A fine scale study of selected environmental and floristic parameters in three populations of *Euphrasia vigursii* (Davey), a rare annual endemic to Devon and Cornwall

L. GRANADOS[1] and S. D. LANE[2]

School of Biological Science, University of Plymouth, Plymouth PL4 8AA

ABSTRACT

Euphrasia vigursii is an endangered hemiparasitic annual, endemic in Devon and Cornwall. This investigation has evaluated fine scale patterns of floristic composition and nutrient distribution in selected populations of *E. vigursii* in Devon and Cornwall to increase understanding of their ecology for use in future management strategies in Devon. Two particular questions were formulated:
1. Is *E. vigursii* immediately surrounded by other particular plant species?
2. If the soil was analysed in the direct location of the site of *E. vigursii* would the pH, Nitrogen, Phosphorus and Potassium content be different from the areas where *E. vigursii* is not present?
Phytosociological analysis indicated that *E. vigursii* is associated with heath and acidic grassland communities typically containing *Ulex gallii*, *Agrostis curtisii*, *Calluna vulgaris*, together with *Molinia caerulea* and *Potentilla erecta* mire. Within the individual sites spatial scale comparison (macro vs. micro) indicated significant differences in Phosphorus levels and pH levels but these were not consistent across the sites. Germination of *E. vigursii* at microenvironment level was closely correlated with the presence of *A. curtisii* rather than its other known host species *Ulex gallii*. This is contrary to published research which suggests that *E. vigursii* avoids the more open, species-poor areas dominated by *A. curtisii*. Correlations between the environmental parameters assessed may reflect present management regimes within the Dartmoor populations.

KEYWORDS**:** spatial scale, species distribution, hemiparasitic, soil nutrients, conservation, Vigurs' Eyebright.

INTRODUCTION

E. vigursii (Vigurs Eyebright) is confined to Cornwall and Devon where it is considered endangered and is classified as vulnerable (Cheffings & Farrell 2005). Until 1979 it had been located in 53 sites in Cornwall; later surveys have revealed only 25 active sites. This represents approximately 50% loss of localities in Cornwall mainly due to habitat destruction (French *et al.* 1999). In Devon there are only 2 sites, rediscovered in 1995 and 1998 and situated on the north-west perimeter of Dartmoor National Park. Ecologists at the National Park aim to conserve and increase the population of *E. vigursii* as part of the Dartmoor Biodiversity Action Plan, as it has been categorised in the priority list of the UK steering group report on biodiversity as being of 'global conservation concern' (HMSO 1995). In order to establish a management strategy that would address the objectives of Dartmoor National Park authority, a greater understanding of the ecology of *E. vigursii* and specifically knowledge of the local populations is essential.

The processes and mechanisms that result in species being rare and endemic are complex traits involving interactions of abiotic, biotic and historical factors. Investigating the factors which influence the distribution of *E. vigursii* must therefore involve an amalgamation of demographic, genetic, resource allocation (Davy & Jefferies 1981; Palmer 1987; Schemske *et al.*, 1974) alongside historical systematic and stochastic perturbations (Shaffer 1981).

E. vigursii is a hemiparasitic summer annual, an erect to 20 cm branched therophyte (Grime 1996) located in heathland containing *Ulex gallii* and *Agrostis curtisii* in both Devon and Cornwall. The leaves are dull greyish green often suffused with violet or black (Stace 1999) due to anthocyanin pigment (Pankhurst 1977). The corolla is usually lilac/purple/reddish and on the upper leaves and bracts are long glandular hairs. *E. vigursii* is only one of four diploids in the genus and considered a stable hybrid between *Euphrasia micrantha* and

