in Highland Scotland. *Scottish Forestry,* 68.

Wright, A., Schnitzer, S.A. and Reich, P.B., 2014. Living close to your neighbors: the importance of both competition and facilitation in plant communities. *Ecological Society of America,* 95 (8), pp. 2213-2223.

Zangerl, A.R., 2003. Evolution of induced plant responses to herbivores. *Basic and Applied Ecology* 4, pp. 91-103.

Appendices

Chi-square test for association between survey year and severity of browsing

Genstat Undergraduate Release 18.1 10 April 2019 16:51:10

Genstat Teaching and Learning Edition
Genstat Procedure Library Release PL26.1

Data imported from Excel file: C:\Users\Catherine\Desktop\spreadsheets\chi.xlsx
on: 10-Apr-2019 16:52:15
taken from sheet "Sheet1", cells A2:C1289

Identifier	Minimum	Mean	Maximum	Values	Missing
species				1288	0

Identifier	Values	Missing	Levels
year	1288	0	2

Identifier	Values	Missing	Levels
browsing	1288	0	3

	_counts		
year	2009	2018	Count
browsing			
heavy	339	458	797
light	156	103	259
none	82	150	232
Count	577	711	1288

	_counts		
year	2009	2018	Count
browsing			
heavy	26	36	62
light	12	8	20
none	6	12	18
Count	45	55	1288

Chi-square test for association between browsing and year

Likelihood chi-square value is 35.02 with 2 d.f.

Probability level (under null hypothesis) $p < 0.001$

browsing	year	Observed	Fitted	Residual
heavy	2009	339.00	357.04	-2.10
	2018	458.00	439.96	2.07
light	2009	156.00	116.03	5.30
	2018	103.00	142.97	-5.88
none	2009	82.00	103.93	-3.32
	2018	150.00	128.07	3.11

Cramer's coefficient (V) calculation method

V **=** √ 35.02 ÷ 1288 (2-1) = 0.165

Two-way analysis of variance (ANOVA) for testing the interaction of bramble presence and browsing damage (independent variables), on sapling height (dependent variable).

JASP Results

ANOVA

ANOVA - SAPLING HEIGHT#

Cases	Sum of Squares	df	Mean Square	F	p
BRAMBLE!	358387	1	358387	58.820	< .001
BROWSING LEVEL!	1.141e+6	2	570296	93.600	< .001
BRAMBLE! ∗ BROWSING LEVEL!	105030	2	52515	8.619	< .001
Residual	4.296e+6	705	6093		

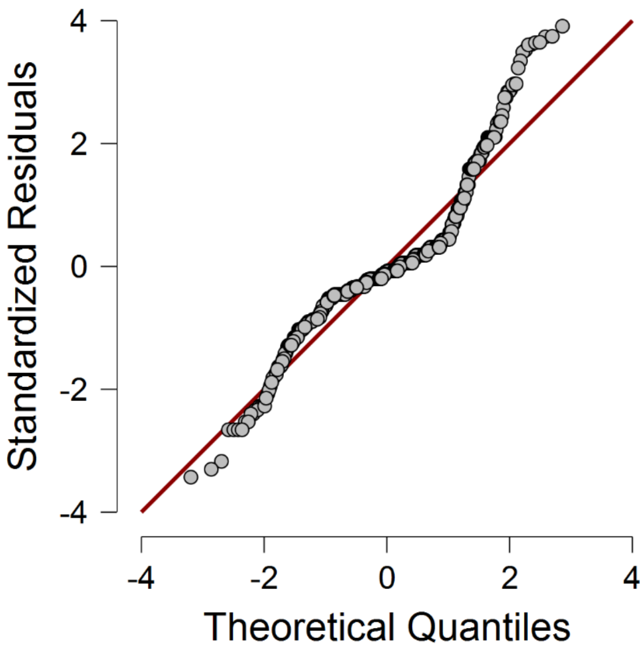
Note. Type III Sum of Squares

Assumption Checks

Test for Equality of Variances (Levene's)

