Vegetation survey at Devil's Dyke, Cambridgeshire

Introduction

There are four main linear earthworks or dykes in Cambridgeshire. The most impressive earthwork is Devil's Dyke with its 12 km length that connects Reach village with Wood Ditton (Figure 1.). Its precise purpose is still unknown. In 1850 when quarrying of the coprolites for superphosphate the fields were dug up to 7 m to expose greensand and the phosphatic nodules were separated from the clayey matrix by washing (Avery, 1990). This created a 'slurry' topsoil which has a prismatic structure. Devil's Dyke was excavated in 1923/1924 by Sir Cyril Fox who revealed that the dyke was built upon ground covered by Roman pottery from the 3rd century. It lies on chalk and is regarded as a Site for Special Scientific Interest (SSSI) supporting a unique species-rich habitat. It used to be grazed by sheep, but its management has changed to mowing. Chalk grassland is a uniform habitat, abiotic factors affect the ecology of plants and animals in a relatively equal way. In this vegetation survey we assessed the role of biotic (plant composition) and abiotic (slope aspect, soil temperature, soil moisture content) factors which influence the composition of chalk grassland vegetation. Ellenberg indicator values were considered and literature on soil nitrogen influence, habitat management and biotic factors was reviewed.

Figure 1. Devil's Dyke is a fragmented earthwork surrounded by agricultural fields. Use of inorganic fertilizers on the fields may have an indirect effect of the Dyke's soil composition (Picture available at: https://billboyheritagesurvey.wordpress.com/2014/03/14/walls-of-the-kingdom/).

Study site and methods

Devil's Dyke is located in east Cambridgeshire (national grid reference: TL 568660 to TL 653584). There are 16 gaps through the Dyke. Groups of 5-6 students carried out vegetation surveys on approximately 21 m long transects. A transect run across the two tops of the opposite slopes (Figure 2). Soil temperatures and samples were collected from the top and bottom of the slopes and in the middle of the Dyke. Species were recorded on the slopes in 25 cm intervals touching a metering tape. Species were recorded in the middle section of the dyke by a pin frame. Soil samples were weighted (100 g) and dried at 105° C, pH was measured, and the soil moisture was calculated.

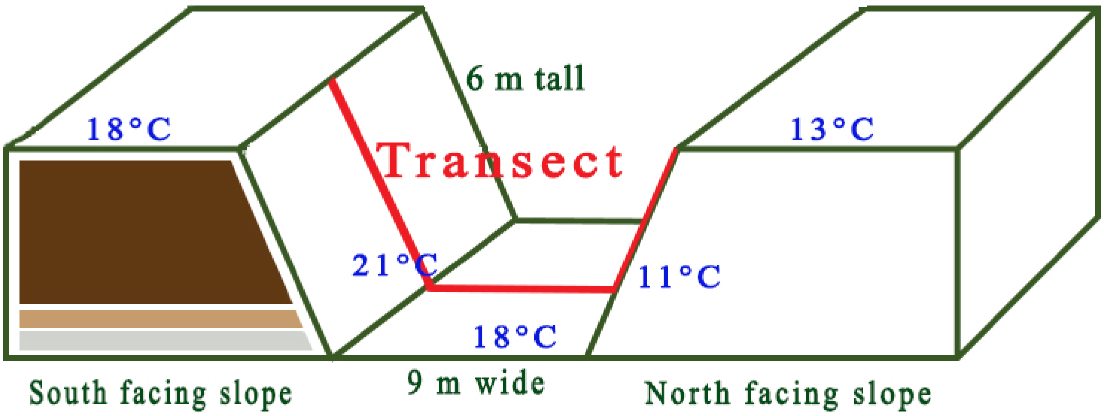

Figure 2. The line transects (red line) ran across the Dyke while the pin frame transects only ran in the middle section of the Dyke. Temperatures showed a significant difference between the two slopes. Soil sampling locations were the same as the soil temperature measurement locations.

Results

The soil temperatures were as expected, the soil on the north facing slope was much colder (11-13°C) than on the south facing slope (18-21°C). The steep slopes had a gradient of 51 - 57.7% (27-30°). The soil samples (n = 5) were slightly alkaline (pH = 7.12-7.81), the highest pH was recorded on the top of the north-facing slope (Table 1).

Table 1. Properties of five soil samples. By dividing the dry weight by the loss of weight during the drying process the soil moisture was calculated.

Slope	Slope area	Soil temperature	Dry weight (g)	Loss of weight during drying(g)	%Soil Moisture	pH
N-facing	Top	13°C	71.58	28.42	39.70382788	7.81
N-facing	Bottom	11°C	63.86	36.14	56.59254619	7.51
Middle		18°C	69.93	30.07	43.000143	7.54
S-facing	Top	18°C	70.08	29.92	42.69406393	7.63
S-facing	Bottom	21°C	62.65	37.35	59.61691939	7.12

Soil dry weights ranged between 62.65 g to 71.58 g and the soil moisture ranged from 39.7% to 59.61%. In total 14 species were recorded, and 3 plant individuals were identified to family level (Table 2). The vegetation composition differed significantly between the north and south-facing slopes (Figure 3) but their species richness was similar. Pin frame transect's vegetation mostly consisted of grasses (Poaceae) (Figure 4).

Table 2. Species recorded in the line and pin frame transects. Most species were from the daisy family Asteraceae.

