

6 Regeneration of Devil's-bit Scabious from the seed bank

This study explores the re-establishment possibilities of the host plant Devil's-bit Scabious from the soil seed bank.

Main question

Are viable Devil's-bit Scabious seeds present in the soil seed bank of the mire vegetations?

6.1 Methods

Five soil samples (0-5 centimetres plus the litter layer) were collected by means of a soil corer in each of the four experimental blocks, and in the area known as the Lows north and Ashcott plot. The soil samples were spread out in a seed tray on top of layer of kiln-dried sand, watered and placed in a polytunnel. The seed trays were covered by horticultural fleece to protect them from influx of other seeds. The trays were watered every week and any emerging seedlings were identified and recorded. If necessary, seedlings were grown on in pots to enable identification.

6.2 Results

No Devil's-bit Scabious seedlings emerged from the soil samples. There was a high proportion of rushes present in all samples, mainly Soft Rush and Bulbous Rush and the proportion of grasses was low (see figure 6.1). One specimen of Ivy-leaved Bellflower germinated in a soil sample originating from block 1, while six specimens of Bog Pimpernel emerged from a soil sample collected on Ashcott plot. Please refer to appendix IV for further information about recorded species.

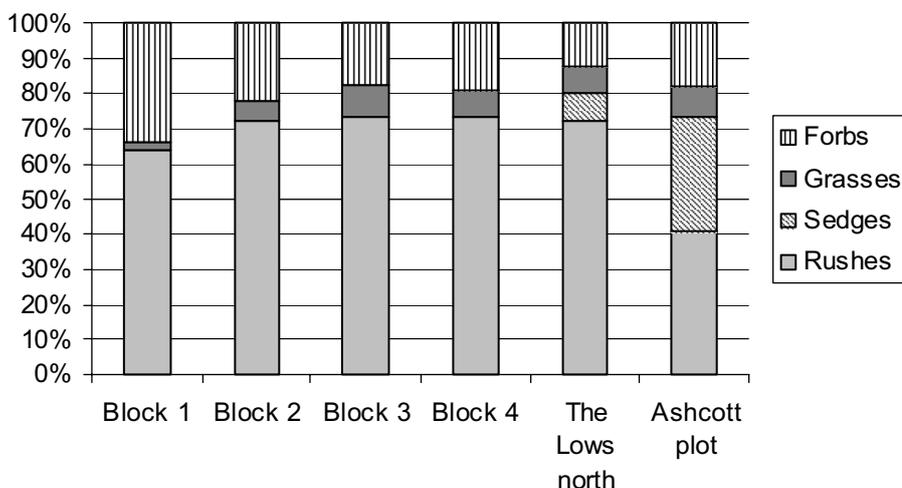
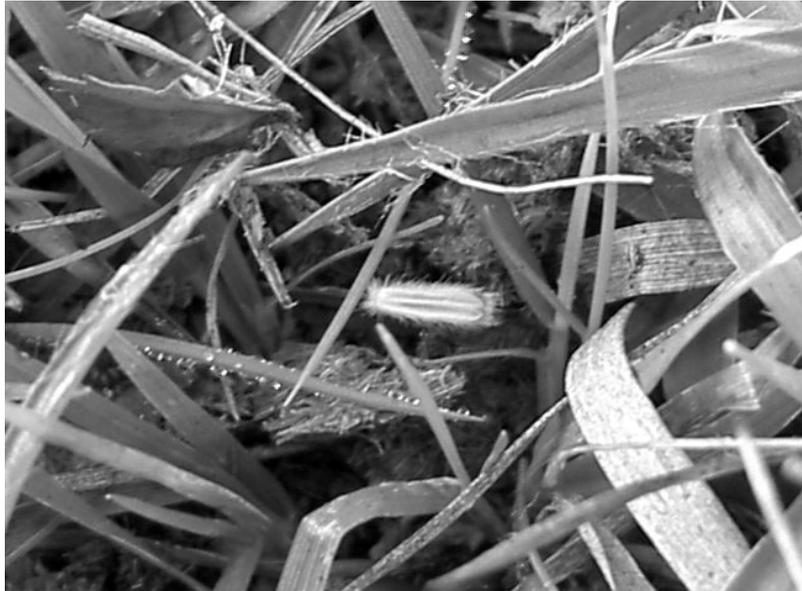


Figure 6.1 The mean proportion of forbs, grasses, sedges and rushes emerging from the five soil samples originating from the four experimental blocks and the Lows north and Ashcott plot.

6.3 Discussion & Conclusion

Seedlings emergence techniques are widely used when the aim is to establish seed bank densities (Simpson and others 1989). It provides an estimate of viable seeds in the soil based on germination of seeds maintained under conditions favourable to germination. A limitation of this method is that one can never be sure that germination conditions for all species in the sample are met. However, this method is desirable over direct counting of seeds as this is extremely tedious and gives no information about viability (Simpson and others 1989). A good number of seedlings emerged from the samples, and, in agreement with findings by several other authors (eg several references in Grime 1989; Bekker

and others 1997), the species composition in the grassland seed bank flora and the aboveground plant community was strikingly dissimilar, containing large amounts of non-target species such as Soft Rush and Bulbous Rush (Bakker & Berendse 1999). Although other rare forbs like Bog Pimpernel and Ivy-leaved Bellflower were encountered in some of the soil samples, Devil's-bit Scabious did not emerge from any of the samples and it is therefore assumed that the possibilities for regeneration of the butterfly's host plant from the soil seed bank are very limited or nonexistent.



A seed of the host plant Devil's-bit Scabious

7 Devil's-bit Scabious' micro-scale habitat characteristics

This section explores the habitat characteristics of Devil's-bit Scabious at micro-scale in the study area.

Main question

What factors are associated with the presence and/or abundance of Devil's-bit Scabious in the study area?

Research questions

1. What biotic factors are associated with the presence and/or abundance of Devil's-bit Scabious in the study area?
2. What abiotic factors are associated with the presence and/or abundance of Devil's-bit Scabious in the study area?

7.1 Methods

Of 29 quadrats in which Devil's-bit Scabious was present and 29 quadrats without the species, all species and their percentage cover were recorded. The vegetation cover was assessed by estimating the percentage cover of Purple Moor-grass, fine grasses (including sedges), rushes, Devil's-bit Scabious, other forbs, scrub and litter. Furthermore, vegetation structure height was assessed in all quadrats by means of 15 measurements with a sward stick (Stewart and others 2001). For each quadrat, soil variables were estimated by calculating an Ellenberg score for fertility, pH and moisture with help of the software program Mavis (Mavis plot analyser Version 1.00). Each score was cover-weighted using the formula $\text{Score} = \frac{\sum (E * c)}{\sum c}$, in which E = Ellenberg score for each species and c = cover value for each species. For each plot, a percentage competitor, stress tolerator and ruderal score based upon the proportion of each species attributable to different parts of the C-S-R triangle (Grime and others 1988) was calculated in Mavis. For further analysis, species percentage scores were log-transformed ($\log(\text{score}+1)$). With help of the software program Canoco for windows version 4.5, patterns of variation in floristic composition and their relationship with the environmental variables were explored. Linear ordination methods (Principal Component Analysis and Redundancy analysis) were used as the beta diversity in community composition was not high (length longest gradient < 3) (Lepš & Šmilauer, 2003). Further tests in SPSS 12.0.1 were used to detect any significant differences. The data was not normally distributed (Shapiro-Wilk tests) and variances were significantly not equal (Levene's test). Therefore, non-parametric tests have been used. The quadrats with and without Devil's-bit were tested for significant differences in terms of the variables pH, fertility, moisture, % competitors, % stress tolerators, % ruderals, % litter, % scrub, % coarse grasses, % fine grasses, % Juncus spp, % forbs, number of species, average vegetation structure height and standard deviation (SD) of vegetation structure height. Furthermore, stepwise linear regression analysis was carried out to identify predictors for percentage cover of Devil's-bit Scabious. The variables pH, fertility, moisture, % competitors, % stress tolerators, % ruderals, % litter, % scrub, % coarse grasses, % fine grasses, % juncus spp, % forbs, number of species, average vegetation structure height and SD of vegetation structure height were used as independent variables, and % Devil's-bit Scabious as dependant variable.

7.2 Results

In the text and figures, quadrats in which Devil's-bit Scabious was present are referred to as S-quadrats and quadrats without the species are referred to as X-quadrats. For further data, see Borsje (2004b).

In the Principal Component Analysis of the plant species composition of the 29 quadrats with Devil's-bit Scabious and the 29 quadrats without the species, four axes with eigenvalues of 0.17, 0.12, 0.08 and 0.07 were found. Together these axes explained 30.6 % of the total species variance. The PCA axis 1 scores can be interpreted in terms of abundances of the plant species ($R^2=0.99$, $p<0.0011$, $F=1507.80$, $df=21$) in the following way:

$$PCA_1 = 1.06 + \sum \beta_n * \log(\text{abundance} + 1)$$

The plant species Purple Moor-grass, Tormentil, Devil's-bit Scabious, Catsear, Carnation Sedge *Carex panacea*, Yorkshire Fog *Holcus lanatus* and Bent spp explain most of the variation.

Redundancy analysis was carried out on the species data with environmental variables Ellenberg moisture, pH and fertility values, mean vegetation structure, standard deviation of the vegetation structure height % stress tolerators, % ruderals, % competitors and % litter and scrub cover. The analysis resulted in 4 axes with eigenvalues of 0.14, 0.08, 0.05 and 0.04, of which the first three axes were statistically significant (axis 1: $F=7.927$ $p=0.002$, axis 2: $F=4.641$ $p=0.004$, axis 3: $F=3.099$ $p=0.04$). The first three axes correlate well with the environmental data ($r=0.93$, 0.86 and 0.84 respectively). The first axis correlates most strongly with Ellenberg moisture ($r=-0.835$ $p<0.001$), Ellenberg pH ($r=0.709$ $p<0.001$), % competitors ($r=-0.806$ $p<0.001$) and % ruderals ($r=0.794$ $p<0.001$). The second axis correlates with average for the vegetation structure height ($r=0.394$ $p=0.002$), standard deviation of the vegetation structure height ($r=0.441$ $p=0.001$) and the percentage scrub ($r=-0.577$ $p<0.001$). The third axis correlates significantly with the variables pH ($r=-0.632$ $p=0.005$), fertility ($r=-0.416$ $p=0.001$) and % stress-tolerators ($r=0.449$ $p<0.001$).

Monte Carlo permutation tests have been carried out to identify the variables that explain most of the variance in species composition. It was found that the variables moisture, pH, % competitors, % ruderals and % scrub all had a significant effect on the species composition (Bonferroni correction applied; $\alpha/10=0.005$). Together, these variables account for 77% of the total variance explained by all environmental variables.

In the distance biplot of the samples with the environmental variables (fig 7.1), samples with Devil's-bit Scabious present are shown with an S, while samples where the plant is absent are shown with an X. The correlation biplot of the species and the samples (same coding of the samples) is shown in figure 7.2. It seems that a dissimilarity in terms of species composition exists between X-quadrats and S-quadrats. The main group of X-quadrats seems to have higher moisture levels, higher percentages of litter, and a higher percentage of competitors than S-quadrats, while S-quadrats seem to have a higher pH value, higher fertility levels and a higher percentage of ruderals. From the correlation biplot we can infer that X-quadrats are associated with higher abundances of Purple Moor-grass, Sharp-flowered rush *Juncus acutiflorus*, Common Sedge *Carex nigra* and to a lesser extent Bog Myrtle, while the S-quadrats have higher abundances of fine grasses (eg Bent spp, Sweet Vernal-grass) and forbs (eg Catsear, Tormentil).

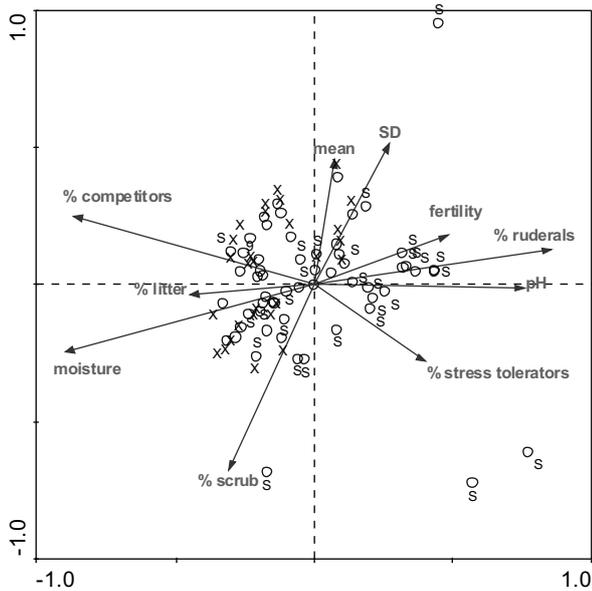


Figure 7.1 Distance biplot of the samples and environmental variables . Mean= average vegetation structure height, SD= standard deviation of vegetation structure height. Quadrats containing Devil's-bit Scabious have the label S, while those without the plant have the label X.