[1]e-mail:lisette.granados@ntlworld.com
[2]e-mail: slane@plymouth.ac.uk

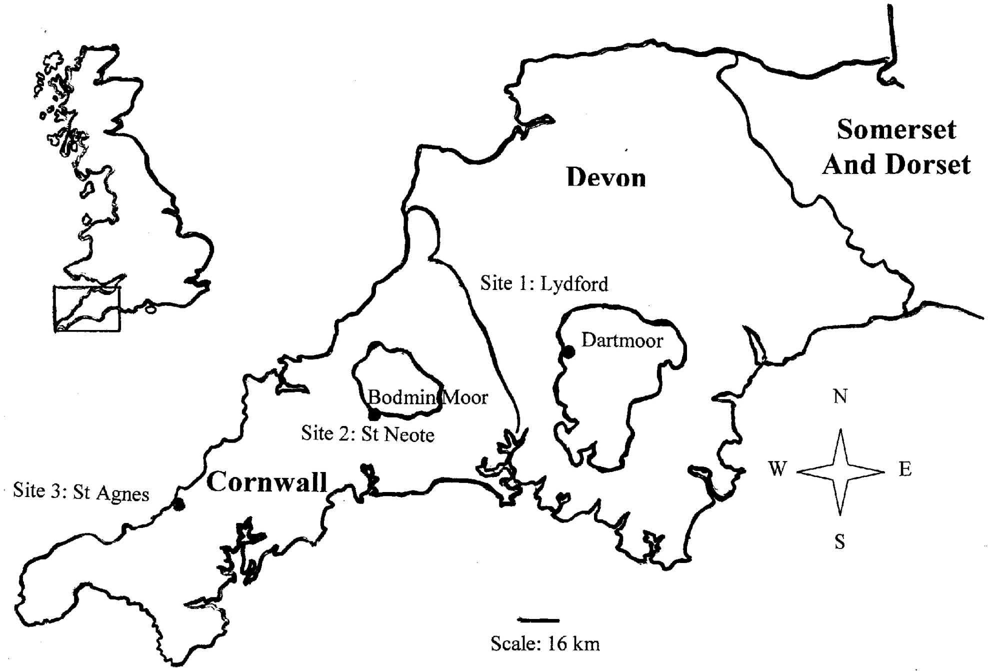

FIGURE 1. Location of study sites in Devon and Cornwall.

Euphrasia anglica (Pankhurst 1977). An open grass sward provided by regular grazing and controlled burning (swaling) is considered characteristic of the habitat in which *E. vigursii* is found (Norman Baldock, Ecologist Dartmoor National Park; pers. comm.. 2000). Very little specific research on *E. vigursii* has been conducted: therefore, the aims of this study have been to evaluate some of the ecological and environmental parameters influencing three separate populations of *E. vigursii* to gain better understanding of its ecology and habitat requirements and to answer two specific questions:

1. Is *E. vigursii* immediately surrounded by other particular plant species?
2. If the soil was analysed in the direct location of *E. vigursii* would the pH, Nitrogen, Phosphorus and Potassium content differ from areas where *E. vigursii* is not present?

MATERIALS AND METHODS

Two surveys were carried out at each of three locations in Devon and Cornwall (Fig. 1). The first survey entailed micro sampling of the target species *E. vigursii* to determine at individual plant level the composition of neighbouring plant associations together with recordings of soil nutrients (Potassium, Phosphorus and Nitrogen) and pH status. The second survey involved macrosampling to give a general indication of the vegetative community composition in which *E. vigursii* was found together with the soil nutrient and pH status within areas where *E. vigursii* was not present.

SITE 1

Lydford, Dartmoor National Park, Devon.
Altitude: 320 m. Sample site size: 10 m × 50 m
In the surveyed area *Ulex* spp. (gorse) and heather formed a mosaic of islands surrounded by pathways containing a grass and herbaceous sward. *E. vigursii* was located in most instances at the parameter of mature and new vegetative growth of *U. gallii* and where *A. curtisii* in the ‘pathways’ was of low sward height and also where periodic swaling had taken place.

SITE 2

St. Neot, Bodmin Moor Cornwall.
Altitude: 170 m. Sample site size: 7 m × 50 m.
The surveyed area contained a linear grass

and herbaceous sward, 15 m wide, which cut through a patchy landscape of gorse, heather and scrubland at the perimeters. *E. vigursii* was situated within the short grass sward from the edge of tall *Ulex* spp. at the perimeter of the survey area to within 5 m of the linear grass sward.