Common name	Latin name	Family
Biting stonecrop	*Sedum acre*	Crassulaceae
Chalk milkwort	*Polygala calcarea*	Polygalaceae
Devil's bit scabious	*Succisa pratensis*	Dipsacaceae
Dewberry	*Rubus caesius*	Rosaceae
Dwarf thistle	*Cirsium acaule*	Asteraceae (Compositae)
Field scabious	*Knautia arvensis*	Dipsacaceae
Horseshoe vetch	*Hippocrepis comosa*	Fabaceae
Ivy	*Hedera helix*	Araliaceae
Montagne's Cylinder-moss	*Entodon concinnus*	Entodontaceae
Mouse-ear hawkweed	*Pilosella officinarum*	Asteraceae (Compositae)
Ribwort plantain	*Plantago lanceolata*	Plantaginaceae
Selfheal	*Prunella vulgaris*	Lamiaceae
Smooth hawk's beard	*Crepis capillaris*	Asteraceae (Compositae)
Meadow hawkweed	*Hieracium caespitosum*	Asteraceae (Compositae)

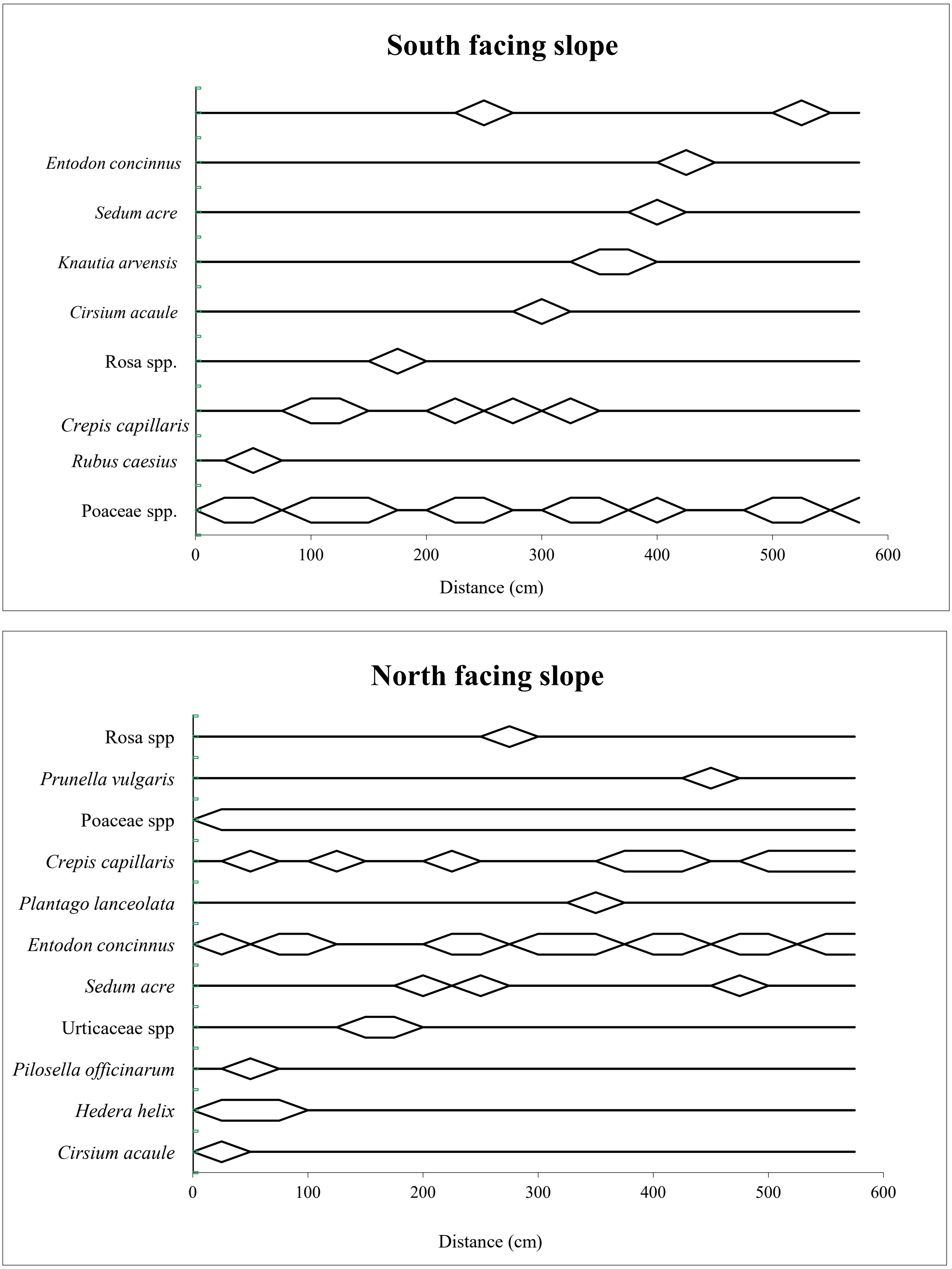

Figure 3. Kite diagrams showing the different vegetation compositions on the slopes. In a chalk sward approximately 35% of the species of herbaceous plants have rosette growth habit (e.g. *Hieraceum polisella, Plantago lanceolata)*. The leaves close to the ground are more protected from the wind, grazing and trampling and with their large leaf surface they can photosynthesize efficiently. The mat growth habits is efficient in eliminating competition (i.e. *Hippocrepis comosa)*. Specialised water storage parts allow *Sedum acre* to cope with dry habitat. Other plants have long roots (i.e. *Scabiosa columbaria)* which allows the taproot to penetrate deep into the soil.