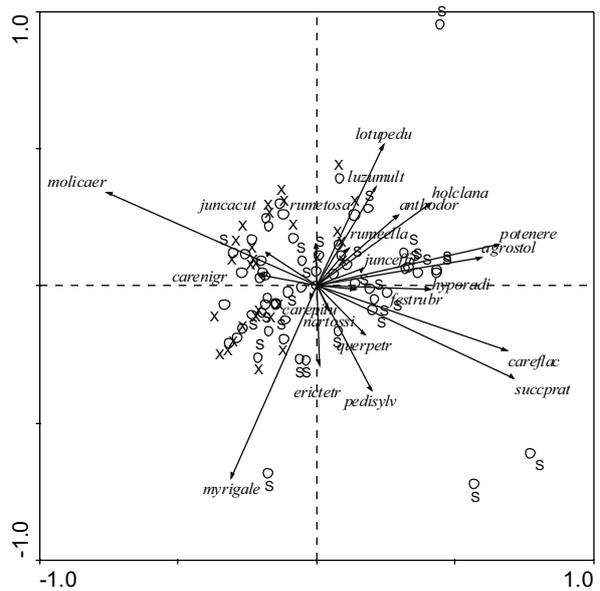


Figure 7.2: Correlation biplot of the samples and species. Quadrats containing Devil's-bit Scabious have the label S, while those without the plant have the label X. Plant species are assigned by the first four letters of the latin genus and species names, except for *Rumex acetosa* and *Rumex acetosella*. These species are assigned by rumetosa and rumeella respectively.

Mann-Whitney U tests confirmed these suspicions; the values of the variables moisture, % competitors and % litter were significantly lower for quadrats containing Devil's-bit Scabious, while the values of the variables pH, fertility, and % ruderals were higher for quadrats containing Devil's-bit Scabious (see fig 7.4, 7.5 and 7.6). Furthermore, it was found that the % fine grasses, % forbs and number of species were significantly higher for quadrats containing Devil's-bit Scabious while the percentage coarse grasses was significantly lower for quadrats with Devil's-bit Scabious present (see fig 7.3).

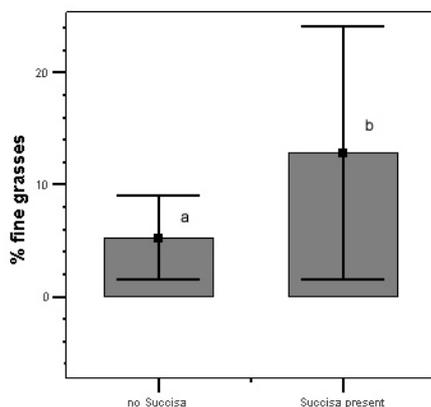


Fig 7.3: Mean % of fine grasses for quadrats with Devil's-bit Scabious (*Succisa*) and quadrats without Devil's-bit Scabious. Error bars show Mean +/- 1.0 SD.

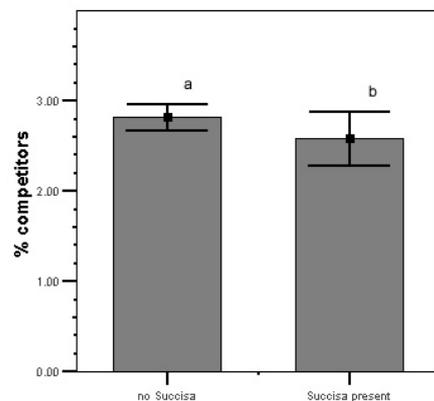


Fig 7.4: Mean % of competitors for quadrats with Devil's-bit Scabious (*Succisa*) and quadrats without Devil's-bit Scabious. Error bars show Mean +/- 1.0 SD.

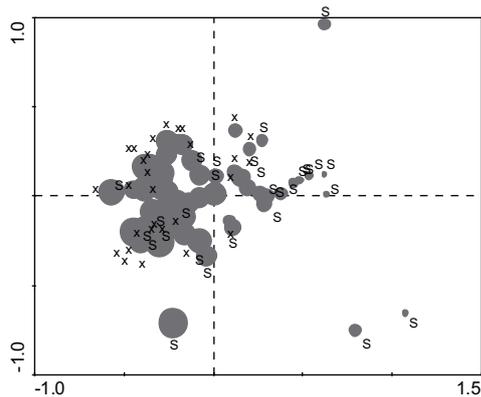


Fig 7.5: Attribute plot of the quadrats with (label S) and without (label X) Devil's-bit Scabious. Size of the samples is scaled to the value for the variable Ellenberg moisture score.

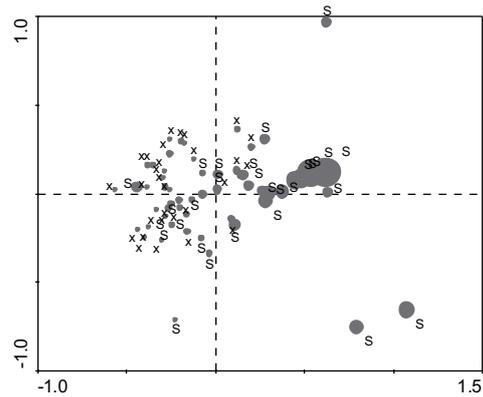


Fig 7.6: Attribute plot of the quadrats with (label S) and without (label X) Devil's-bit Scabious. Size of the samples is scaled to the value for the variable Ellenberg pH score.

Linear stepwise regression showed that of all the variables entered, pH, % competitors, % ruderals and % fine grasses were statistically significant predictors for % Devil's-Bit Scabious cover ($R^2=0.893$). This resulted in the regression model:

$$\% \text{ Devil's-bit Scabious} = 22.18 + 1.36 (\text{pH}) + -0.97 (\% \text{ C}) + -1.04 (\% \text{ R}) + -0.46 (\text{Fine grasses})$$

It is interesting to note that the coefficient for fine grasses is negative which suggest a negative relationship between the percentage Devil's-bit Scabious and percentage fine grasses. However, Mann-Whitney test have already shown that the percentage fine grasses is higher in S-quadrats than in X-quadrats, and a regression carried out solely with the variable fine grasses does result in a positive relationship (see figure 7.7). It is interesting to note that a number of quadrats do contain higher percentages of fine grasses, however, Devil's-bit Scabious is absent (see figure 7.8).

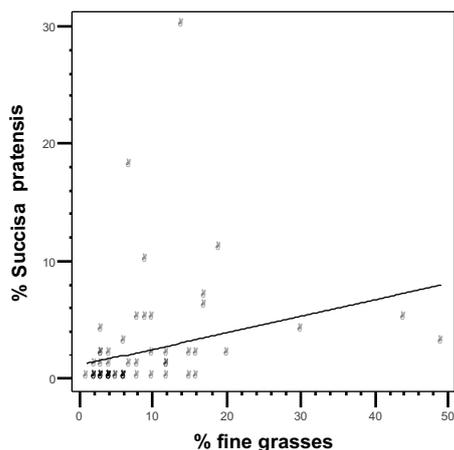


Fig 7.7: Scatterplot for % fine grasses against % Succisa pratensis (Devil's-Bit Scabious). Fitted regression line: $\% \text{ succisa} = 1.13 + 0.140 (\% \text{ fine grasses})$.

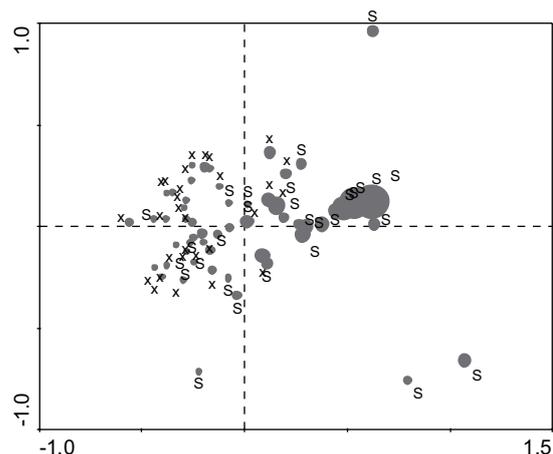


Fig 7.8: Attribute plot of the quadrats with (label S) and without (label X) Devil's-bit Scabious. Size of the samples is scaled to the value for % fine grasses.

7.3 Discussion and conclusion

This study on the habitat characteristics at micro-scale of Devil's-bit Scabious is carried out with a small number of samples (quadrats), still, the results are in agreement with the present knowledge on the ecology of the plant.

The quadrats containing Devil's-bit Scabious were typically more species-rich and contained more fine grasses than the quadrats without the species, while the quadrats without Devil's-bit Scabious had higher abundances of Purple Moor-grass, and a higher proportion of competitors in the species composition. The fact that the plant was mostly absent from these "highly competitive quadrats" is in agreement with Grime's C-S-R theory (1979), which states that Devil's-bit Scabious, as a typical stress tolerator; exploits sites where the growth of potential dominants is restricted by a low level of soil fertility and/or cutting and grazing regimes (Grime and others 1988). As soon as the dominance of highly competitive species like Purple Moor-grass is reduced, other less vigorous species are given a chance to compete, resulting in more species-rich, botanically interesting vegetation communities (Bakker 1989; Grubb 1977; Crofts & Jefferson 1999).

Samples containing Devil's-bit Scabious were drier and less acidic than samples without the species present. Species that were most strongly correlated with the samples without Devil's-bit Scabious were Purple Moor-grass, Bog Myrtle, Sharp-flowered Rush, and Common Sedge. These species are all able to cope with prolonged flooding in winter (Weeda and others 2003). Locations with Devil's-bit Scabious might be at a little higher altitude in the landscape resulting in a slightly drier environment; Grime and others (1988) mentions that Devil's-bit Scabious is seldom found in waterlogged sites, and if so, mainly on tussocks of other species. The pH range where Devil's-bit Scabious can be found is quite broad, roughly from 3.5-8.5, however, maximum frequency is reached in the range of 5.5-6.5. The pH range of Devil's-bit Scabious' main competitor in the study area, Purple Moor-grass, is also quite broad, however, the optimum for this species is clearly in more acidic environments (pH <4) (Grime and others 1988). The quadrats without Devil's-bit Scabious might be too wet or too acidic for the species.

However, this conclusion is probably too hasty. The vegetation in the study area is in transition; after severe drainage caused by nearby peat excavation and several years with a lack of vegetation management, the area is now subject to restoration management. Water levels have been restored and grazing and topping management has been put in place. The actual conditions that allowed Purple Moor-grass to reach its dominant position (lack of vegetation management, increased availability of nutrients as a result of peat oxidation caused by drainage, ability to cope with strong fluctuations of the water table) are changed to conditions more favourable for species-rich communities.

But Purple Moor-grass is capable of sustaining its own dominance; it produces copious amounts of acid, slow decomposing litter, thereby suffocating other plant species (Weeda and others 2003). Moreover, Purple Moor-grass is very efficient in reuse of nutrients. Before shedding, it withdraws nutrients from the above ground biomass to its roots and this contributes largely to the competitive vigour of the species (Berendse and others 1987; Weeda and others 2003). As a result, reducing the dominance of Purple Moor-grass is a slow process, which is most successful if its nutrient cycling is hampered by early cutting or grazing (Weeda and others 2003; Crofts & Jefferson 1999).

Although conditions for less vigorous plant species to flourish might be present or the conditions might at least become more favourable to them, this does not mean that all target species of the target community are able to react quickly to these changes in the environment. Re-colonization of restored patches might be slow or even absent. Two important constraints are impoverished seed banks and limited dispersal capacities of plant species (Bakker & Berendse 1999). Seed banks of grasslands all over Europe contain large amounts of non-target species while rare and often endangered species are under-represented or absent (Bakker & Berendse 1999; Thompson 2000). Adams (1955) mentions that seeds of Devil's-bit Scabious remain viable for at least a year, however, it is thought that no buried

seed bank exists (Grime and others 1988, see also chapter 6). Seeds of Devil's-bit Scabious have no well-defined dispersal mechanism, and are poorly dispersed (Grime and others 1988), mostly falling close to the parent plant. Moreover, small populations of Devil's-bit Scabious suffer from a reduced germination percentage, reduced number of seedlings in the population and higher seedling mortality (Hooftman & Diemer 2001; Vergeer and others 2003; 2004).

Even though suitable conditions for Devil's-bit Scabious might occur in several compartments of the study area, the species might still not be able to recolonize these areas from the scattered small populations that are still present. The observation that several quadrats contained fine grasses and forbs, but contained no specimens of Devil's-bit Scabious might indicate that re-colonization of suitable habitat by Devil's-bit Scabious is a slow and difficult process.



Devil's-bit Scabious with Catsear, Tormentil, Bog Asphodel and Bog Myrtle in one of the more species-rich patches on the study site (July 2004).