SITE 3

St. Agnes, nr Redruth, Cornwall.
Altitude: 85 m. Sample site size: 3·5 m × 50 m
In the surveyed area there was a blanket of dwarf gorse and heather species with pathways formed by walkers and erosion by the weather. *E. vigursii* was situated approximately 20 m from the cliff edge on one of the many worn paths that connect the coastal path that runs along the cliff edge with a parallel inland pathway. It was present amongst shorter vegetation at each side of the pathway although a greater percentage of the population was situated north east facing and was therefore sheltered from south-westerly winds.

SURVEY METHODS

Each survey site was marked out into a 1 m^2 grid framework and random co-ordinates used for macro sampling (1 m^2 quadrats). Micro sampling used 40 mm circular quadrats that were positioned non-randomly; the quadrat was placed over the target species (*E. vigursii* in the centre) and species frequency within the microsampling area recorded. Soil samples were collected 10 mm from the stem of *Euphrasia vigursii.* For the macro survey a 1 m^2 collapsible quadrat was randomly positioned in the survey area and the percentage cover for each species was recorded. Identification of the floristic species was carried out using keys by Stace (1999), Hubbard (1985) and Fitter *et al.* (1995).

Soil samples were taken from the centre of the quadrat using a 15 mm × 150 mm metal corer, to a depth of 25 mm to 75 mm depending on soil texture. In each survey site 60 soil samples were taken; 30 in the macro quadrats and 30 in the circular micro quadrats.

ANALYSIS OF SOIL SAMPLES

In total the surveys yielded 180 soil samples. Each was crushed and put through a 2 mm metal sieve before testing for pH, Potassium, Phosphorus, and Nitrogen using recommended methodology (ADAS Bulletin RB 427) for NPK and pH while C: N ratio was determined with a Leco FP 2000 C and N Analyser.

COMMUNITY CLASSIFICATION AND PHYTOSOCIOLOGY

In order to define the floristic community in which *E. vigursii* occurs the floristic data (using percentage cover data) were classified using two-way indicator species analysis and the computer program TWINSPAN. The TABLEFIT programme was then used to link the resulting communities in to the categories of the National Vegetation Classification (Dinsdale 1997).

The total micro floristic data (frequency data) were also run through TWINSPAN and Detrended Correspondence Analysis computer program applied using PC ORD in order to examine which were the associative and most frequent floristic species with *E. vigursii*. This was carried out for the micro floristic data between and in each individual site.

RESULTS

Floristic data and soil cores were obtained from a total of 180 quadrats collected from the three sites. The 90 micro quadrats yielded 21 plant species in total while the macro quadrats contained 28 plant species (Table 1). Bare ground and dead material were also recorded . All the species occurred at both survey scales, apart from *Poa* spp. which was only found only in the micro quadrats.

CLASSIFICATION AND PHYTOSOCIOLOGY

Interpretation of two-way indicator species analysis and definition of plant communities

The classification groups resulting from TWINSPAN analysis and synoptic frequency of occurrence within each group are shown in Table 2. Five TWINSPAN groups were defined and their associated NVC plant communities categorised (Table 3). Groups 1 and 2 were heath communities of Site 3, St Agnes. In group 1 *Agrostis curtisii* , *Erica cinerea*, *Potentilla erecta*, and *Ulex gallii*, *Thymus* spp., *Serratula tinctoria* and *Ulex europaeus* were frequent; however, there was a low frequency of *Erica tetralix*. In group 2 *Ulex gallii*, *Thymus species*, *Erica tetralix*, *Carex flacca*, *Serratula tinctoria*, *Viola* spp., *Agrostis curtisii* and *Potentilla erecta* were frequent. Dead material was a feature of both groups 1 and 2 and bare ground was a feature of the group 2.