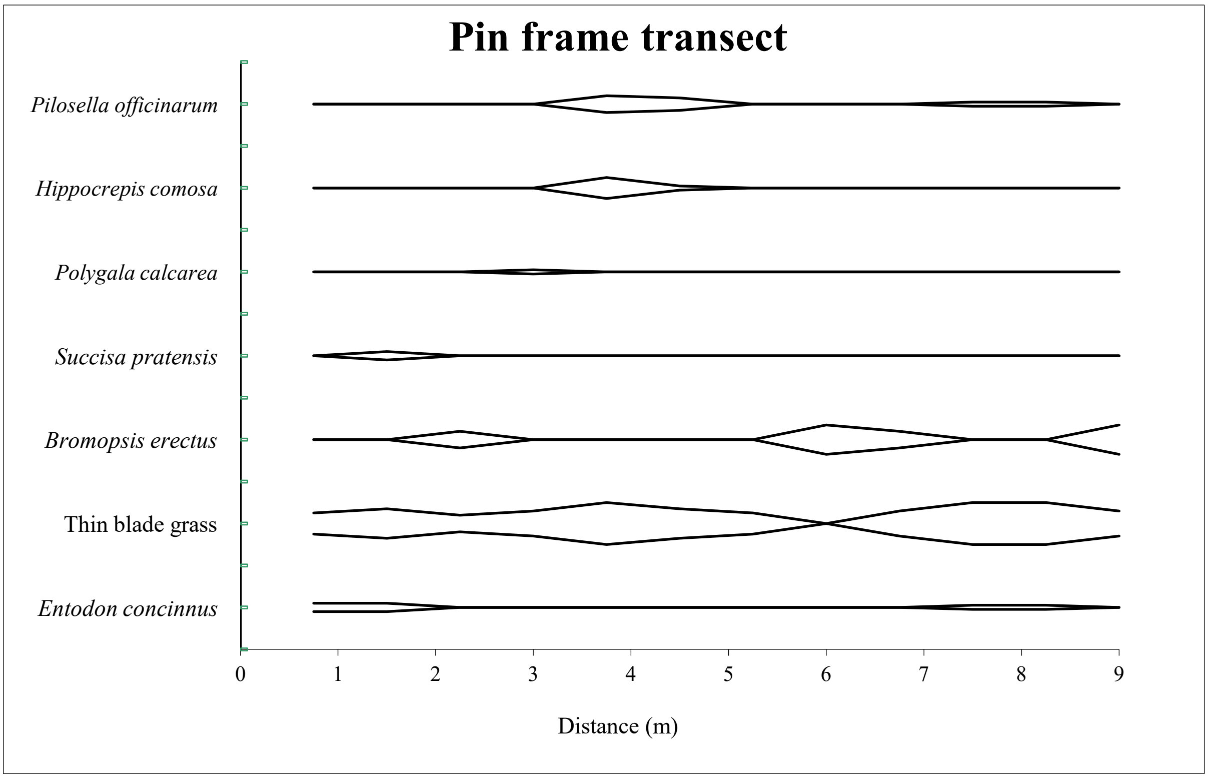

Figure 4. Species recorded in the pin frame transect. The low number of different forbs can be explained by the high amount of trampling (biotic factor) in the middle section of the Dyke.

Discussion

Abiotic factors

Soil pH (pH = -log (H^+)) affects numerous soil chemical reactions, processes and microorganism activity. pH influences nutrient availability (Pietri et al., 2008; Kemmitt et al., 2005; Kemmitt et al., 2006), solubility of metals (Firestone et al., 1983; Flis et al., 1993), and carbon availability (Andersson et al., 2000). Our samples were relatively constant in terms of pH values (pH = 7.12-7.81, Figure 5). The rate of weathering in chalk soil is reduced as a result of relatively high pH because of the high calcium carbonate levels. The largest soil temperature difference was between the bottom of the north-facing slope (11°C) and the bottom of the south-facing slope (21°C). Temperature is one of the most limiting factors of vegetation. It is influenced by the solar radiation (Figure 6), causing differences in vegetation assemblages (Figure 3) and microbial activities (Rousk et al., 2009; Pietikäinen et al., 2005). The soil at Devil's Dyke is well aerated which causes the soil to warm up quicker than a soil with high water content. The soil moisture contents were higher compared to Chappell et al. (1971) where soil samples were from 0-25 mm and 25-50 mm depths and collected in Hampshire. Their results varied between 20.5-38.8% which is higher than our measurements (39.7-59.6%). Our sampling was after a week of heavy precipitation which may be the reason for our high values.