8 Effects of the grazing regimes on Devil's-bit Scabious

The attributes of different types of grazing management could have different effects on the growth form of Devil's-bit Scabious. For example, it is known that sheep select for Devil's-bit Scabious, grazing the plant down tightly, which might prevent flowering and thus reproduction. Without the ability to set seed, the chances of the species increasing its cover and spreading to areas in which it is now absent are minimal. The aim of this experiment is to investigate the effects of the restoration management in the form of sheep grazing and cattle grazing on the host plant Devil's-bit Scabious. Furthermore, the aim is to identify any possible bottlenecks that, under the present management, might exist when the aim is to restore the cover and frequency of Devil's-bit Scabious to a level that allows re-establishment of the butterfly, and to restore the vegetation to "favourable condition".

Main question

How do the restoration grazing regimes affect the Devil's-bit Scabious plants in the study areas?

Research questions

1. Do the variables number of leaves in the rosette, number of buds, length and width of the largest leaf and biomass of the plants at the start of the experiment differ between the groups of plants subject to the three treatments (cattle grazing, sheep/goat grazing and control)?
2. Do the variables number of leaves in the rosette, number of buds, length and width of the largest leaf, biomass, number of stem leaves, number of flowering stems, number of flowers and height of the flowering stem differ after they have been subject to the treatments and do any significant differences in terms of the variables number of eaten stems and number of eaten flowers exist between the three treatments?
3. Have any of the measured characteristics of the plants at the beginning of the experiment had any effect on the measured plant characteristics and expressed life history functions at the end of the experiment?
4. Has the height and type of the surrounding vegetation around a plant had any effect on the abovementioned variables measured at the end of the experiment?

Hypotheses

- The biomass of Devil's-bit Scabious plants subject to sheep/goat grazing will be lower than that of plants subject to cattle grazing, and grazing on Devil's-bit Scabious will result in a reduced ability to attempt reproduction since the flowers are consumed. Biomass of ungrazed control plants will be highest and these control plants will be most successful in their attempts to reproduce⁷.
- In the treatment cattle grazing, plants growing in unpalatable or less preferred vegetation will have a higher biomass and will be more successful in their attempts to reproduce. For sheep grazing, this effect is not expected as sheep are able to select for certain species from a mixture.

8.1 Methods

In May 2004, Devil's-bit Scabious plants were randomly selected in the Lows south and on Ashcott plot. In the Lows south the plants have been subject to grazing with North Devon cattle, stocking level 1.7LU per hectare⁸. The thirty plants on Ashcott plot have been subject to grazing with Shetland sheep and domestic goats, stocking level 0.85 LU per hectare⁹, and thirty control plants were present within an enclosure in the Lows south.

⁷ A successful attempt to reproduce is defined as the ability to put up a flowering stalk and to bear flowers.

⁸ Assuming for cattle: 1 animal = equivalent to 0.5 Livestock Unit (LU).

⁹ Assuming for sheep & goats: 1 animal = equivalent to 0.125 Livestock Unit (LU).

Of these randomly selected plants, number of rosette leaves, number of buds and length and width of the largest leaf of each plant were measured. In September 2004, 30 plants were again selected in the area subject to sheep/goat grazing and in the area subject to cattle grazing. A number of control plants within the enclosure were affected by grazing by cattle because they were located too close to the fence. Since the density of Devil's-bit Scabious in the enclosure was low, only 28 control plants could be used for further recording. The variables number of leaves in the rosette, length and width of the largest rosette leaf, number of flowering stems, number of stems eaten, number of flowers, number of flowers eaten and the length of the flowering stems were recorded. Furthermore, around each plant five vegetation height measurements were carried out using a sward stick (Stewart and others 2001). The first bit of vegetation touched by the perspex plate was recorded in five different categories: Purple Moor-grass, Bog Myrtle, fine grasses, forbs or scrub.

For statistical analysis, biomass per plant at the start and at the end of the experiment was calculated as the product of the number of leaves of the rosette and the length and width of the largest leaf (Vergeer and others 2003). The number of stem leaves, flowers and flowers eaten per flowering stem were added up for plants that had more than one flowering stem. For the length of the flowering stem, the mean of the stems present was used for further analysis. Of the five vegetation height measurements taken around each plant, a mean was calculated and a score (between 1 and 5) for each of the categories Purple Moor-grass, Bog Myrtle, fine grasses, forbs or other scrub was assigned to each plant. Analysis was carried out with the SPSS 12.0.1 for windows software package.

The variances were significantly not homogenous, therefore, to test for significant differences between treatments, non-parametric Kruskal-Wallis and Mann-Whitney U tests were used. In total 88 plants were used for the analysis, 30 plants subject to sheep/goat grazing, 30 plants subject to cattle grazing and 28 control plants.

When planning the experiment, it was not known that on the study site that was going to be subject to sheep grazing, goat grazing would also be introduced. The fact that one of the three treatments consisted of mixed sheep and goat grazing makes it difficult to attribute the results of this treatment to one of these grazing animals, or to discern the effects of the two types of grazing animal. However, because the ratio of sheep:goats was roughly 4:1, and goats preferably browse while the effects of grazing were studied on a herb, it is assumed that the effects of the treatment are most likely the result of sheep grazing, and the grazing in the concerning area will be further referred to as sheep grazing.

8.2 Results

For further data, see Borsje (2004b). At the start of the experiment, no significant differences existed between the plants subject to the three treatments in terms of number of leaves in the rosette and number of buds, however, the length of the largest leaf is longer of the plants under sheep grazing and the width of the largest leaf is wider of control plants than for plants under cattle grazing, and the leaves of the plants under sheep grazing are also wider than the leaves of plants under cattle grazing. This does not affect the biomass of the plants, as no significant differences exist at the start of the experiment (see figure 8.1).

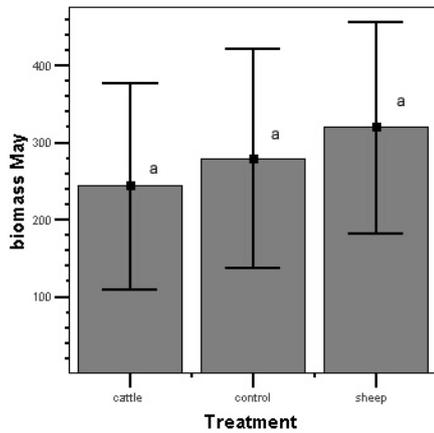


Figure 8.1: Bars represent biomass of the plants at the start (May) of the experiment. Error bars show Mean +/- 1.0 SD. Bars with the same letter do not differ significantly. $n_{\text{cattle}}=30$, $n_{\text{control}}=30$, $n_{\text{sheep}}=30$. Error bars show Mean +/- 1.0 SD.

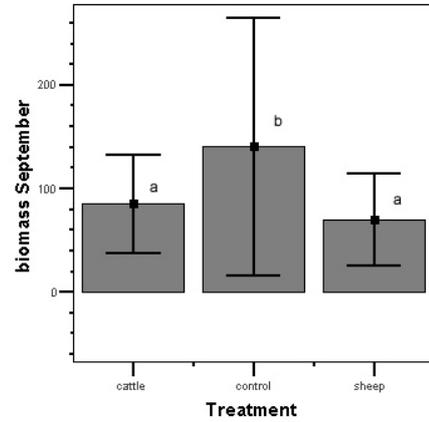


Figure 8.2: Bars represent biomass of the plants at the end (September) of the experiment. Error bars show Mean +/- 1.0 SD. Bars with the same letter do not differ significantly. $n_{\text{cattle}}=30$, $n_{\text{control}}=28$, $n_{\text{sheep}}=30$. Error bars show Mean +/- 1.0 SD.

At the end of the experiment, the biomass of the control plants was higher than the biomass of the grazed plants (figure 8.2). However, the number of leaves in the rosette did not differ significantly. The high biomass is caused by the significantly higher values for length and width of the rosette leaves of the control plants compared to the grazing treatments (see figure 8.3 and 8.4).

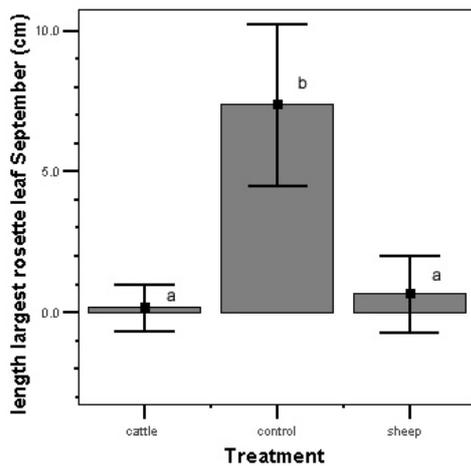


Figure 8.3: Bars represent the variable length largest rosette leaf of the Devil's-bit Scabious plants in May. Error bars show Mean +/- 1.0 SD. Bars with the same letter do not differ significantly. $n_{\text{cattle}}=30$, $n_{\text{control}}=28$, $n_{\text{sheep}}=30$.

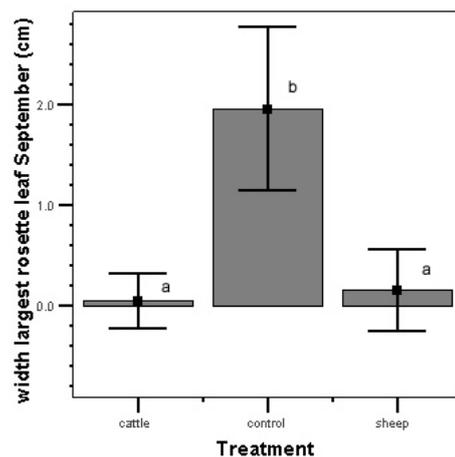


Figure 8.4: Bars represent the variable width largest rosette leaf of the Devil's-bit Scabious plants in May. Error bars show Mean +/- 1.0 SD. Bars with the same letter do not differ significantly. $n_{\text{cattle}}=30$, $n_{\text{control}}=28$, $n_{\text{sheep}}=30$.

Of the control plants, 25 plants flowered, while only three cattle grazed plants and 11 sheep grazed plants flowered (see fig 8.5). With a mean of 2.25 flowering stalks per plant, the number of flowering stalks was higher for the control plants than for the grazed plants, while the number of flowering stalks was higher for sheep grazed plants as compared to cattle grazed (means of 0.47 and 0.10 respectively).

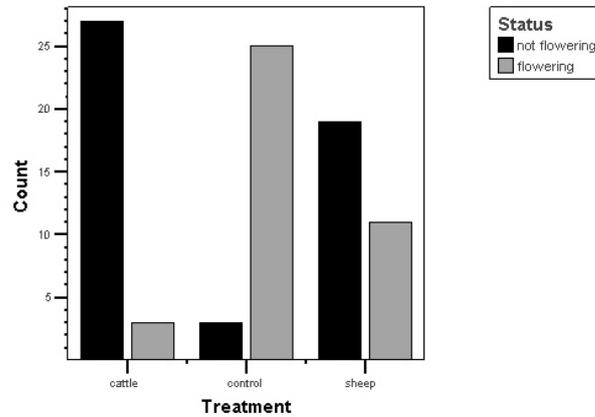


Fig 8.5: Bars represent the number of flowering and flowerless plants per treatment.

Also the number of flowers per plant differed markedly between treatments. Control plants had a mean number of flowers of 8.6 and a maximum of 14 flowers per plant, while the mean number of flowers per plant for the plants under cattle and sheep grazing was only 0.10 with a maximum of one flower per plant and 0.70 with a maximum of three flowers per plant respectively (see figure 8.6). The mean length of the flowering stalks was also significantly higher for control plants than for the grazed plants, while the plants under sheep grazing had longer stalks than the plants under cattle grazing.

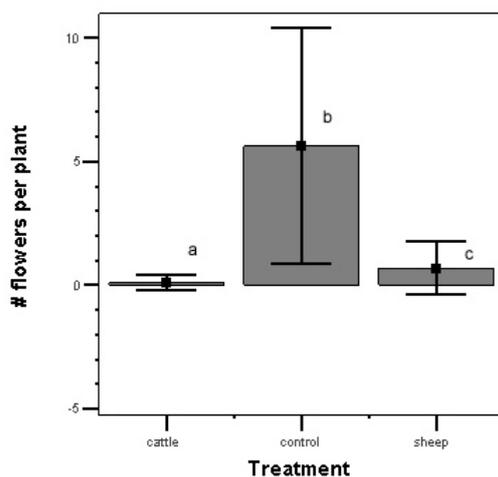


Figure 8.6: Bars represent the variable mean number of flowers for Devil's-bit Scabious plants in September. Error bars show Mean +/- 1.0 SD. Significant differences exist between all treatments. $n_{cattle}=30$, $n_{control}=28$, $n_{sheep}=30$.