Group 3 were heath communities of Site 1, Lydford. *Agrostis curtisii*, *Ulex gallii*, *Thymus* spp., *Potentilla erecta*, *Galium saxatile* and

TABLE 1. ASSOCIATES OF *EUPHRASIA VIGURSII* IN MACRO AND MICRO SURVEY SITES IN DEVON AND CORNWALL

Macro		Micro
Bare ground	Dead material	
Agrostis capillaris	*Pilosella officinarum*	*Agrostis capillaris*
Agrostis curtisii	*Plantago lanceolata*	*Agrostis curtisii*
Anthoxanthum odoratum	*Polygala serpyllifolia*	*Carex flacca*
Calluna vulgaris	*Potentilla erecta*	*Erica cinerea*
Carex flacca	*Pteridium aquilinum*	*Erica tetralix*
Dactylis glomerata	*Rubus fruticosus*	*Euphrasia vigursii*
Danthonia decumbens	*Senecio jacobaea*	*Galium saxatile*
Erica cinerea	*Serratula tinctoria*	*Hypericum* spp.
Erica tetralix	*Stachys officinalis*	*Hypochaeris radicata*
Euphrasia anglica	*Teucrium scorodonia*	*Lotus corniculatus*
Euphrasia micrantha	*Thymus* spp.	*Pilosella officinarum*
Euphrasia vigursii	*Ulex europaeus*	*Poa* spp
Galium saxatile	*Ulex gallii*	*Potentilla erecta*
Holcus lanatus	*Vaccinium myrtillus*	*Senecio jacobaea*
Hypericum spp.	*Viola* spp.	*Serratula tinctoria*
Hypochaeris radicata		*Thymus* spp.
Lotus corniculatus		*Ulex gallii*
Molinia caerulea		*Viola* spp.

Molinia caerulea were frequent but with low frequencies of *Danthonia decumbens*, *Pilosella officinarum*, *Erica cinerea*, *Carex flacca* and bare ground.

Group 4 and 5 were a mixture of heath, mire, and under shrub communities of Site 2, St Neot. In group 4 *Agrostis curtisii*, *Potentilla erecta*, *Pteridium aquilinum*, *Molinia caerulea*, and *Ulex europaeus* were frequent with a low frequency but high abundance of *Ulex gallii*. Less common was *Agrostis capillaris*. In group 5 *Agrostis curtisii*, *Potentilla erecta*, *Pteridium aquilinum*, *Agrostis capillaris*, *Senecio jacobaea*, *Molinia caerulea* and *Galium saxatile* and *Hypochaeris radicata* were frequent with *Ulex gallii*, *Euphrasia vigursii*, *Carex flacca*, *Euphrasia anglica and Anthoxanthum odoratum* less so.

Euphrasia vigursii was found to be most frequent in group 2 (7 quadrats) at Site 3 compared to its presence in Site 3, group 1 (1 quadrat); Site 1, group 3 (1 quadrat) and Site 2, group 5 (4 quadrats). In group 2 it was associated with NVC U3, H4 and H8 (Table 3). The quadrats in which *E. vigursii* was found in the other groups were classified as NVC: U3; M25a – *Erica tetralix* sub community; H4 and H8b *Danthonia decumbens* sub community.

DIRECT ORDINATION WITH *E. VIGURSII* USING DETRENDED CORRESPONDENCE ANALYSIS (DCA)

The distribution of the floral species from all three sites formed distinct floristic groups with the exception of *Erica cinerea*, *Hypochaeris radicata* and *Agrostis curtisii* (Fig. 2).

There was close correlation between *A. curtisii* and *E. vigursii* in terms of how frequent *A. curtisii* was encountered in each of the micro quadrats at all of the sites.

When the sites were individually analysed using DCA there were still strong correlations between *A. curtisii* and *E. vigursii* (Fig. 2) although not all the species named were present within each site.

In Site 1 there were close correlations of *E. vigursii* with *A. curtisii*, *Potentilla erecta*, and *Pilosella officinarum*. Species which showed as outliers in this site were *Lotus corniculatus*, *Ulex gallii*, *Thymus* spp. and *Erica tetralix*.

In Site 2 *E. vigursii* was strongly correlated with *A. curtisii* and *P. erecta* and associated with *Agrostis capillaris*, *Viola* spp. and bare ground whilst the species that show as outliers were *Galium saxatile*, *Carex flacca* and *Hypochaeris radicata*.