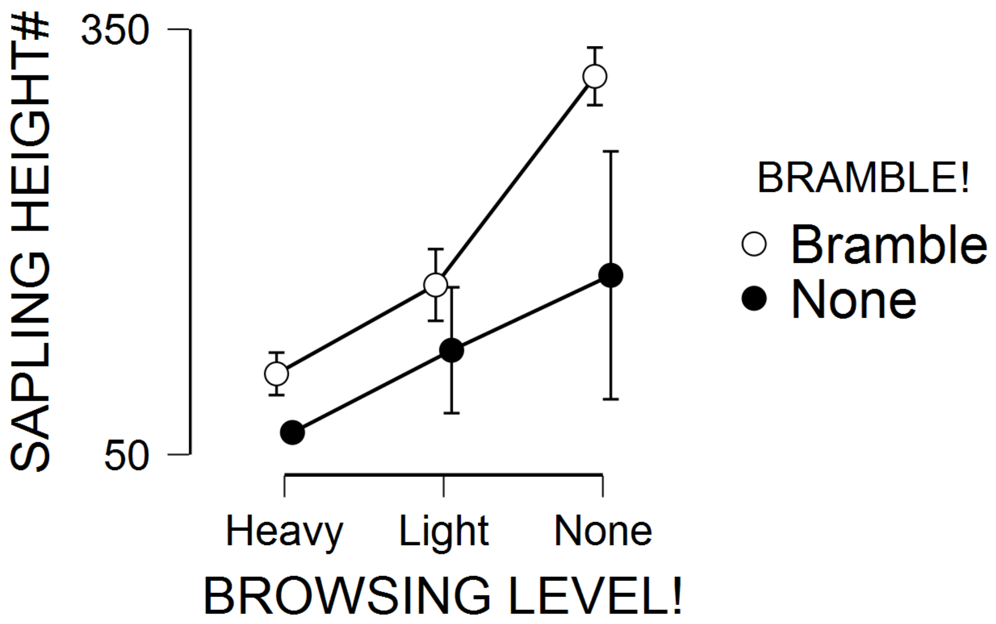
F	df1	df2	p
71.65	5	705	< .001

Q-Q Plot



Descriptives

Descriptives Plot



Descriptives

Descriptive Statistics

	SAPLING HEIGHT#		
	Heavy	**Light**	**None**
Valid	458	103	150
Missing	0	0	0
Mean	71.90	157.1	303.7
Std. Deviation	44.67	112.5	129.2
Minimum	10.00	15.00	30.00
Maximum	410.0	460.0	600.0

Descriptives

Descriptive Statistics

	SAPLING HEIGHT#	
	Bramble	**None**
Valid	281	430
Missing	0	0
Mean	225.2	72.96
Std. Deviation	139.6	57.78
Minimum	30.00	10.00
Maximum	600.0	480.0

Simple Main Effects - BRAMBLE!

Level of BROWSING LEVEL!	Sum of Squares	df	Mean Square	F	p
Heavy	101413	1	101413	16.644	< .001
Light	43195	1	43195	7.089	0.008
None	249985	1	249985	41.029	< .001

Marginal Means

Marginal Means - BRAMBLE! ✻ BROWSING LEVEL!