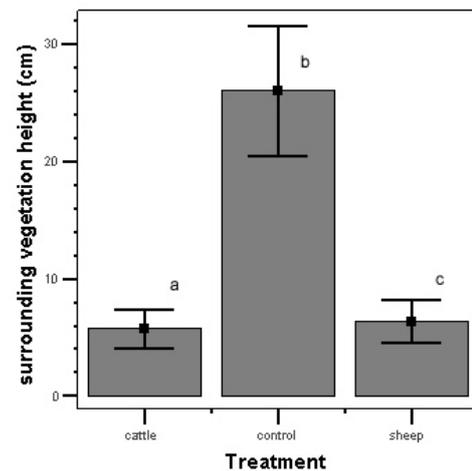


Figure 8.7: Bars for the variable height of the surrounding vegetation. Error bars show Mean +/- 1.0 SD. Significant differences exist between all treatments. $n_{cattle}=30$, $n_{control}=28$, $n_{sheep}=30$.

The vegetation around control plants was significantly higher than the vegetation around grazed plants (see figure 8.7).

While in the grazed plots the plants did not get the chance to develop flowers at all, the plants in the ungrazed plots did. In the ungrazed plots some of the flowers were bitten off the stalk and were thus recorded as eaten. More eaten flowers were recorded on ungrazed plants than on grazed plants. This is because in the grazed treatments, the whole flowering stalk was eaten including any possible flowers, which made it not possible to record individual eaten flowers. The mean number of flowers eaten for control plants (5.44 per plant) indicates that grazing occurred inside the enclosure where the control plants were located. It is thought that the grazing inside the enclosure can be attributed to roe deer since roe deer are very abundant in the area. Rabbit grazing seems less likely as they are not often seen in the study area.

The mean height of the surrounding vegetation, or the type of surrounding vegetation had apparently no effect on the biomass of the plants or the ability to attempt to reproduce, since no significant correlation between these variables was found.

8.3 Discussion and conclusion

At the start of the experiment, the leaves of the plants due to be subject to sheep grazing were slightly longer than those of the plants due to be subject to cattle grazing, however, plants did not differ significantly in terms of number of leaves in the rosette, number of buds, width of the largest leaf or in estimated biomass. Therefore, it is assumed that any differences found between the three groups of plants at the end of the experiment are attributable to the treatments.

Effects of grazing

Plants subject to sheep grazing and cattle grazing were heavily affected; the number of flowering plants was low in both categories, while the mean number of flowers per plant and the mean length of the flowering stalk was also significantly lower than that of control plants. It can be concluded that both types of grazing management do affect Devil's-bit Scabious plants.

Differential effects of grazing

Sheep are known to select for Devil's-bit Scabious and to concentrate grazing on the more palatable, herb-rich patches in which Devil's-bit Scabious is often found (Warren 1994; Butterfly Conservation 2001; Crofts & Jefferson 1999) while cattle can not graze selectively. It was hypothesized that sheep grazing would result in small rosettes with a low biomass, and a reduced success in terms of reproduction attempts compared to plants being grazed by cattle or not being grazed at all.

In contrast to this expectation, plants subject to sheep grazing were more successful in their attempts to reproduce than plants subject to cattle grazing; the number of flowering plants, the number of flowers per plant, the number of flowering stalks per plant and the mean length of the flowering stalk were all higher of the plants subject to sheep grazing than of plants subject to cattle grazing.

It is thought that the observed results are linked to the different stocking levels of the two experimental areas. The stocking level in the cattle grazed area was very high with 1.7 LU per hectare during the 20 weeks of the experiment. To put this stocking rate into perspective; 2.0 LU per hectare is the average stocking rate for sheep and beef production on improved grassland (Crofts & Jefferson 1999) and the recommended stocking rate for M25 mire vegetations, based on the likelihood of significant vertebrate interest, is only 0.5-0.625 LU per hectare (Crofts & Jefferson 1999). The stocking level in the sheep grazed area was calculated by assuming that one goat is equivalent to one sheep in terms of livestock units, resulting in a stocking level of 0.85 LU per hectare. This stocking level comes much closer to the recommended stocking level of 0.625 LU per hectare.

As a result of the high grazing pressure in the cattle grazed area, almost all biomass was removed during the grazing season, resulting in a tight and very short sward. As a result, the Devil's-bit Scabious plants have not been successful in their attempts to reproduce because the plants including the flowering stalks were being grazed down continuously. The high stocking levels in the area are part of the restoration management aimed at reducing the domination of Purple Moor-grass in favour of forb species and fine grasses. By means of the high stocking levels, the dominance of Purple Moor-grass is reduced through continuous removal of its re-growth. This will favour target species like less vigorous herbs and fine-leaved grasses that are less capable to compete for water, light and nutrients. Devil's-bit Scabious is one of these target species, not only because it is part of a well-developed mire community, but also because it is the host plant of the Marsh Fritillary butterfly. The aim is to restore the habitat of this butterfly species in order to make re-establishment possible. However, the results of this experiment show that the stocking level in the area seriously hindered the ability of the host plant to reproduce. As a result, the chances on increase in cover or colonization of "empty" areas are minimal, especially because no persistent seed bank of the species is thought to exist (Adams 1955; Grime and others 1988, see also chapter 6).

In the area subject to sheep grazing, a more heterogeneous vegetation in terms of vegetation height was present, although patches containing Devil's-bit Scabious and fine grasses were grazed down short (personal observation). Even though the grazing pressure in this area was only half that of the cattle area, still not many Devil's-bit Scabious plants managed to produce any reproductive organs and the plants that did flower had short flowering stalks, mostly bearing only one flower. These short flowering stalks bearing only a few flowers are similar to the "secondary" flowering stalks found on Devil's-bit Scabious plants some time after they have been subject to a hay cut (personal observation). Adams (1955) found that plants whose leaves were cut to 3 centimetres every week during May and June, also had considerably shorter flowering stems than those of a control group. On Ashcott plot, Devil's-bit Scabious plants that had been grazed by sheep had considerably less flowering stalks, flowers and shorter flowering stalks than the control group. Furthermore, it was observed that the sheep had preferentially grazed patches in which Devil's-bit Scabious was present. This suggests that even at low grazing pressures, sheep grazing is likely to have detrimental effects on the reproductive success of Devil's-bit Scabious and therefore on its ability to spread and increase its cover in the area.

It was hypothesized that plants growing in patches of unpalatable Bog Myrtle or less preferred Purple Moor-grass would be less affected by the grazing treatments, because the grazing animals would avoid these patches. However, no significant difference between the type of surrounding vegetation and any characteristics of the Devil's-bit Scabious plants was found. This can probably be attributed to the high stocking levels in the area, which has forced the animals to graze the sward down completely. If the grazing pressure would have been lower, the animals could have been more selective about where they would and would not graze and unpalatable or less preferred vegetation would have been left alone or grazed less intensively (Bakker 1989).

Observations relevant to the conservation of the Marsh Fritillary butterfly

The estimated biomass of the plants subject to sheep grazing and cattle grazing did not differ significantly at the end of the experiment. Even though the grazing pressure in the sheep grazed area was only half that of the grazing pressure in the cattle grazed area, the effects on the biomass of Devil's-bit Scabious were similar. This strongly suggests that, even at low stocking rates close to the recommended stocking rate for mire vegetation with considerable invertebrate interest (Crofts & Jefferson 1999), the sheep graze preferably in the more palatable fine grass patches, or might even select for Devil's-bit Scabious, thereby affecting the biomass of Devil's-bit Scabious plants heavily. The available biomass of the host plant is an important factor in the ecology of the Marsh Fritillary butterfly as it is a cluster laying species. When ovipositing, females select for large lush plants (Emmett & Heath 1990; Thomas & Lewington 1991), while small plants reduced to tight rosettes are avoided (Warren 1994). Moreover, later on in the year when the eggs have hatched, the groups of larvae finish their "plant of birth" quickly, and need more large host plants with a high biomass nearby to be able to feed sufficiently. If sheep grazing is to be continued in the future after the site has been sufficiently restored, this might hinder re-establishment of the butterfly because of the effect sheep grazing would

have on the butterfly's host plant. The aim is to graze the area with cattle in the future (English Nature 2003), but because of the isolation of the site from the main grazing units, it is difficult to find a contractor who is prepared to graze the area with cattle.

The estimated biomass of the ungrazed plants was higher than that of the grazed plants, however, the difference is not large and the number of leaves in the rosette did not differ significantly between treatments. The higher biomass of the control plants was caused by the longer length and width of the rosette leaves of the control plants. It is interesting to note that the difference in terms of biomass was relatively small for the control plants compared to the grazed plants, and no difference was detected in the number of rosette leaves, which was low for all treatments compared to the start of the experiment. The loss of leaves in the grazed treatments can be attributed to the grazing action of the animals. Adams (1955) has shown that plants growing in long grass had fewer rosette leaves than plants growing in short grass or on bare soil. The loss of leaves for the control plants can probably be attributed to the height of the surrounding vegetation, which was significantly higher (mean 26 centimetres) for control plants than for plants subject to grazing (mean 6 centimetres).

It is interesting to note that none of the treatments control, sheep grazing or cattle grazing seemed to result in host plants having properties that make them suitable for ovipositing by the female butterfly; the biomass of the plants is low and rosette leaves are few. For optimum growth of Devil's-bit Scabious, plants growing on the periphery of a tussock or a tussocky area have advantages. They are protected by the presence of the tussocks against too heavy grazing, as would happen in fine grass patches. However, they are also not completely smothered by the high surrounding vegetation; at least at one side of the plant enough light is present which makes production and maintenance of abundant rosette leaves worthwhile and feasible. Anecdotal evidence suggests that ovipositing females select for these large 'periphery plants' (pers. comm. M. Yeandle and C. Bulman). Cattle grazing with a low stocking rate of 0.1-0.4 LU/ha, as recommended by Butterfly Conservation, could encourage the development of such large host plants suitable for egg-laying by creating a sward where these periphery conditions could be frequently found.



The sheep on Ashcott plot preferably grazed the fine grass patches where Devil's-bit Scabious was present (September 2004).

9 Re-establishment of Devil's-bit Scabious by transplants

Devil's-bit Scabious often performs poorly during ecological restoration experiments that involve sowing of the species (Warren and others 2002; Hooftman and others 2003 ; Pywell and others 2003). Hooftman and others (2003) and Hooftman & Diemer (2002) found low germination percentages for Devil's-bit Scabious, and Vergeer (pers. comm.) found that germination percentages vary considerably from year to year. Establishment of Devil's-bit Scabious by transplants might avoid the difficult germination and establishment phase altogether. This experiment investigates whether establishment of Devil's-bit Scabious in the study area by means of transplants is a possibility, and whether success rates are influenced by cattle grazing. A successful establishment for a plant is here defined as a plant that is still alive at the end of the experiment.

Main question

Is re-establishment of Devil's-bit Scabious by means of transplants a possibility in the study area and what factors influence the success rate?

Hypotheses

- Establishment success will be influenced by the biomass of the transplants at the start of the experiment, and the success rate will be significantly lower for plants subject to cattle grazing, as these plants have to cope with defoliation, and for transplants growing in high surrounding vegetation, as these plants have to cope with a more competitive vegetation.
- At the end of the experiment, transplants will have a lower biomass than autochthonous¹⁰ plants, and transplants will be less successful in their attempts to reproduce¹¹.

Research questions

1. Have any of the measured plant characteristics number of leaves in the rosette, number of buds, length of the largest rosette leaf and width of the largest rosette leaf of the transplants at the start of the experiment had any influence on the establishment success?
2. Do the ungrazed and grazed plants differ in terms of the plant characteristics number of leaves in the rosette, length of the largest rosette leaf, width of the largest rosette leaf, number of leaves on the stem, number of stems flowering, number of stems eaten, number of flowers, number of flowers eaten and the length of the flowering stalk at the end of the experiment and does grazing influence the establishment success?
3. Does the height of the surrounding vegetation influence the success of establishment?
4. Are there any differences between planted and autochthonous plants in terms of biomass and the number of plants having success in their attempts to reproduce?

¹⁰ Autochthonous plants are defined as Devil's-bit Scabious plants that were already present in the study area.

¹¹ A successful attempt to reproduce is defined as the ability to put up a flowering stalk and to bear flowers.

9.1 Methods

In May 2004, 80 pot-grown specimens of Devil's-bit Scabious were planted in a compartment of the study area where the species was absent. Each plant was planted in a hole with a diameter of 7 centimetres and a depth of 12 centimetres filled with potting compost. Half of the plants have been subject to grazing with Red Devon cattle (stocking density 1.7 LU per hectare), the other half of the plants were planted within an enclosure. The cattle broke into the enclosure in early June, therefore, 12 control plants had to be excluded from the experiment because they were damaged by the cattle. At the time of planting, the variables number of leaves in the rosette, number of buds, length of the largest rosette leaf and width of the largest rosette leaf were measured. In September 2004, the plants were visited again and the variables number of leaves in the rosette, length of the largest rosette leaf, width of the largest rosette leaf, number of leaves on the stem, number of stems flowering, number of stems eaten, number of flowers, number of flowers eaten and the length of the flowering stalk were measured of the plants that were still present. Furthermore, around each plant five vegetation height measurements were carried out using a sward stick (Stewart and others 2001) and the first bit of vegetation touched by the perspex plate was recorded in five different categories: Purple Moor-grass, Bog Myrtle, fine grasses, forbs or scrub.