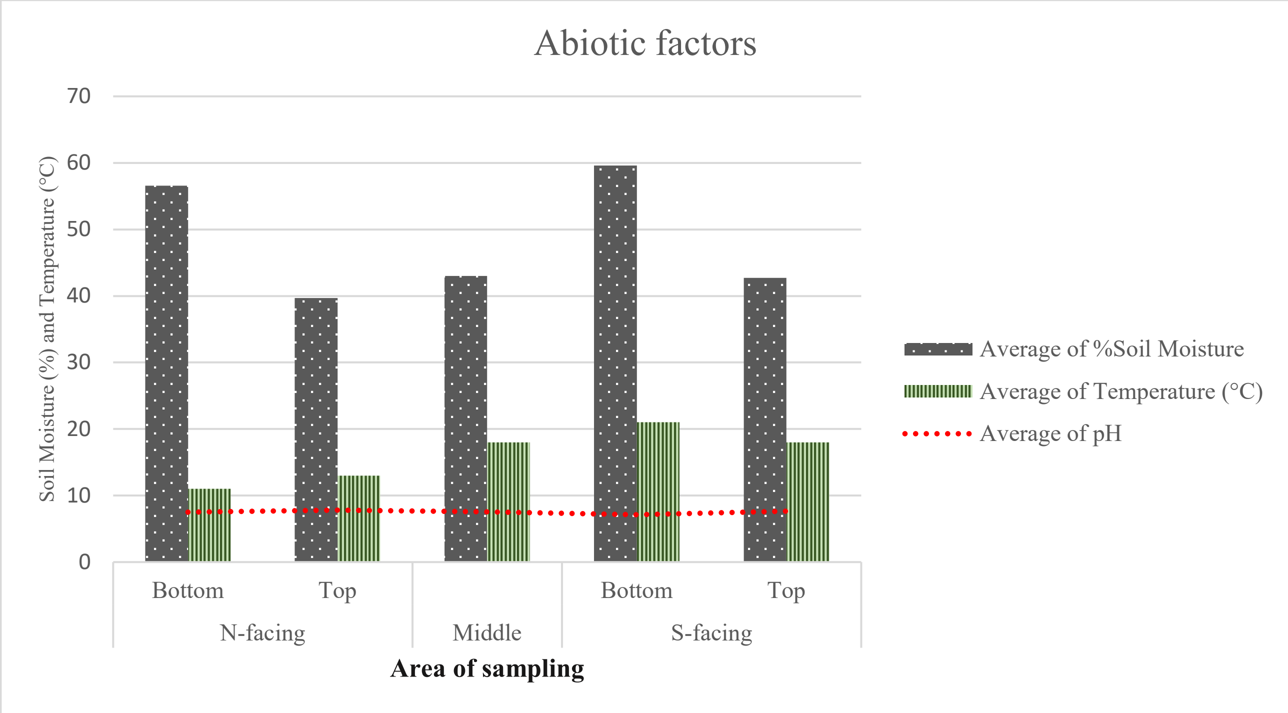

Figure 5. Result of abiotic factors. The pH values did not vary greatly between the different areas of sampling. For soil moisture (%), there is no significant difference between the different slopes but there is a clear difference between the top and bottom measurements. Temperature of the south-facing slopes were higher as expected cause by solar radiation (see Figure 6).

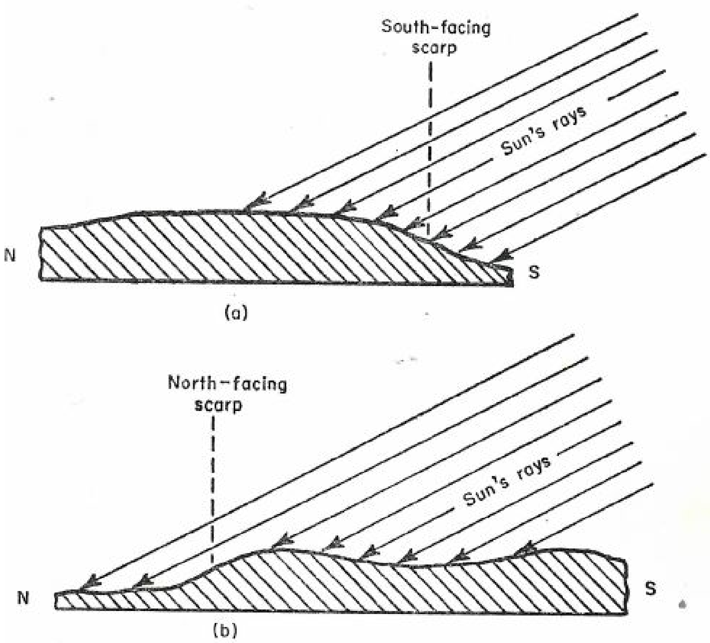

Figure 6. The aspect of a soil affects the amount of solar radiation and therefore its temperature. South-facing slopes receive the sun rays directly while the north-facing slopes receive sun rays at a different angle which causes them to be colder (Sankey, 1966).

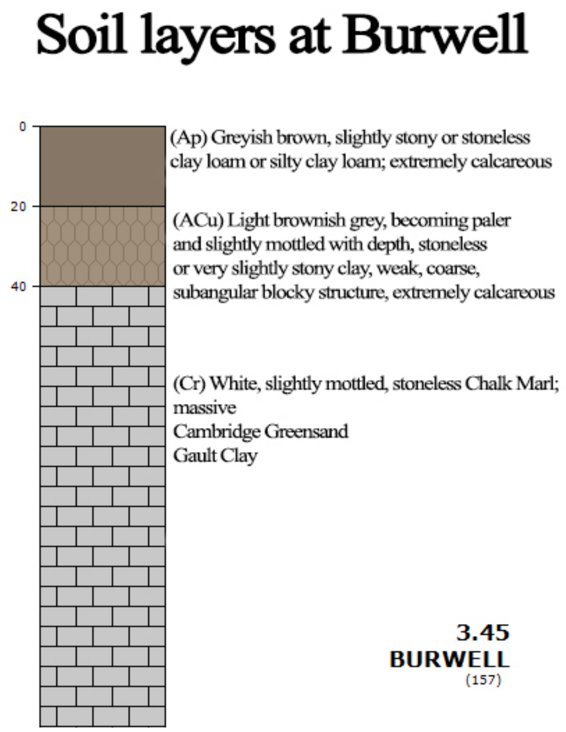

Figure 7. Illustration of the soil layers at Devil's Dyke. The top 20cm is the most calcareous layer and the C horizon is gault clay.

The soil moisture contents were the highest at the bottom of the slopes which was expected as the topsoil is a well-drained layer (Figure 7). The moisture content of the south-facing slopes was 6-8% higher than on the north-facing slopes which is the opposite of Bennie et al. (2006) findings. Their volumetric soil moisture content was 10-20% lower on the south-facing slopes than on the north-facing slopes. Gay et al. (1982) showed how the perennial and biennial plants' nitrogen, phosphorus and potassium concentrations fluctuate seasonally at Devil's Dyke and has an effect on the mycorrhiza density. Soil nitrogen level is another important abiotic factor although different studies have sometimes controversial results (Table 3).

Table 3. Studies have shown that the Ellenberg N values have been increasing in the last decades. The effect of nitrogen in grasslands is complex and hard to do research and eliminating other abiotic and biotic factors. Species richness reduction has been shown in most of the studies. This short review considers what negative effect nitrogen may cause and what is the authors' suggestion.