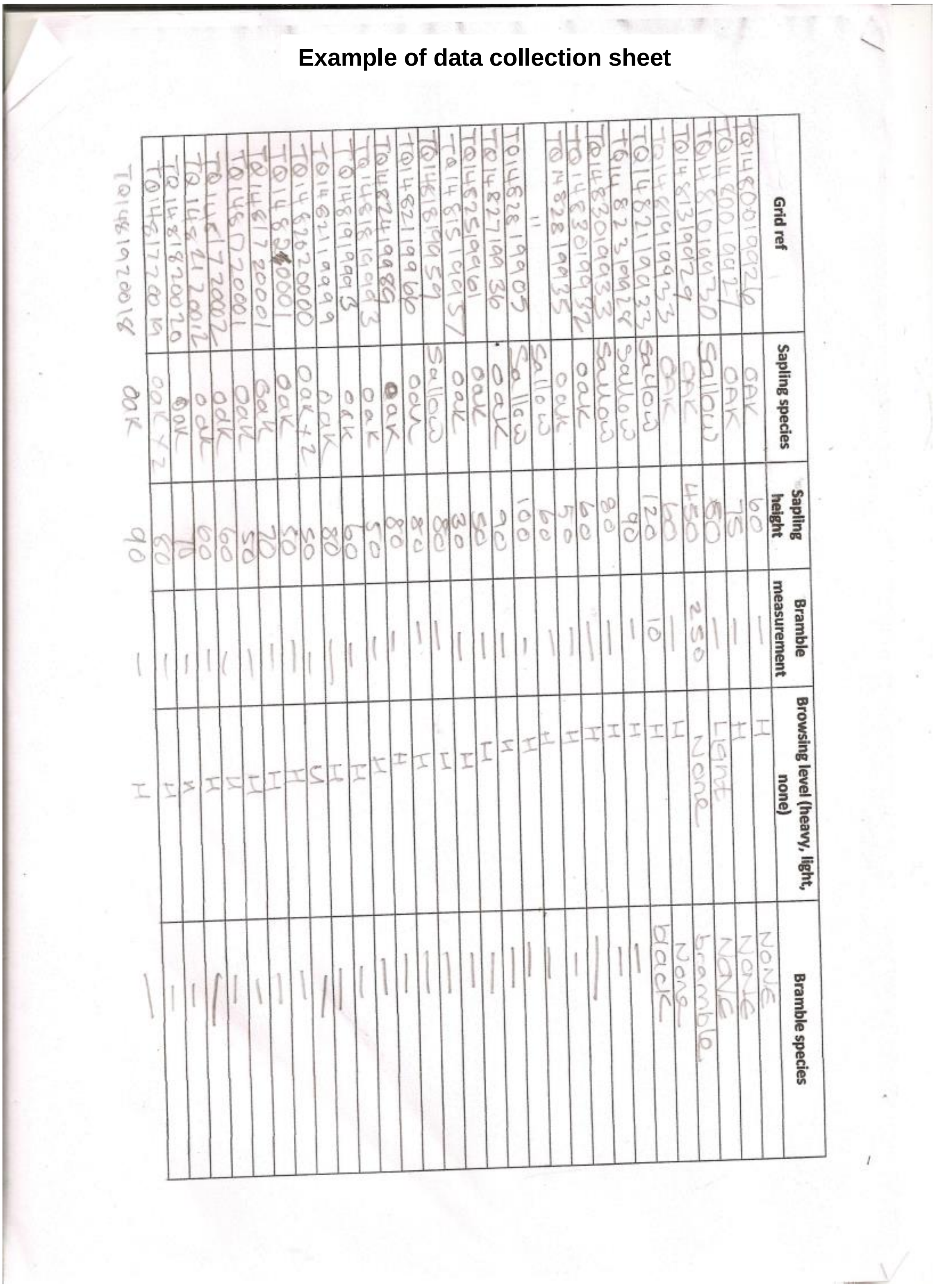
BRAMBLE!	BROWSING LEVEL!	Marginal Mean	SE	Lower CI	Upper CI
Bramble	Heavy	106.93	9.330	88.61	125.25
	Light	169.60	9.013	151.90	187.30
	None	316.76	6.693	303.62	329.91
None	Heavy	65.57	3.963	57.79	73.35
	Light	123.57	14.751	94.61	152.53
	None	176.43	20.862	135.47	217.39

Descriptives

Descriptives - SAPLING HEIGHT#

BRAMBLE!	BROWSING LEVEL!	Mean	SD	N
Bramble	Heavy	106.93	62.90	70
	Light	169.60	109.94	75
	None	316.76	119.84	136
None	Heavy	65.57	37.26	388
	Light	123.57	114.47	28
	None	176.43	151.43	14

Example of data collection sheet



Grid ref	Sapling species	Sapling height	Bramble measurement	Browsing level (heavy, light, none)	Bramble species
TQ1480019926	OAK	60	—	H	NONE
TQ1480019927	OAK	75	—	H	NONE
TQ1481019930	Sallow	50	—	Light	NONE
TQ1481319929	OAK	450	250	None	bramble
TQ1481919933	OAK	60	—	H	None
TQ1482119923	sallow	120	10	H	black
TQ1482319928	sallow	90	—	H	—
TQ1483019933	Sallow	80	—	H	—
TQ1483019932	oak	60	—	H	—
TQ1482819935	oak	50	—	H	—
"	Sallow	60	—	H	—
TQ1482819905	Sallow	100	—	H	—
TQ1482719936	oak	90	—	H	—
TQ1482519961	oak	50	—	H	—
TQ1481519957	oak	30	—	H	—
TQ1481819959	Sallow	80	—	H	—
TQ1482119966	oak	80	—	H	—
TQ1482419989	oak	80	—	H	—
TQ1481819993	oak	50	—	H	—
TQ1481919993	oak	60	—	H	—
TQ1482119999	oak	80	—	H	—
TQ1482020000	oak +2	50	—	H	—
TQ148240001	oak	50	—	H	—
TQ1481720001	oak	70	—	H	—
TQ148[illegible]720001	oak	50	—	H	—
TQ1481720002	oak	60	—	H	—
TQ1482120012	oak	60	—	H	—
TQ1481820020	oak	70	—	H	—
TQ1481720019	oak x2	60	—	H	—
TQ1481920018	oak	90	—	H	—