For analysis, biomass per plant at the start and at the end of the experiment was calculated as the product of the number of leaves in the rosette and the length and width of the largest leaf (Vergeer and others 2003). The number of stem leaves, flowers and flowers eaten per flowering stem were added up for plants which had more than one flowering stem, and for the length of the flowering stem, the mean of the stems present was used for further analysis. Of the five vegetation height measurements taken around each plant, a mean was calculated and a score (between 1 and 5) for each of the categories Purple Moor-grass, Bog Myrtle, fine grasses, forbs or scrub was assigned to each plant. Analysis was carried out with the SPSS 12.0.1 for windows software package. The data was not normally distributed, and the variances were significantly not homogenous. Therefore, non-parametric tests were used.

The characteristics of transplants were also compared with the characteristics of plants that were already present in the study area (autochthonous plants) and were either protected from grazing or subject to grazing by cattle. The autochthonous plants are the same plants as the control plants and cattle grazed plants in chapter 8.

9.2 Results

For further data, see Borsje (2004b).

Comparison of ungrazed transplants and transplants subject to grazing

There were no significant differences in terms of number of rosette leaves and the number of buds at the start of the experiment. Only the shape of the rosette leaves differed slightly with plants subject to grazing having wider leaves than the control plants, however, this does not result in a higher biomass for grazed plants. Therefore, all differences subsequently found can be attributed to the treatments.

All control plants had established by the end of the experiment (100%), while 31 out of 40 plants (78%) established under grazing. It is interesting to mention that all the control plants that had been damaged by the cattle in June and had been excluded from the experiment also managed to establish successfully. No significant initial differences have been found in terms of number of rosette leaves, number of buds, length and width of the largest leaf and biomass, for plants that established successfully and plants that died during the experiment ($n_{\text{died}}=9$, $n_{\text{established}}=31$). Also the vegetation height around the plants did not differ significantly for plants that died and plants that established successfully.

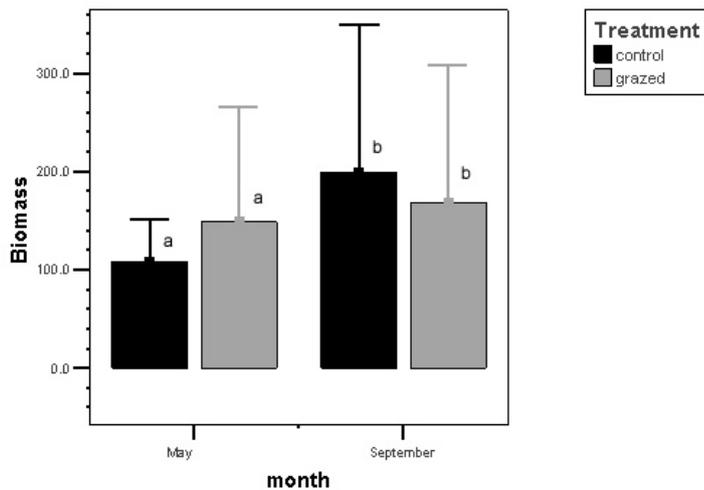


Fig 9.1: The bars represent the biomass of the planted Devil's-bit Scabious plants at the start (May) and end (September) of the experiment. Error bars show Mean +/- 1.0 SD. Bars with the same letter within one category (May or September) do not differ significantly. May: $n_{\text{control}}=40$, $n_{\text{grazed}}=40$, September: $n_{\text{control}}=28$, $n_{\text{grazed}}=31$.

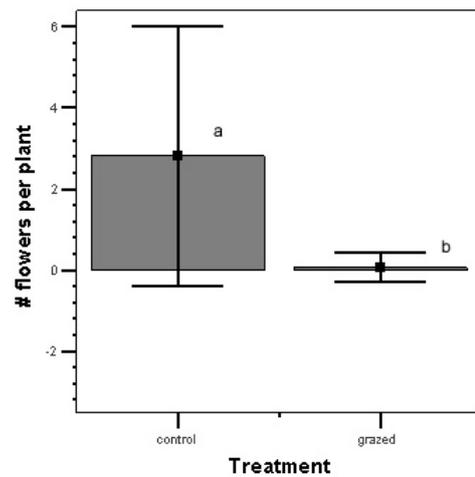


Fig 9.2: Bars represent the mean number of flowers recorded for Devil's-bit Scabious transplants under the two treatments "control" and "grazed". Error bars show Mean +/- 1.0 SD. $n_{\text{control}}=28$, $n_{\text{grazed}}=31$.

At the end of the experiment, there was no significant difference in terms of biomass between control plants and plants subject to grazing (see figure 9.1). Also the number of rosette leaves did not differ significantly between treatments, however, rosette leaves of control plants were now slightly longer than those of grazed plants.

The plants subject to grazing have been severely hindered in their attempts to reproduce; only one of the established plants subject to grazing managed to flower (3%), while 20 of the 28 control plants flowered (71%). Consequently, control plants had significantly more stem leaves than grazed plants, as only plants with flowering stalks bear stem leaves.

The number of flowers per plant ranged from 0 to 14 with a mean of 2.80 per plant for control plants, while the only plant that flowered in the grazed treatment had two flowers (see fig 9.2). The flowering stalks of control plants were a lot higher (mean of 43 centimetres) than the flowering stalk of the only flowering grazed plant (20 centimetres). As expected, no bitten off stems were found on control plants, however of one plant, a flower was eaten. On only one grazed plant, a bitten off flower stem was found while no eaten flowers were recorded on grazed plants. This is attributable to the fact that of the grazed plants, the whole flowering stalk was eaten including any possible flowers, which made it impossible to record individual eaten flowers.

Comparison of transplants and autochthonous plants protected from grazing

It is interesting to compare the characteristics of the transplants ($n_{\text{planted}} = 28$) with autochthonous plants ($n_{\text{autoch}}=28$). At the start of the experiment in May, the autochthonous plants had a significant higher biomass than the pot-grown plants, caused by a higher number of leaves in the rosette and wider and longer leaves for the autochthonous plants (see figure 9.3). The number of buds per plant did not differ significantly. In September however, the biomass¹² of the transplants was slightly higher, although this difference was not significant (see figure 9.3). The number of leaves in the rosette and the length of the largest leaf did also not differ significantly.

Only the width of the largest leaf was wider for transplants than for autochthonous plants. Of the plants already present in the study area, 23 out of 28 flowered (82%), while of the planted plants 17 out of 28 plants flowered (61%). The characteristics of flowering were significantly different; the

¹² For both groups of plants, only plants that bore rosette leaves have been used for comparison of biomass, as no rosette leaves present results in a biomass of 0, $n_{\text{autoch}} = 26$ $n_{\text{planted}} = 25$.

values for number of stems flowering, the number of flowers and the length of the flowering stalk were all higher for plants already present as opposed to planted plants. The mean vegetation height around the plants did not differ significantly between the two groups of plants.

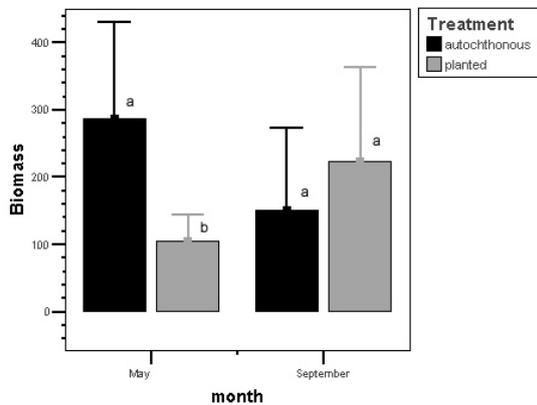


Fig 9.3: Bars represent biomass for planted and autochthonous specimens of Devil's-bit Scabious at the start (May) and end (September) of the experiment, both groups of plants are **protected from grazing**. Error bars show Mean +/- 1.0 SD. Only in May biomass differs significantly between transplants and autochthonous plants. May: $n_{\text{plant}}=40$, $n_{\text{autoch}}=30$, September: $n_{\text{plant}}=28$, $n_{\text{autoch}}=30$.

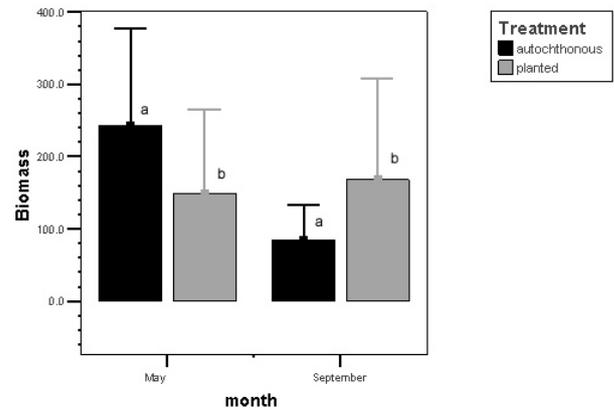


Fig 9.4: Bars represent biomass for planted and autochthonous specimens of *Succisa pratensis* at the start (May) and end (September) of the experiment, both groups of plants have been **subject to grazing**. Error bars show Mean +/- 1.0 SD. Biomass differs significantly in May and September. May: $n_{\text{plant}}=40$, $n_{\text{autoch}}=30$, September: $n_{\text{plant}}=31$, $n_{\text{autoch}}=30$.

Comparison of transplants and autochthonous plants subject to grazing

The same comparison can be made for transplants and autochthonous plants that have both been subject to cattle grazing. At the start of the experiment, the biomass of the autochthonous plants was higher than that of the transplants, with the values for number of leaves in the rosette and the length of the largest leaf also being higher. However, the width of the largest leaf was significantly higher for transplants. The number of buds did not differ significantly. At the end of the experiment however, biomass was significantly higher for planted plants, as a result of wider and longer leaves, since no significant difference exists in number of leaves in the rosette (see figure 9.4). The surrounding vegetation was also significantly higher for planted plants. Because only three of the 30 autochthonous plants (10%) and only one of the 31 transplants flowered (3%), the variables associated with flowering are not compared for the two groups of plants.

9.3 Discussion & Conclusion

Establishment of the Devil's-bit Scabious transplants has been successful during the first six months; 100% of the plants protected from grazing had established by the end of the experiment, while still 78% percent of the plants managed to establish under a fairly intensive grazing regime (1.7 LU per hectare). On top of establishing, a large number of control plants (71%) also managed to flower during the experiment, while grazed plants were a lot less successful in their attempts to reproduce as only 3% flowered. No studied characteristics of the plants at the time of planting were found to have an influence on the failure of establishment, as plants that died and plants that survived did not differ significantly in terms of any of the plant characteristics at the start of the experiment. Vegetation height around transplants did also not influence the survival of the transplants.

When comparing the transplants with autochthonous plants, differing results were found for plants subject to grazing and plants protected from grazing. At the start of the experiment, autochthonous plants had a significant higher biomass than the transplants, with more rosette leaves per plant. However, at the end of the experiment, biomass did not differ significantly between planted plants and autochthonous plants that were protected from grazing, while of the two groups of plants subject to grazing, the planted plants had a significantly higher biomass than the autochthonous plants. The catch

up of the planted plants might be attributable to the reduced root competition as a result of the created gap during planting, and the nutrients available in the potting compost that was used to fill the gap. Davies and others (1999) found gaps to be ineffective in assisting establishment of pot plants. They created 15 and 30 centimetres diameter gaps by applying glyphosate herbicide on the surface and plants were planted when mineral soil became exposed. Their study might not have reduced root competition completely. In this study, a soil core was removed including the roots of competitors, which might have aided establishment.

Although the transplants seem to not have suffered much from the planting, as reflected in the same or even higher biomass for planted plants as opposed to autochthonous plants, the planting seems to have affected the ability to reproduce; more autochthonous plants flowered and they had longer flowering stalks and more flowers than planted plants. It is possible that the planted plants have allocated more resources to vegetative growth, for example to the development of an extensive root system, so that less resources were available for reproduction. Furthermore, autochthonous plants probably had a large well-developed root system, which may have allocated more nutrients that could be allocated to reproduction.

The establishment success of Devil's-bit Scabious plantlets can however not be judged from this short period of time. Neighbouring competitors might also benefit from the nutrients that have become available in the gap, thereby lowering the plantlets' chances on survival in the longer term. Moreover, Davies and others (1999) found unexpected high mortality during the first autumn and winter of their study. Although the species they planted initially showed high survival rates, a lot of the species had high mortality rates in the subsequent three years of the study. Notably stress-tolerators like Clustered Bellflower *Campanula glomerata*, Harebell *Campanula rotundifolia* and Small Scabious *Scabiosa columbaria* had high survival rates in the first year of the experiment (78%, 76% and 96% respectively), whereas after three years all Clustered Bellflower and Harebell plants had died while the survival percentage of Small Scabious was only 1%. Devil's-bit Scabious is also a stress tolerator and is a close relative of Small Scabious and might therefore have similar mortality rates in the coming years.