Abiotic factor	Where	Negative effect	Suggestion	Reference
- Atmospheric N deposition	UK	- Long-term, chronic N reduces plant species richness - Linear correlation with inorganic N deposition	-N deposition alters topsoil pH - Soil pH needs decades to recover	Stevens et al., 2004
- N deposition - Mean temperature	UK	- Species richness decreases in acid grasslands and heathlands	- Species richness in chalk grassland is not affected by N deposition - Climatic effect included - Species richness reduction is not caused by competitive exclusion but by the fast-growing dominant species	Maskell et al., 2010
- N deposition	EU	- Reduction of species richness	- Enhanced growth of "tall" grasses and stress-tolerant competitor species caused by increased N levels	Bobbink et al., 1998
- N deposition - P levels	UK	- Reduction of species diversity - Decrease of characteristic calcareous grass species and rare species	- No negative effect on species richness - P limitation may be the reason for the difference between acid grassland/ heathland and chalk grassland response	Van den Berg et al., 2011
- N levels - Climate	UK	- Reduction of stress-tolerant species - Increase in Ellenberg N values	- Shift toward mesotrophic grassland communities	Bennie et al., 2006
- N availability	BE, NL	- Decline in α-, γ-diversity because of N increase	- Removal of above-ground phytomass	Williems et al., 1993; Jacquemyn et al., 2003

Ellenberg indicator values

A quantitative approach was developed by Ellenberg (1988) which consisted of abiotic values to describe the plant's light (L), moisture (F), reaction (R, pH), nitrogen (N) and salt (S) preferences and limits. Considering the species that were recorded in our vegetation survey (Table 4), their indicator values are relatively similar to each other. They are generally light-loving plants, their F values suggest the variation of dry-site indicators to moist-site indicators. *Succisa pratensis* and *Rubus caesius* were recorded near the bottom of the south-facing slope, the area had the highest soil moisture content. Their R values show a higher variation in their soil pH than our soil measures indicated. The plants' N values suggest infertile to intermediate fertile soils.

Table 4. Ellenberg indicator values for the recorded species at Devil's Dyke. These values are debated to be affected by other factors. Significant effects of radiation and slope aspect were found for Ellenberg values where L, N and F scores are lower for steep and south-facing aspects (Bennie et al., 2006; Amezaga et al., 2004; Gelbard et al., 2003). *R. caesius* and *H. helix* differ from most of the other species N values (N = 6). They are all missing from saline environments (S values), *S. acre* is the only species that could persist in the presence of salt.

Name	LO*	L	FO	F	RO	R	NO	N	SO	S
*Bromopsis erecta***	8	7	3	4	8	8	3	3	0	0
Cirsium acaule	9	9	3	4	8	8	2	3	0	0
Crepis capillaris	7	7	5	4	6	7	4	4	0	0
Hedera helix	4	4	5	5	●	7	●	6	0	0
Hippocrepis comosa	7	8	3	3	7	8	2	2	0	0
Knautia arvensis	7	7	4	3	●	8	4	4	0	0
Pilosella officinarum	7	8	4	4	●	7	2	2	0	0
Plantago lanceolata	6	7	●	5	●	6	●	4	0	0
Polygala calcarea	7	7	3	3	9	8	2	2	0	0
Prunella vulgaris	7	7	5	5	7	6	●	4	0	0
Rubus caesius	6	7	●	7	8	7	7	6	0	0
Sedum acre	8	8	2	2	●	7	1	2	1	1
Succisa pratensis	7	7	7	7	●	5	2	2	0	0

*LO: Light (original)
L: Light (final)
FO: Moisture (original)
F: Moisture (final)
RO: Reaction (original)
R: Reaction (final)
NO: Nitrogen (original)
N: Nitrogen (final)
SO: Salt (original)
S: Salt (final)

** Green: middle section of the dyke
Blue: north-facing slope
Orange: south-facing
White: both slopes

Biotic factors

Soil pH affects biomass composition of fungi and bacteria greatly (Rousk et al., 2009). The soil microbial community (especially mycorrhiza community) is a crucial biotic factor, affecting nutrient transformations (decomposition) and the regeneration of minerals which affects plant productivity (Table 5, Figure 8). Turf-compatible, short-lived (annuals, biennials and pauciennials) plants are able to regenerate in a continuous turf but the incompatible species require a gap (Grubb, 1976). The latter species are greatly affected by root competition from matrix-forming perennials (Fenner, 1978). Competition for pollinators is another biotic factor that has been shown at Devil's Dyke by Lack (1982). He suggested that selection against interspecific pollen transfer led to flower specializations and an earlier flowering group of plants. Anthropogenic management is also an important biotic factor to consider (Table 6). Our vegetation survey showed the different vegetation composition between the north-facing and south-facing slopes, the varying abiotic factors and hypothesized biotic factors. Long-term monitoring of Devil's Dyke will be able to provide data to compare its management's effects (mowing *versus* grazing).

Table 5. Studying biotic factors requires methods to eliminate abiotic factors' influence on the studied biotic factors. These are strongly connected and often hard to distinguish. The following table summarizes research done on biotic factors in chalk grasslands. It is important to consider plant-microbe-insect interactions and not only plant-microbe or plant-insect linkages. Mycorrhizas are fungi that have a symbiotic association with the plant roots and has been shown to promote aphid presence on *Plantago lanceolata* (Gange et al., 1999).