TABLE 2. SPECIES COMPOSITION OF THE THREE COMMUNITY TYPES DEFINED BY TWO-WAY INDICATOR SPECIES ANALYSIS OF THE QUADRAT DATA FROM THE THREE SITES OF *EUPHRASIA VIGURSII* IN DEVON AND CORNWALL

Species	Twinspan group				
	1	2	3	4	5
Ulex gallii	V	VI	VI	III	III
Euphrasia vigursii	II	III	I		III
Thymus spp.	V	VI	IV		
Erica tetralix	II	VI	IV		
Carex flacca	VI	IV	III	II	III
Hypochaeris radicata	IV	IV		II	IV
Dactylis glomerata	II	III			
Teucrium scorodonia		III			
Stachys officinalis		III			
Serratula tinctoria	VI	VI			
Viola spp.	V	VI	II		II
Erica cinerea	VI	III	III		II
Plantago lanceolata	II	II			II
Ulex europaeus	IV	II		V	II
Agrostis curtisii	III	VI	VI	VI	VI
Potentilla erecta	VI	VI	VI	VI	VI
Vaccinium myrtillus			III		
Pilosella officinarum		II	III		
Danthonia decumbens			III		
Euphrasia micrantha			I		
Calluna vulgaris			IV		II
Polygala serpyllifolia			III	II	II
Euphrasia anglica			II	II	III
Galium saxatile			VI	II	VI
Lotus corniculatus		II	II	II	
Molinia caerulea			VI	VI	IV
Hypericum spp.				II	II
Pteridium aquilinum				VI	VI
Senecio jacobaea				III	VI
Anthoxanthum odoratum					III
Holcus lanatus					IV
Agrostis capillaris			I	III	VI
Rubus fruticosus					II
Bare ground	II	IV	II	II	III
Dead material	VI	IV			

Key to species frequency in each group:
l = 1–5%; ll = 6–20%; lll = 21–40%; lV = 41–60%; V = 61–80%; Vl = 81–100%

TABLE 3. CORRELATION OF NVC COMMUNITIES WITH INDICATOR SPECIES GROUPS AND STUDY SITES

Two way indicator species groups	NVC communities
1	H6 *Erica vagans– Ulex europaeus* heath
	H8 *Calluna vulgaris – Ulex gallii* heath
	H4 *Ulex gallii – Agrostis curtisii* heath
2	H8 *Calluna vulgaris – Ulex gallii* heath
	U3 *Agrostis curtisii* heath
3	U3 *Agrostis curtisii* heath
	H4 *Ulex gallii – Agrostis curtisii* heath
	H8 *Calluna vulgaris – Ulex gallii* heath
4	U3 *Agrostis curtisii* heath
	U20 *Pteridium aquilinum – Galium saxatile* community
	W25 *Pteridium aquilinum – Rubus fruticosus* underscrub
	M25 *Molinia caerulea – Potentilla erecta* mire
5	U3 *Agrostis curtisii* heath
	W25 *Pteridium aquilinum – Rubus fruticosus* underscrub
	M25 *Molinia caerulea – Potentilla erecta* mire
Site	**NVC communities**
Site 1	U3 *Agrostis curtisii* heath
	H4 *Ulex gallii – Agrostis curtisii* heath
	H8 *Calluna vulgaris – Ulex gallii* heath
Site 2	U3 *Agrostis curtisii* heath
	U20 *Pteridium aquilinum – Galium saxatile* community
	M25 *Molinia caerulea – Potentilla erecta* mire
	W25 *Pteridium aquilinum – Rubus fruticosus* underscrub
Site 3	H4 *Ulex gallii – Agrostis curtisii* heath
	H6 *Erica vagans – Ulex europaeus* heath
	H8 *Calluna vulgaris – Ulex gallii* heath
	U3 *Agrostis curtisii* heath

In Site 3 close associations were apparent between *E. vigursii*, *Hypochaeris radicata* and *Agrostis curtisii* as well as *Ulex gallii* and *Potentilla erecta*. Species that were outliers and therefore showed less of an association were *Serratula tinctoria*, *Carex flacca*, *Erica tetralix* and *Erica cinerea*.