Although the initial establishment of Devil's-bit Scabious has been successful, further monitoring in the coming years is recommended before conclusions can be drawn.



A Devil's-bit Scabious transplant that has been subject to grazing (November 2004).

10 Conclusions, Discussion & Recommendations

The purpose of this study is to answer the following questions:

Is a sustainable re-establishment of the Marsh Fritillary feasible in the Avalon Marshes?

What are suitable measures to achieve both restoration of the vegetation and habitat restoration for the Marsh Fritillary butterfly, and do any bottlenecks occur during the habitat restoration phase or will they arise when maintaining the habitat conditions in the future?

These questions were answered by carrying out a number of experiments, which are discussed separately below. This discussion is followed by a general conclusion and discussion, and recommendations.

1. Is suitable Marsh Fritillary habitat present on Shapwick Heath NNR and what areas on the reserve have a high potential for the species?

The mire patches The Lows north, The Lows south and Ashcott plot have a high potential for the butterfly. However, Purple Moor-grass encroachment is a considerable problem in these areas at the moment. It will take a number of years before the mire patches are restored to Marsh Fritillary habitat. Once restored, the patches comprise a considerable area of continuous Marsh Fritillary habitat, while the future management of the patches, extensive cattle grazing, is sympathetic to the needs of the butterfly.

2. Is a sustainable re-establishment of the Marsh Fritillary butterfly in a viable meta-population structure feasible in the Avalon Marshes?

The scenario studies carried out with help of the Incidence Function Model suggest that Shapwick Heath NNR and the surrounding nature reserves have a high potential for realising the re-establishment of the Marsh Fritillary butterfly in a viable meta-population structure. Re-establishment requires that the former habitat in the Lows and on Ashcott plot is restored. In addition, further habitat creation is necessary near Ashcott plot. The habitat creation would be in areas that have been re-profiled after peat excavation, and natural colonization of the host plant Devil's-bit Scabious in these areas indicates the potential of these areas for the butterfly. The viable Shapwick meta-population can be further extended to include the former colony on Catcott Heath, and the former colony on Street Heath with the aid of stepping stone patches in re-profiled peat excavations on Ham Wall NNR. It is rare that an entire viable Marsh Fritillary meta-population can be present within a single nature reserve and this will facilitate sympathetic habitat management in all patches in the meta-population. The model results have clearly shown that the Avalon Marshes could be one of the key areas for the conservation of the Marsh Fritillary in the United Kingdom if all conservation bodies in the area contribute to providing Marsh Fritillary habitat.

3. Is it possible to realize favourable conditions for germination and/or establishment of Devil's-bit Scabious by means of different management regimes and the resulting differences in habitat characteristics at micro-scale?

The seeds of Devil's-bit Scabious that were sown have not germinated. It is thought that this can be attributed to the viability of the sown seeds and not to the conditions created by application of the different treatments. It is therefore recommended that the seeding is repeated in half of the plots, this time in a higher density of 5kg seeds per hectare and coinciding with the natural seed fall in autumn. This enables further monitoring of the seeding in March 2004, while the second seeding will hopefully

result in reasonable germination percentages, which makes evaluation of the effects of the applied treatments on the establishment of Devil's-bit Scabious possible.

4. Is it possible to significantly reduce the cover of Purple Moor-grass and scrub species in favour of the cover of forbs and fine grasses by means of different management regimes?

This part of the study consists of a long-term experiment in which monitoring should take place for at least three years, and any conclusions drawn at this point would be premature. The results after the first year do however show some notable trends. Especially the low cover of Purple Moor-grass and scrub species in the rotovated plots is interesting. If subsequent vegetation management could prevent further increase in cover of Purple Moor-grass and provide appropriate circumstances for establishment of fine grasses and forb species, this treatment could be very successful in achieving a reduction in cover of Purple Moor-grass and scrub species in favour of fine grasses and forbs. Since not enough re-growth occurred after the hay cut in July to allow a proper second hay cut, it is recommended that in the following years of the experiment the first hay cut is applied in June just after monitoring has been completed. Hopefully, this will result in more vegetation re-growth in September, which will justify the second hay cut and improve the treatment. Moreover, early cutting is thought to be most effective in reducing the dominance of Purple Moor-grass by hampering its nutrient cycling. The same accounts for early grazing. Therefore, ideally, grazing in the Lows south should commence as early in spring as possible.

5. Are viable Devil's-bit Scabious seeds present in the soil seed bank of the mire vegetations?

Because Devil's-bit Scabious seedlings did not emerge from any of the soil samples it is assumed that the possibilities for regeneration of the butterfly's host plant from the soil seed bank are very limited or nonexistent.

6. What factors are associated with the presence and/or abundance of Devil's-bit Scabious in the study area?

Quadrats with Devil's-bit Scabious had a higher abundance of fine grasses and were more species-rich, while quadrats without the species had a higher abundance of Purple Moor-grass and a higher proportion of competitors in the species composition. The observation that several quadrats contained fine grasses and forbs, but contained no specimens of Devil's-bit Scabious suggests that re-colonisation of the species into patches where suitable conditions prevail is limited. Constraints are probably the absence of a seed bank and limited dispersal capacities of the species. Re-colonization of suitable habitat through natural means is possibly a slow and difficult process for Devil's-bit Scabious.

7. How do the restoration grazing regimes affect Devil's-bit Scabious plants in the study areas?

The characteristics of Devil's-bit Scabious plants subject to cattle grazing and sheep grazing were compared with the characteristics of plants protected from grazing. It was thought that the Devil's-bit Scabious plants would be most heavily affected by sheep grazing, as sheep are known to graze preferentially in the fine grass patches where Devil's-bit Scabious is often found and even select for the host plant. Both grazing treatments affected the Devil's-bit Scabious plants significantly. In contrast to expectation, cattle grazed plants were more heavily affected than sheep grazed plants. The observed results can be attributed to the different stocking levels in the two areas. The stocking level in the cattle grazed area was very high and came close to the stocking rate for beef production on improved grassland. This resulted in a very short, tight sward over the whole site; Devil's-bit Scabious

plants were grazed down completely and not able to reproduce. The stocking level in the sheep grazed area came more close to the recommended stocking rate for M25 mire vegetations with significant invertebrate interest. Nevertheless, only very few Devil's-bit Scabious plants in the sheep grazed area managed to flower, indicating that even at low stocking levels, sheep grazing has detrimental effects on the reproductive success of Devil's-bit Scabious and therefore on its ability to spread and increase its cover in the area. Moreover, the biomass of the plants was low and rosette leaves were few. The available biomass of the host plant is an important factor in the ecology of the Marsh Fritillary butterfly. Females select for large host plants with abundant rosette leaves available and the larvae also require these large plants to be able to feed sufficiently. The results of this experiment show that even at low stocking rates, close to stocking rates recommended for this type of vegetation with considerable invertebrate interest, the Devil's-bit Scabious plants are heavily affected and unsuitable in terms of the requirements of the butterfly. If sheep grazing is to be continued in the future after the site has been sufficiently restored, this might hinder re-establishment of the butterfly because of the effect sheep grazing would have on the butterfly's host plant. The aim is to graze the area with cattle in the future, but because of the isolation of the site from the main grazing units, it is difficult to find a contractor who is prepared to graze the area with cattle.

8. Is establishment of Devil's-bit Scabious by means of transplants a possibility in the study area and what factors influence the success rate?

Establishment of Devil's-bit Scabious transplants during the first six months has been successful; all plants protected from grazing established while a large proportion of the plants subject to grazing established. Besides the successful establishment, a large number of ungrazed plants managed to flower, although the number of flowering plants, the number of flowers and the number of flowering stalks per plant was lower for planted plants than for autochthonous plants. The establishment success of Devil's-bit Scabious transplants can however not be judged from this short period of time only. Similar studies have shown that although establishment rates are often high after the first year, considerable mortality rates have been recorded in subsequent years. Although the initial establishment of Devil's-bit Scabious has been successful, further monitoring in the coming years is recommended before conclusions can be drawn.

General conclusion & discussion

Is a sustainable re-establishment of the Marsh Fritillary feasible in the Avalon Marshes?

The former habitat in the patches The Lows north, The Lows south and Ashcott plot is unsuitable for the Marsh Fritillary at the moment, but the areas have a high potential for the butterfly. Once restored, the patches comprise a considerable area of continuous Marsh Fritillary habitat, while the future management of the patches, extensive cattle grazing, is sympathetic to the needs of the butterfly.

The scenario studies carried out with help of the Incidence Function Model have shown that the Avalon Marshes have a high potential for realizing the re-establishment of the Marsh Fritillary butterfly in a viable meta-population structure. Re-establishment requires that the former habitat on Shapwick Heath, in the Lows north and south and on Ashcott plot, is restored. In addition, further habitat creation is necessary near Ashcott plot. The habitat creation would be in areas that have been re-profiled after peat excavation, and natural colonization of the host plant Devil's-bit Scabious in these areas indicates the potential of these areas for the butterfly. The viable Shapwick meta-population can be further extended to include the former colony on Catcott Heath, and the former colony on Street Heath with the aid of stepping stone patches in re-profiled peat excavations on Ham Wall reserve. The presence of the entire viable Marsh Fritillary meta-population within nature reserves will facilitate sympathetic habitat management in the patches in the meta-population. The model results have clearly shown that the Avalon Marshes could be one of the key areas for the conservation

of the Marsh Fritillary in the United Kingdom if all conservation bodies in the area contribute to providing Marsh Fritillary habitat.

What are suitable measures to achieve both restoration of the vegetation and habitat restoration for the Marsh Fritillary butterfly, and do any bottlenecks occur during the habitat restoration phase or will they arise when maintaining the habitat conditions in the future?

Completely answering the second main question of this study is only possible after certain experiments have been monitored for at least three years. However, some of the experiments have already put forward some important points.

Bottlenecks concerning the restoration phase

A condition that has to be met in order to realize re-establishment of the Marsh Fritillary butterfly in the areas is re-establishment of the host plant in parts where it is now absent and increase in cover where the species is present. The aim of the current intensive grazing regimes is to restore the vegetation to “favourable condition”, however, it is likely that they will not result in re-establishment and increase in cover for Devil’s-bit Scabious. Constraints are the absence of a seed bank and limited dispersal capacities of the species. Moreover, this study has shown that the high stocking rates prevent flowering and setting seed of the few remaining Devil’s-bit Scabious plants, and thus hinders dispersal and increase in cover. If the aim is to achieve both restoration of the vegetation to favourable condition and restoration of the habitat of the Marsh Fritillary butterfly, re-establishment and increase in cover of the host plant Devil’s-bit Scabious is required, and additional measures might be necessary to achieve this.

Possible measures are protection of certain areas from grazing. This will allow Devil’s-bit Scabious to flower and set seed. If it is possible to cut these areas early, this will affect Purple Moor-grass heavily, but will not hinder reproduction of Devil’s-bit Scabious since the species flowers late; even in plots cut for hay in July the species managed to flower during this experiment. Another possibility is to lower the stocking rates in the area, but this will probably interfere with the aim of achieving favourable condition in terms of the vegetation, since the high stocking rates have been put in place to counteract Purple Moor-grass and scrub encroachment.

Other possible measures are sowing or planting of Devil’s-bit Scabious. This can be especially useful in compartments where the species is now absent, since poor dispersal capacities and the absence of a seed bank will be the initial constraints here. Suitable management regimes under which planting and sowing of Devil’s-bit Scabious is most successful are being investigated as part of this study, but conclusions can only be drawn after the experiments have been monitored for a few years.

Bottlenecks concerning the habitat maintenance phase

Restoration management in one of the experimental areas consisted of sheep grazing. The results of the study investigating the effects of grazing on Devil’s-bit Scabious plants suggest that even at low stocking rates, sheep select for the patches containing Devil’s-bit Scabious and possibly also select for the species itself. This selective grazing results in small plants with a low biomass, while the female butterfly requires large host plants with a high biomass for egg laying. If sheep grazing is to be continued in the future after the site has been sufficiently restored, this might hinder re-establishment of the butterfly because of the effect sheep grazing would have on the butterfly’s host plant. The aim is to graze the area with cattle in the future, but because of the isolation of the site from the main grazing units, it is difficult to find a contractor who is prepared to graze the area with cattle.

Recommendations

Re-establishment of the Marsh Fritillary butterfly

Firstly, it should be emphasized that re-establishment of the Marsh Fritillary butterfly will be most successful when all conservation bodies in the area contribute to providing Marsh Fritillary habitat, thus ensuring that the amount of available habitat in the meta-population is maximized.

To enable a successful re-establishment of the Marsh Fritillary butterfly, it is recommended that:

- The former habitat in the Lows north and south and on Ashcott plot on Shapwick Heath NNR is restored, with additional habitat restoration/creation in overgrown areas and re-profiled peat excavations.
- This viable meta-population is further extended to include the former colony on Catcott Heath and Street Heath. This requires habitat restoration on Street Heath and on Catcott Heath, with further habitat restoration/creation in re-profiled peat excavations on Ham Wall NNR.