Biotic factor	Effect	Reference
Invasion	Negative	Crawley et al., 1999; Belnap and Phillips, 2001; Davis et al., 2001
Mycorrhiza	Positive	Swaty et al., 1998
Butterfly communities	Positive	Krauss et al., 2003; Van Swaay, 2002
Species turnover	x	Chase et al., 2000; Hunter and Price, 1992
Gap colonization and grazing	Positive	Bullock et al., 1995; Helden and Dittrich, 2016
Herbivory	Negative	Bakker and Olff, 2003; Van der Putten et al., 2001
Invertebrate diversity	Positive	Woodcock et al., 2005; Littlewood et al., 2012; Siemann, 1998
Pathogens	Negative	Van der Putten et al., 2001
Fragmentation	Negative	Eriksson et al., 2002
Succession	Negative	Hobbs and Mooney, 1986; Schippers at al., 1999

Table 6. Management and restoration are anthropogenic factors influencing both abiotic (e.g. soil composition) and biotic (e.g. pollination) factors in chalk grassland communities. Most papers suggest further studies since the ideal management is still unknown. The main management types are mowing, grazing or burning.

Topic	Where	Biotic (B)/ abiotic factor (A)	Negative effect	Suggestion	Reference
Management	GE, NL, UK	- Fragmentation (B) - Species interactions (B)	- Fragmentation - Mowing -Gaps in our knowledge - Restricted information availability - Limited international cooperation	- Extensive grazing -Farmer compensation - Further studies in: plant-herbivory and plant-pollinator interaction - Integrated conservation	Wallis De Vries et al., 2002
Restoration and Management	NL	- History of land use (B)	- Land abandonment - Domination by *Brachypodium pinnatum* - *Bromus erectus* in UK, GE, BE	- Mowing & hay removal - Follow 4 stages of restoration - Further studies in sheep grazing	Willems, 2001
Management	GE	- 50 year long management (B)	- 5 out 6 regions showed negative trends in species richness - Nitrogen input - Grassland eutrophication	- 1 region showed increased species richness - More long-term studies - More arthropod studies	Wesche et al., 2012
Management and Soil Nutrients	UK	- Environmentally Sensitive Areas Scheme (B) -Nutrients (A)	- Use of inorganic fertilizers - High soil P concentrations - Scheme does not show improvement after intensive farming	- Reduction of fertilizers - Sod removal	Critchley et al., 2001
Restoration and Management	EU	- Fragmentation (B) - Pollination (B)	- Fragmentation - Loss of habitat - Reduction of patch area - *B. pinnatum* - Mowing	- Grazing by sheep (seed dispersal) - Further arthropod and long-term studies	Butaye et al., 2005
Management	UK	- α-, β-,γ- diversity changes (B)	- Taxonomic homogenization - Succession - Nitrogen (?)	- Nitrogen is not accountable for declining species richness - Reduction of species richness because of increased competitive exclusion - Impact of management > N deposition - Reduction of possibilities for colonization by mesotrophic species	Newton et al., 2012

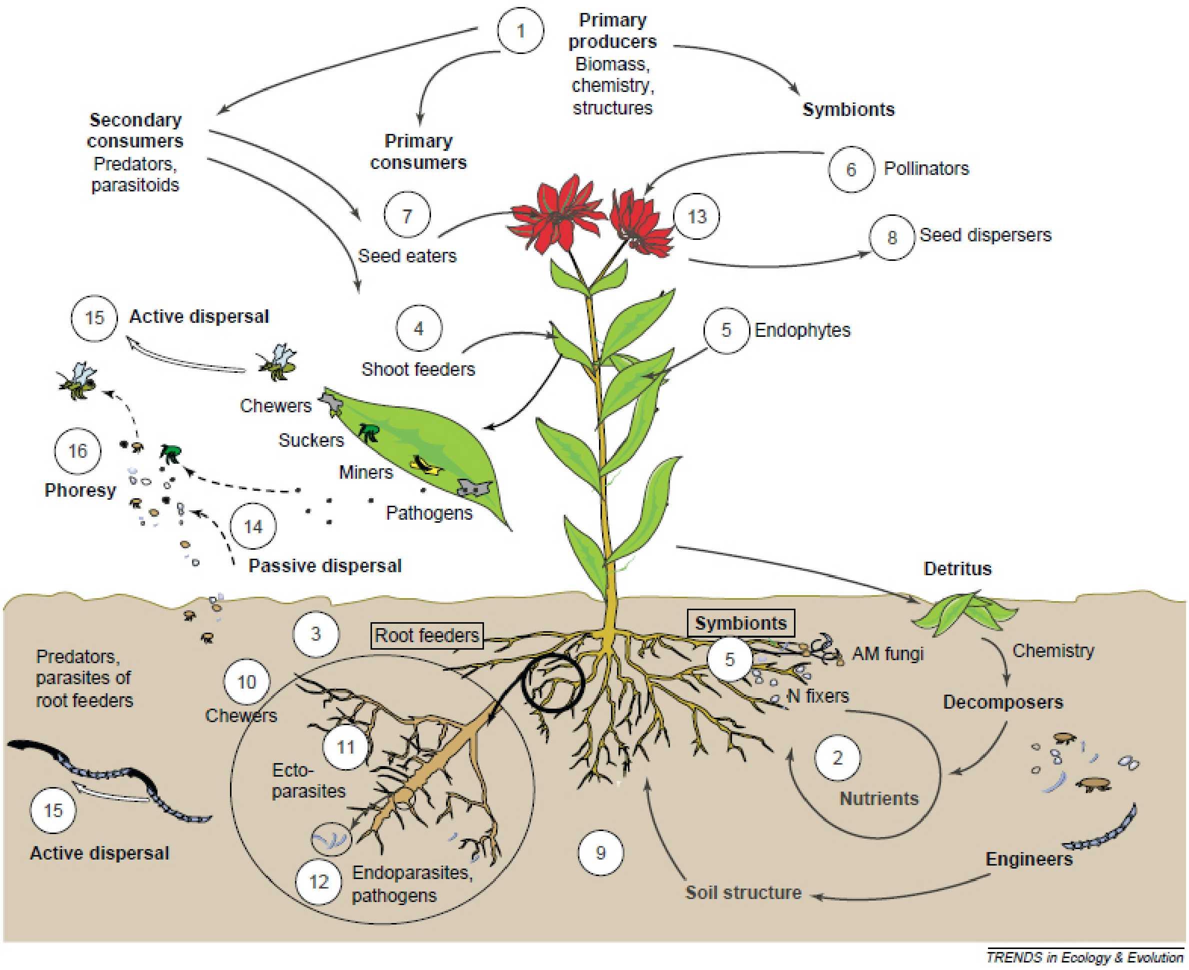

Figure 8. Aboveground and belowground species linkages play a crucial role in ecosystems (De Deyn et al., 2005). The chalk soil is abundant in Ca^{2+}, K^{+} and Mg^{+} ions which makes it a good base which provides a suitable habitat for nitrifying bacteria. It has been shown that the mycorrhiza of the matrix-forming perennials play a key role in the turf-incompatible species (Francis and Read, 1994) in chalk grasslands. Loranger et al. (2012) assessed 105 physiological, morphological and phenological traits of 51 grassland species to see the differences in rates of herbivory. Leaf lignin concentration seems to reduce coleopteran herbivores. Biodiversity of this ecosystem is driven by bottom-up (competition for resources: ④⑥⑦) and top-down (control by pathogens or predators: ③④⑩⑪⑫) effects and symbiosis (⑤).

Final word count: 1082

References

Amezaga, I., Mendarte, S., Albizu, I., Besga, G., Garbisu, C. and Onaindia, M. 2004. Grazing intensity, aspect, and slope effects on limestone grassland structure. *Rangeland Ecology and Management*, Vol 57(6), pp. 606-612

Andersson, S., Nilsson, S.I. and Saetre, P. 2000. Leaching of dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) in mor humus as affected by temperature and pH. *Soil Biology and Biochemistry*, Vol 32(1), pp. 1-10

Bakker, E.S. and Olff, H. 2003. Impact of different-sized herbivores on recruitment opportunities for subordinate herbs in grasslands. *Journal of Vegetation Science*, *Vol* 14(4), pp. 465-474

Belnap, J. and Phillips, S.L. 2001. Soil biota in an ungrazed grassland: response to annual grass (Bromus tectorum) invasion. *Ecological applications*, *Vol* 11(5), pp. 1261-1275

Bennie, J., Hill, M.O., Baxter, R. and Huntley, B. 2006. Influence of slope and aspect on long-term vegetation change in British chalk grasslands. *Journal of ecology*, Vol 94(2), pp. 355-368

Bullock, J.M., Hill, B.C., Silvertown, J. and Sutton, M. 1995. Gap colonization as a source of grassland community change: effects of gap size and grazing on the rate and mode of colonization by different species. *Oikos*, Vol 72(2), pp. 273-282

Butaye, J., Adriaens, D. and Honnay, O. 2007. Conservation and restoration of calcareous grasslands: a concise review of the effects of fragmentation and management on plant species. *Base*, Vol 9(2), pp. 111-118

Chappell, H.G., Ainsworth, J.F., Cameron, R.T. and Redfern, M. 1971. The effect of trampling on a chalk grassland ecosystem. *Journal of Applied Ecology*, Vol 8(3), pp. 869-882

Chase, J.M., Leibold, M.A., Downing, A.L. and Shurin, J.B. 2000. The effects of productivity, herbivory, and plant species turnover in grassland food webs. *Ecology*, *Vol* 81(9), pp. 2485-2497

Critchley, C.N.R., Chambers, B.J., Fowbert, J.A., Bhogal, A., Rose, S.C. and Sanderson, R.A. 2002. Plant species richness, functional type and soil properties of grasslands and allied vegetation in English Environmentally Sensitive Areas. *Grass and Forage Science*, Vol 57(2), pp. 82-92

Davis, M.A., Grime, J.P. and Thompson, K. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology*, *Vol* 88(3), pp. 528-534

De Deyn, G.B. and Van der Putten, W.H. 2005. Linking aboveground and belowground diversity. *Trends in Ecology & Evolution,* Vol 20(11), pp. 625-633

Ellenberg, H. 1988. *Vegetation ecology of central Europe*. Cambridge University Press.

Firestone, M.K., Killham, K. and McColl, J.G. 1983. Fungal toxicity of mobilized soil aluminum and manganese. *Applied and environmental microbiology*, Vol 46(3), pp. 758-761

Flis, S.E., Glenn, A.R. and Dilworth, M.J. 1993. The interaction between aluminium and root nodule bacteria. *Soil Biology and Biochemistry,* Vol 25, pp. 403-417

Gange, A.C., Bower, E. and Brown, V.K. 1999. Positive effects of an arbuscular mycorrhizal fungus on aphid life history traits. *Oecologia, Vol* 120, pp. 123-131

Gay, P.E., Grubb, P.J. and Hudson, H.J. 1982. Seasonal changes in the concentrations of nitrogen, phosphorus and potassium, and in the density of mycorrhiza, in biennial and matrix-forming perennial species of closed chalkland turf. *The Journal of Ecology*, Vol 70(2), pp. 571-593

Gelbard, J.L. and Harrison, S. 2003. Roadless habitats as refuges for native grasslands: interactions with soil, aspect, and grazing. *Ecological Applications*, Vol 13(2), pp. 404-415

Helden A.J. and Dittrich A.D.K. 2016: Hemiptera community and species responses to grassland sward islets. *Entomologica Austriaca Vol* 23, pp. 19–28