Habitat restoration experiments

To continue the initiated experiments and to further investigate the habitat restoration potential, future work should comprise:

- application of the treatments in the experimental plots for at least three consecutive years, with monitoring of the vegetation in June. The timing of the hay cuts should be June for one hay cut and June and September for two hay cuts. Furthermore, grazing on the Lows south and on Ashcott plot should ideally commence as early in spring as possible;
- reseeding half of the sown plots in a density of 5kg seeds per hectare coinciding with the natural seed fall in autumn, and subsequent monitoring of germination and establishment of Devil's-bit Scabious for at least three consecutive years;
- experiments that investigate factors that influence viability and germinability of Devil's-bit Scabious seeds;
- monitoring of the fate of the Devil's-bit Scabious transplants.

Furthermore, consideration should be given to the possibilities of protecting some patches containing Devil's-bit Scabious from grazing, in order to encourage dispersal and increase in cover of the host plant.

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References

- ADAMS, A.W. (1955). Devil's-bit Scabious Moench. *Journal of Ecology* 43 : 709-718.
- ALLABY, M. (1998). *Oxford Dictionary of Ecology*. Oxford University Press, Oxford
- ANTHES, N. (2002). Lebenszyklus, Habitatbindung und Populationsstruktur des Goldenen Scheckenfalters *Euphydryas aurinia* Rott. im Alpenvorland. Diplomarbeit, Westfälische Wilhelms-Universität Münster.
- ASHER, J., WARREN, M., FOX, R., HARDING, P., JEFFCOATE, G. & JEFFCOATE, S. (2001). *The Millenium Atlas of Butterflies in Britain and Ireland*. Oxford University Press, Oxford.
- AUSDEN, M & TREWEEK, J. (1995). Grasslands. In: *Managing habitats for conservation*. Eds: W.J. Sutherland & D.A. Hill. Cambridge University Press, Cambridge.
- AVERIS, A., AVERIS, B. BIRKS, J., HORSFIELD, O, THOMPSON, D. & YES, M. (2004). *An illustrated guide to British upland vegetation*. JNCC, Peterborough.
- BAKKER, J.P. (1989). *Nature management by Grazing and Cutting*. Kluwer Academic Publishers, Dordrecht.
- BAKKER, J.P., POSCHLOD, P. STRYKSTRA, R.J., BEKKER, R.M. & THOMPSON, K. (1996). Seed banks and seed dispersal: important topics in restoration ecology. *Acta Botanica Neerlandica* 45: 461-490.
- BAKKER, J.P. & BERENDSE, F. (1999). Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends in Ecology and Evolution* 14: 63-68.
- BAKKER, J.P., GROOTJANS, A.P., HERMY, M. & POSCHLOD, P. (2000). How to define targets for ecological restoration? *Applied Vegetation Science* 3: 3-6.
- BAKKER, J.P., ELZINGA, J.A. & DE VRIES, Y. (2002). Effects of long-term cutting in a grassland system: perspectives for restoration of plant communities on nutrient poor soils. *Applied Vegetation Science* 5: 107-120.
- BEKKER, R.M., VERWEIJ, G.L., SMITH, R.E.N., REINE, P., BAKKER, J.P. & SCHNEIDER, S. (1997). Soil seed banks in European Grasslands: does land use affect regeneration perspectives? *Journal of Applied Ecology* 34: 1293-1310.
- BARNETT, L.K. AND WARREN, M.S. (1995c). Species Action Plan Marsh Fritillary *Eurodryas aurinia*. Butterfly Conservation, Wareham.
- BERENDSE, F. & AERTS, R. (1984). Competition between *Erica tetralix* L. and Purple Moor-grass (L.) Moench as affected by the availability of nutrients. *Acta Oecologia Oecologia Plantarum* 5: 3-14.
- BERENDSE, F., BELTMAN, B., BOBBINK, R., KWANT, R. & SCHMITZ, M. (1987). Primary production and nutrient availability in wet heathland ecosystems. *Acta Oecologica Oecologia Plantarum* 8: 265-279.
- BLACKSTOCK, T.H., STEVENS, D.P., STEVENS, P.A., MOCKRIDGE, C.P. & YEO, M.J.M. (1998). Edaphic relationships among *Cirsio-Molinietum* and related wet grassland communities in lowland Wales. *Journal of Vegetation Science* 9: 431-444.

- BLACKSTOCK, T.H., RIMES, C.A., STEVENS, D.P., JEFFERSON, R.G., ROBERTSON, H.J., MACKINTOSH, J. & HOPKINS, J.J. (1999). The extent of semi-natural grassland communities in lowland England and Wales: a review of conservation surveys 1978-96. *Grass and Forage Science* 54: 1-18.
- BORSJE, H.J. (2004a). *Future fliers? Study on the re-establishment possibilities of extinct butterfly species on Shapwick Heath NNR*. Unpublished MSc-thesis, Wageningen University & Research Centre, The Netherlands.
- BORSJE, H.J. (2004b) Restoring a butterfly's habitat. Re-establishment and increase in cover of *Succisa pratensis*, host plant of the Marsh Fritillary butterfly. Unpublished MSc-thesis, Wageningen University, the Netherlands.
- BÜHLER, C. & SCHMID, B. (2001). The influence of management regime and altitude on the population structure of Devil's-bit Scabious: implications for vegetation monitoring. *Journal of applied ecology* 38: 689-698.
- BULMAN, C.R. (2001). *Conservation Biology of the Marsh Fritillary butterfly Euphydryas aurinia*. Unpublished PhD Thesis, University of Leeds, Leeds.
- BUTTERFLY CONSERVATION (2001). *Managing Damp Grassland For Marsh Fritillary – technical advice note*. Butterfly Conservation, Wareham.
- BUTTERFLY CONSERVATION (2004). *The Marsh Fritillary needs your help; a guide to managing Damp Grassland*. Butterfly Conservation, Wareham.
- CHINERY, M. (1998). *Collins guide to the butterflies of Britain and Europe*. HarperCollinsPublishers, London.
- CRITCHLEY, C.N.R, CHAMBERS, B.J., FOWBERT, J.A., SANDERSON, R.A., BHOGAL, A. & ROSE, S.C. (2002). Association between lowland grassland plant communities and soil properties. *Biological Conservation* 105: 199-215.
- CROFTS, A, & JEFFERSON. R. G (Eds) (1999). *The lowland grassland management handbook, 2nd Edition*. English Nature, Peterborough.
- DAVIES, A., DUNNETT, N.P. & KENDLE, T. (1999). The importance of transplant size and gap width in the botanical enrichment of species-poor grasslands in Britain. *Restoration Ecology* 7: 271-280.
- EBERT, G. & RENNWALD, E. (1991). *Die Schmetterlinge Baden-Württembergs, Bd. 1. Tagfalter*. Eugen Ulmer GmbH&Co, Stuttgart.
- ELLENBERG, H., WEBER, H.E., DÜLL, R., WIRTH, V., WERNER, W. & PAULIBEN, D. (1992). *Zeigerwerte von Pflanzen in Mitteleuropa, 2nd ed. Scripta Geobotanica* 18: 1-258.
- EMMET, A.M. & HEATH, J. (1990). *The moths and butterflies of Great Britain and Ireland, vol 7 Part I. Hesperiiidae to Nymphalidae*. Harley Books, Colchester.
- ENGLISH NATURE (SOMERSET TEAM). (2003). *Shapwick Heath NNR Management Plan 2003-2008*.
- FENNER, M. (1985). *Seed Ecology*. Chapman & Hall, London.

- FULLER, R.M. (1987). The changing extent and conservation interest of lowland grasslands in England and Wales: a review of grassland surveys 1930-1984. *Biological Conservation* 40: 281-300.
- GIBSON, C.W.D. & BROWN, V.K. (1991). The nature and rate of development of calcareous grassland in southern Britain. *Biological Conservation* 58: 297-316.
- GRIFFIS, K.L., MANN, S.S. & WAGNER, M.R. (2001) The suitability of butterflies as indicators of ecosystem condition: A comparison of butterfly diversity across stand treatments in northern Arizona. In: Van Riper III, C., Thomas, K.A. & Stuart, M.A, eds. *Proceedings of the 5th Biennial Conference of research on the Colorado Plateau*. U.S. Geological Survey/FRESC Report Series USGSFRESC/COPL/2001/24.
- GRIME, J.P. (1979). *Plant strategies and vegetation processes*. Wiley, Chichester.
- GRIME, J.P., HODGSON, J.G. & HUNT, R. (1988). *Comparative Plant Ecology, a functional approach to common British species*. Unwin Hyman, London.
- GRIME, J.P. (1989). Seed banks in Ecological Perspective. In: Leck, M.A., Parker & V.T. Simpson, eds. *Ecology of soil seed banks*, Eds Academic Press, New York.
- GRUBB, P.J. (1977). The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews* 52: 107-145.
- HANSKI, I. (1999). *Metapopulation Ecology*. Oxford University Press, New York.
- HANKSI, I., MOILANEN, A., PAKKALA, T. & KUUSSAARI, M. (1996). The quantitative Incidence Function Model and persistence of an endangered butterfly metapopulation. *Conservation Biology*, 10, 578-590.
- HARTEMINK, N, JONGEJANS, E. & DE KROON, H. (2004). Flexible life history responses to flower and rosette bud removal in three perennial herbs. *Oikos* 105: 159-167.
- HOBSON, R. (1997). A study of *Euphydryas aurinia* on Goss Moor National Nature Reserve in Cornwall: habitat requirements and habitat management. Unpublished MSc Thesis, University of Wales, Bangor.
- HOBSON, R., BOURN, N.A.D., WARREN, M.S. & BRERETON, T.M. (2001). *The Marsh Fritillary in England: A review of status and habitat condition*. Butterfly Conservation Report No. S01-31.
- HOOFTMAN, D.A.P. & DIEMER, M. (2002). Effects of small habitat size and isolation on the population structure of common wetland species. *Plant Biology* 4: 720-728.
- HOOFTMAN, D.A.P., VAN KLEUNEN, M. & DIEMER, M. (2003). Effects of habitat fragmentation on the fitness of two common wetland species, *Carex davalliana* and *Succisa pratensis*. *Oecologia* 134: 350-359.
- ISSELSTEIN, J., TALLOWIN, J.R.B. & SMITH, R.E.N. (2002). Factors affecting seed germination and seedling establishment of fen-meadow species. *Restoration Ecology* 10: 173-184
- JOINT NATURE CONSERVATION COMMITTEE (2004). *Common Standards Monitoring Guidance for Lowland Grassland Habitats Version February 2004*. ISSN 1743-8160 (online): 38-45. Accessed December 2004.

- KENT, M. & COKER, P. (1992). *Vegetation Description and Analysis: A practical approach*. John Wiley & Sons, Chichester.
- KIRBY, P. (2001). *Habitat management for invertebrates. A practical handbook*. RSPB, Sandy.
- KITAJIMA, K. & FENNER, M. (2000). Ecology and regeneration. In: *Seeds, the ecology of regeneration in plant communities*. 2nd edition. Ed: M. Fenner, CABI publishing, Wallingford.
- KOTOROVÁ, I. & LEPŠ, J. (1999). Comparative ecology of seedling recruitment in an oligotrophic wet meadow. *Journal of Vegetation Science* 10: 175-186.
- LEPŠ, J. & ŠMILAUER, P. (2003). *Multivariate Analysis of Ecological Data using CANOCO*. Cambridge university press, Cambridge.
- MAES, D. & VAN DYCK, H. (1999). Dagvlinders in Vlaanderen - Ecologie, verspreiding en behoud. Stichting Leefmilieu, Antwerpen.
- MATUS, G., VERHAGEN, R. BEKKER, R.M. & GROOTJANS, A.P. (2003). Restoration of the *Cirsio-dissecti-Molinietum* in The Netherlands: Can we rely on soil seed banks? *Applied Vegetation Science* 6: 73-84.
- MILLIGAN, A.L., PUTWAIN, P.D., COX, E.S., GHORBANI, J., LE DUC, M.G. & MARSS, R.H. (2004). Developing an integrated land management strategy for the restoration of moorland vegetation on Purple Moor-grass-dominated vegetation for conservation purposes in upland Britain. *Biological Conservation* 119: 371-385.
- MINISTRY OF AGRICULTURE, FISHERIES AND FOOD (1986). *The Analysis of Agricultural Materials*, third edition. Reference Book 427, HMSO, London.
- NEW, T.R., PYLE, R.M., THOMAS, J.A., THOMAS, C.D. & HAMMOND, P.C. (1995). Butterfly conservation management. *Annual reviews of Entomology* 40: 57-83.
- OOSTERMEIJER, J.G.B. & VAN SWAAY, C.A.M. (1998). The relationship between butterflies and environmental indicator values: a tool for conservation in a changing landscape. *Biological Conservation* 86: 271-280.
- PORTER, K. (1981). The population dynamics of small colonies of the butterfly *Euphydryas aurinia*. Ph.D. thesis, University of Oxford.
- PORTER, K. (1982). Basking behaviour in larvae of the butterfly *Euphydryas aurinia*. *Oikos* 38: 308-312.
- PORTER, K. (1983) Multivoltinism in *Apanteles bignellii* and the influence of weather on synchronisation with its host *Euphydryas aurinia*. *Entomol. exp. & appl.* 34: 155-162.
- PROBERT, R.J. (1992). The role of temperature in germination ecophysiology. In: FENNER, M, ed. *Seeds, the Ecology of Regeneration in plant communities*. CAB International Wallingford.
- PROSSER, M.V. AND WALLACE, H.I. (2000). Shapwick Heath, Ashcott Heath and Seventy Acres NVC survey 1999. Ecological surveys, Bangor.
- PYWELL, R.F., BULLOCK, J.M., HOPKINS, A., WALKER, K.J., SPARKS, T.H., BURKE, M. JW. & PEEL, S. (2002). Restoration of species-rich grassland on arable land: assessing the limiting processes using a multi-site experiment. *Journal of Applied Ecology* 39: 294-309

- PYWELL, R.F., BULLOCK, J.M. ROY, D.B., WARMAN, L., WALKER, K.J. & ROTHERY, P. (2003). Plant traits as predictors of performance in ecological restoration. *Journal of Applied ecology* 40: 65-77.
- RODWELL, J.S. ed. (1991). *British Plant Communities. Volume 2. Mires and heath*. Cambridge University Press, Cambridge.
- RODWELL, J.S. ed. (1992). *British Plant Communities. Volume 3. Grasslands and Montane communities*. Cambridge University Press, Cambridge.
- SCHAFFERS, A.P., SÝKORA, K.V. (2000). Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction: a comparison with field measurements. *Journal of Vegetation Science* 11: 225-244.
- SHEPPARD, D. (1999). Grassland management for invertebrates. In: *The Lowland Grassland handbook 2nd edition*. Eds: Crofts, A. & Jefferson, R.G. English Nature, Peterborough.
- SIMPSON, R.L., LECK, M.A. & PARKER, T. (1989). Seed Banks: General Concepts and Methodological Issues. In: Leck, M.A., Parker & V.T. Simpson, eds. *Ecology of soil seed banks*, Eds Academic Press, New York.
- SOONS, M.B. & HEIL, G.W. (2002). Reduced colonization capacity in fragmented populations of wind-dispersed grassland forbs. *Journal of Ecology* 90: 1033-1043.
- SOULÉ, M.E. (1987) *Viable populations for Conservation*. Cambridge University Press, London.
- STEWART, K.E.J., BOURN, N.A.D. & THOMAS, J.A. (2001). An evaluation of three quick methods commonly used to assess sward height in ecology. *Journal of Applied Ecology* 38: 1148-1154.
- THOMAS, C.D. (1994). Extinction, colonization and metapopulations: environmental tracking by rare species. *Conservation Biology* 8: 373-378.
- THOMAS, C.D. (1995). Ecology and conservation of butterfly metapopulations in the fragmented British landscape. In: PULLIN, A.S., ed. *Ecology and Conservation of Butterflies*, p 46-63. Chapman & Hall, London.
- THOMAS, C.D., THOMAS, J.A. & WARREN, M.S. (1992). Distributions of occupied and vacant butterfly habitats in fragmented landscapes. *Oecologia* 92: 563-567.
- THOMAS, J.A. & LEWINGTON, R. (1991). *The butterflies of Britain and Ireland*. Dorling Kindersley, London.
- THOMPSON, K. (2000). The Functional Ecology of Soil Seed Banks. In: FENNER, M., ed. *Seeds, the ecology of regeneration in plant communities. 2nd edition*. CABI publishing, Wallingford.
- VERGEER, P., RENGELINK, R., COPAL, A. & OUBURG, N.J. (2003). The interacting effects of genetic variation, habitat quality and population size on performance of Devil's-bit Scabious. *Journal of Ecology* 91: 18-26.
- VERGEER, P., SONDEREN, E. & OUBURG, N.J. (2004). Introduction strategies put to the test: local adaption versus heterosis. *Conservation Biology* 8: 812-821.
- WAHLBERG, N., MOILANEN, A. & HANSKI, I. (1996). Predicting the occurrence of endangered species in fragmented landscapes. *Science*, 273, 1536-1538.

WAHLBERG, N., KLEMETTI, T. & HANSKI, I. (2002). Dynamic populations in a dynamic landscape: the metapopulation structure of the Marsh Fritillary butterfly. *Ecography* 25: 224-232.

WAMELINK, G.W.W., JOOSTEN, V., VAN DOBBEN, H.F. & BERENDSE, F. (2002). Validity of Ellenberg indicator values judged from physico-chemical field measurements. *Journal of Vegetation Science* 13: 269-278.

WARREN, M.S. (1994). The UK status and suspected metapopulation structure of a threatened European butterfly, the Marsh Fritillary *Eurodryas aurinia*. *Biological Conservation* 67: 239-249.

WARREN, J., CHRISTAL, A. & WILSON, F. (2002). Effects of sowing and management on vegetation succession during grassland habitat restoration. *Agriculture, Ecosystems and Environment* 93: 393-402.

WEEDA, E.J., WESTRA, R., WESTRA, CH. & WESTRA, T. (2003) *Nederlandse Oecologische Flora. Wilde planten en hun relaties, deel 3 en 5*. KNNV uitgeverij, Utrecht.

WYNHOFF, I., VAN SWAAY, C. AND VAN DER MADE, J. (1999). *Veldgids Dagvlinders*. Stichting Uitgeverij KNNV, Utrecht.

Appendix I - SSSI's and PSA targets

Sites of Special Scientific Interest (SSSI's) are England's most important areas for wildlife and geology. There are 4,112 SSSI's covering an area of more than a million hectares. The sites range from small areas that protect populations of a single species to large expanses of upland moorland or coastal mudflats and marshes.

It is the responsibility of the English Government's nature conservation agency, English Nature, to select and protect SSSI's. The Government's environmental responsibilities are now represented in a broader set of Public Service Agreement (PSA) targets, monitored by the Treasury. The condition of the SSSI land in England has been assessed by English Nature, using categories agreed across England, Scotland, Wales, and Northern Ireland through the Joint Nature Conservation Committee. There are six reportable condition categories: favourable; unfavourable recovering; unfavourable no change; unfavourable declining; part destroyed and destroyed. One of the PSA targets is that 95% of SSSI land should be in "favourable" or "unfavourable recovering" condition by 2010. In essence, if an SSSI is in favourable condition or recovering condition, it means that the habitats and species are in a healthy state, and are being conserved for the future by appropriate management. If an SSSI is assessed as unfavourable, this means there is a current lack of appropriate management, or that there are damaging impacts that need to be addressed. A statement of Common standards for Monitoring has been published by the Joint Nature Conservation Committee (JNCC) in 1988. This statement gives guidance on setting and assessing conservation objectives, and the designation of sites in one of the condition categories.

Source: English Nature(2003). England's best wildlife & geological sites. The condition of Sites of Special Scientific Interest in England in 2003. English Nature, Peterborough.

For more information, see the following websites:

SSSI's and PSA targets: www.english-nature.org.uk/special/SSSi/
Common Standards Monitoring: www.jncc.gov.uk/csm/default.htm

Appendix III – Overview species recorded in experimental blocks

Number of quadrats recorded in each block =64, #Qs = number of quadrats per block in which the species is recorded, min = minimum cover (%) recorded in a quadrat, max = maximum cover (%) recorded in a quadrat and mean = mean cover (%) recorded over all 64 quadrats.

species	block 1				block 2				block 3				block 4			
	# Qs	min	max	mean	# Qs	min	max	mean	# Qs	min	max	mean	# Qs	min	max	mean
Tormentil	62	2	50	14.01	60	1	30	6	52	1	50	5.67	64	1	40	14.34
Purple Moor-grass	62	30	90	66.41	64	40	85	67.53	64	10	90	61.1	64	20	80	56.92
Bog Myrtle	45	2	30	5.17	64	5	30	14.92	62	4	40	14.72	63	1	50	14.84
Creeping Bent	22	1	3	0.625	5	1	4	0.17	16	1	40	1.59	48	1	40	4.97
Heath Wood-rush	61	1	7	2.53	62	1	7	2.08	59	1	5	1.5	62	1	3	1.61
Sweet Vernal Grass	60	1	10	2.58	51	1	4	1.31	61	1	6	1.83	58	1	10	1.91
Yorkshire Fog	17	1	5	0.64									26	1	5	0.83
Downy Birch	5	1	4	0.17	18	1	8	0.88	23	1	6	0.875	14	1	8	0.45
Carnation Sedge	11	1	4	0.375					5	1	10	0.36	12	1	4	0.36
Pill Sedge	4	1	2	0.08	5	1	10	0.44	1	1	4	0.06	3	1	3	0.09
Common Sedge	5	1	2	0.11	2	1	1	0.03	2	1	1	0.03				
Yellow Sedge																
Soft Rush	2	1	3	0.06	1	1	3	0.05					2	1	3	0.06
Sharp-flowered rush					4	3	35	1.14	3	3	60	1.47	7	1	3	0.17
Red Fescue	1	1	2	0.03									1	1	1	0.02
Annual Meadow-grass									1	1	1	0.02				
Bramble spp	3	1	3	0.08	3	1	2	0.06	4	2	9	0.23	2	1	1	0.03
Creeping Willow	1	1	5	0.08												
Sessile Oak	1	1	1	0.02					2	1	1	0.03				
Common Sorrel	12	1	4	0.36												
Catsear	7	1	2	0.17	12	1	5	0.5	14	1	3	0.38	11	1	5	0.3
Greater Birdsfoot Trefoil	1	1	3	0.05									1	1	2	0.03
Common Mouse-ear	1	1	1	0.016	1	1	1	0.02					3	1	1	0.05
Lesser Stitchwort													1	1	1	0.02
Heath Milkwort	1	1	1	0.016									1	1	1	0.02
Sheep's Sorrel	3	3	10	0.3									4	2	3	0.14
Devil's-bit Scabious					3	1	5	0.13	6	1	30	0.89	17	1	11	1.03
Cross-leaved Heath									4	1	2	0.08	3	1	2	0.06
Lousewort					2	1	1	0.03	2	1	1	0.03	1	1	1	0.02
Bog Asphodel					2	2	2	0.06	2	2	2	0.06				
Male Fern					2	1	1	0.03	2	1	1	0.03				
Knotgrass																

Appendix IV – Overview of emerged species during seed bank study

= Number of seedlings, mean = mean number of seedlings over the 5 samples per block.

Species	Block 1		Block 2		Block 3		Block 4		The Lows north		Ashcott plot	
	#	mean	#	mean	#	mean	#	mean	#	mean	#	mean
Tormentil	4	2	3	2	2	1.8	4	1.6	3	1.2	5	2.6
Marsh Pennywort	1	0.2	1	0.3	0	0	1	0.2	1	0.2	3	0.6
Willowherb spp	3	0.6	1	1.75	3	2	2	0.4	0	0	2	0.6
Marsh Valerian	1	0.2	0	0	0	0	0	0	0	0	0	0
Soft Rush	4	4.2	4	11	4	9.2	4	7	5	11.8	5	9.4
Bulbous Rush	4	2.2	4	8.0	4	9.4	4	1.6	4	5.0	4	2.6
Sharp-flowered Rush	0	0	0	0	0	0	2	0.6	0	0	0	0
Creeping Bent	2	0.4	2	1.5	3	2.4	2	1.0	2	0.6	4	2.0
Common Nettle	1	0.2	0	0	0	0	0	0	0	0	0	0
Common Sorrel	0	0	2	1.0	3	0.8	1	0.2	0	0	2	0.4
Lesser Spearwort	0	0	1	0.25	0	0	0	0	0	0	0	0
Greater Birdsfoot Trefoil	0	0	0	0	0	0	1	0.2	0	0	0	0
Bramble spp	0	0	0	0	0	0	0	0	1	0.2	0	0
Downy Birch	0	0	0	0	0	0	0	0	1	0.2	0	0
Carex demissa	0	0	0	0	0	0	0	0	3	3.8	4	9.8
Heath Wood-rush	0	0	0	0	0	0	0	0	1	1.0	0	0
Red Fescue	0	0	0	0	0	0	0	0	0	0	1	0.8
Bog Pimpernel	0	0	0	0	0	0	0	0	0	0	2	1.2
Ivy-leaved Bellflower	1	0.2	0	0	0	0	0	0	0	0	0	0



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Front cover photographs:

Top left: Using a home-made moth trap.

Peter Wakely/English Nature 17,396

Middle left: Co₂ experiment at Roudsea Wood and Mosses NNR, Lancashire.

Peter Wakely/English Nature 21,792

Bottom left: Radio tracking a hare on Pawlett Hams, Somerset.

Paul Glendell/English Nature 23,020

Main: Identifying moths caught in a moth trap at Ham Wall NNR, Somerset.

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