Hobbs, R.J. and Mooney, H.A. 1986. Community changes following shrub invasion of grassland. *Oecologia*, *Vol* 70(4), pp. 508-513

Hunter, M.D. and Price, P.W. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology*, *Vol* 73(3), pp. 724-732

Jacquemyn, H., Brys, R. and Hermy, M. 2003. Short-term effects of different management regimes on the response of calcareous grassland vegetation to increased nitrogen. *Biological Conservation*, Vol 111(2), pp. 137-147

Kemmitt, S.J., Wright, D. and Jones, D.L. 2005. Soil acidification used as a management strategy to reduce nitrate losses from agricultural land. *Soil Biology and Biochemistry*, Vol 37(5), pp. 867-875

Kemmitt, S.J., Wright, D., Goulding, K.W. and Jones, D.L. 2006. pH regulation of carbon and nitrogen dynamics in two agricultural soils. *Soil Biology and Biochemistry*, Vol 38(5), pp. 898-911

Krauss, J., Steffan-Dewenter, I. and Tscharntke, T. 2003. Local species immigration, extinction, and turnover of butterflies in relation to habitat area and habitat isolation. *Oecologia*, *Vol* 137(4), pp. 591-602

Lack, A.J. 1982. The ecology of flowers of chalk grassland and their insect pollinators. *Journal of Ecology,* Vol 70, pp. 773-790

Littlewood, N.A., Stewart, A.J. and Woodcock, B.A. 2012. Science into practice–how can fundamental science contribute to better management of grasslands for invertebrates?. *Insect Conservation and Diversity*, *Vol* 5(1), pp. 1-8

Loranger, J., Meyer, S.T., Shipley, B., Kattge, J., Loranger, H., Roscher, C. and Weisser, W. 2012. Predicting Invertebrate herbivory from plant traits: evidence from 51 grassland species in experimental monocultures. *Journal of Ecology,* Vol 93(12), pp. 2674-2682

Maskell, L.C., Smart, S.M., Bullock, J.M., Thompson, K.E.N. and Stevens, C.J. 2010. Nitrogen deposition causes widespread loss of species richness in British habitats. *Global Change Biology*, Vol 16(2), pp. 671-679

Pietikäinen, J., Pettersson, M. and Bååth, E. 2005. Comparison of temperature effects on soil respiration and bacterial and fungal growth rates. *FEMS Microbiology Ecology*, Vol 52(1), pp. 49-58

Pietri, J.A. and Brookes, P.C. 2008. Nitrogen mineralisation along a pH gradient of a silty loam UK soil. *Soil Biology and Biochemistry*, Vol 40(3), pp. 797-802

Rousk, J., Brookes, P.C. and Bååth, E. 2009. Contrasting soil pH effects on fungal and bacterial growth suggest functional redundancy in carbon mineralization. *Applied and Environmental Microbiology*, Vol 75(6), pp. 1589-1596

Sankey, J. 1966. Chalkland ecology (Ed: Dowdeswell, W.H.) London: Heinemann Educational Books

Schippers, P., Snoeijing, I. and Kropff, M.J. 1999. Competition under high and low nutrient levels among three grassland species occupying different positions in a successional sequence. *New Phytologist*, *Vol* 143(3), pp. 547-559

Siemann, E. 1998. Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology*, *Vol* 79(6), pp. 2057-2070

Stevens, C.J., Dise, N.B., Mountford, J.O. and Gowing, D.J. 2004. Impact of nitrogen deposition on the species richness of grasslands. *Science*, Vol 303(5665), pp. 1876-1879

Swaty, R.L., Gehring, C.A., Van Ert, M., Theimer, T.C., Keim, P. and Whitham, T.G. 1998. Temporal variation in temperature and rainfall differentially affects ectomycorrhizal colonization at two contrasting sites. *New Phytologist*, *Vol* 139(4), pp. 733-739

Van Den Berg, L.J., Vergeer, P., Rich, T.C., Smart, S.M., Guest, D.A.N. and Ashmore, M.R. 2011. Direct and indirect effects of nitrogen deposition on species composition change in calcareous grasslands. *Global Change Biology*, Vol 17(5), pp. 1871-1883

Van der Putten, W.H., Vet, L.E., Harvey, J.A. and Wäckers, F.L. 2001. Linking above-and belowground multitrophic interactions of plants, herbivores, pathogens, and their antagonists. *Trends in Ecology & Evolution*, *Vol* 16(10), pp. 547-554

Van Swaay, C.A.M. 2002. The importance of calcareous grasslands for butterflies in Europe. *Biological Conservation*, *Vol* 104(3), pp. 315-318

Wallis De Vries, M.F., Poschlod, P. and Willems, J.H. 2002. Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. *Biological Conservation*, Vol 104(3), pp. 265-273

Wesche, K., Krause, B., Culmsee, H. and Leuschner, C. 2012. Fifty years of change in Central European grassland vegetation: Large losses in species richness and animal-pollinated plants. *Biological Conservation*, Vol 150(1), pp. 76-85

Willems, J.H. 2001. Problems, approaches, and results in restoration of Dutch calcareous grassland during the last 30 years. *Restoration Ecology*, Vol 9(2), pp. 147-154

Willems, J.H., Peet, R.K. and Bik, L. 1993. Changes in chalk-grassland structure and species richness resulting from selective nutrient additions. *Journal of Vegetation Science*, Vol 4(2), pp. 203-212

Woodcock, B.A., Pywell, R.F., Roy, D.B., Rose, R.J. and Bell, D. 2005. Grazing management of calcareous grasslands and its implications for the conservation of beetle communities. *Biological Conservation*, *Vol* 125(2), pp. 193-202