ENVIRONMENTAL SITE COMPARISON

The macro results for both the UNIANOVA analysis (Potassium and Phosphorus) and for the Kruskal-Wallis test (pH and Nitrogen) indicate significant differences between the sites for environmental variables (P<0·05). Differences were observed in pH between the macro and micro-quadrats in Site 2 and Site 3 but not in Site 1 (Fig. 3). However, mean values for the micro quadrats were higher than for the macro quadrats at all three sites.

On the sites surveyed, *E. vigursii* distribution was strongly linked to soil micro-environment, germination correlating with a pH range from 3·3 to 4·8, a Potassium range of between 15 mg/100 g to 53·60 mg/100 g, a Phosphorus range between 0·04 mg/100 g and 7·44 mg/100 g and a Nitrogen range between 0·34% and 9·62%. Results of the UNIANOVA analysis indicated a significant difference in Phosphorus levels (F = 7·446, P>0·05) but the results for Potassium were not significant. Results of the Kruskal-Wallis test indicated a significant difference in pH (P<0·05) and in Nitrogen (P<0·05) between the spatial scales (micro and macro). Chemical comparisons of the individual sites at micro and macro levels revealed significant differences in Phosphorus levels at Site 1 (t-test, P<0·05), and pH levels at Site 2 and Site 3 (Kruskal-Wallis test, P<0·05). No significant differences were seen in the other parameters recorded. Comparing these results with the descriptive vegetation analyses suggests that *E. vigursii* distributions generally link with higher levels of nutrients and pH.

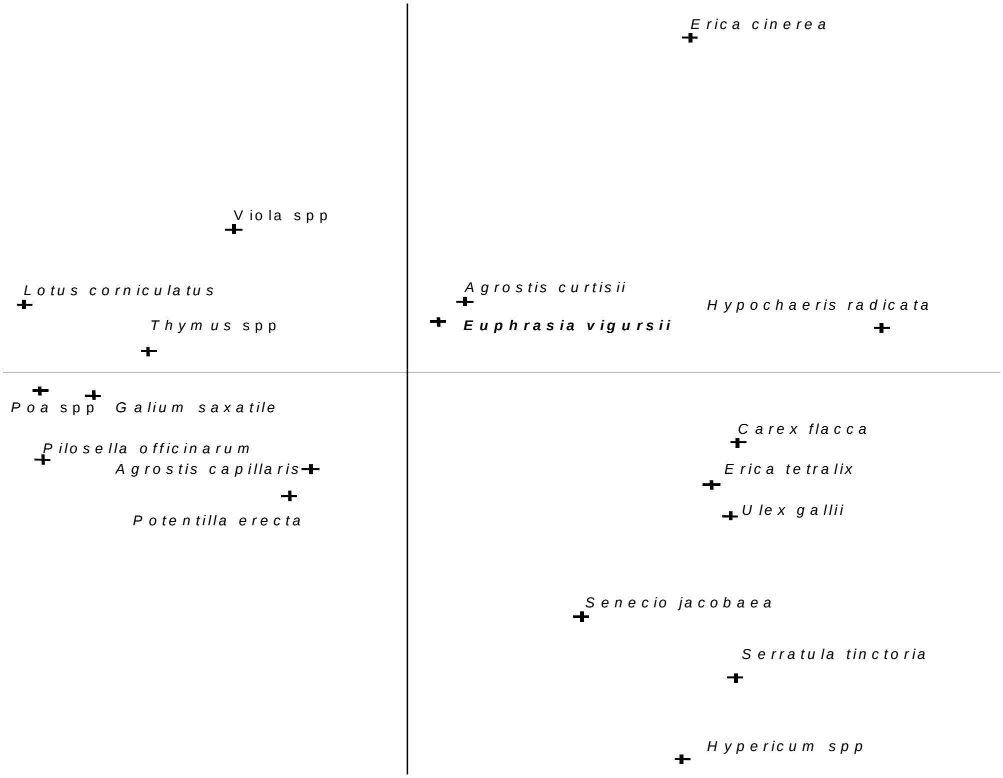

FIGURE 2. Combined Ordination plot of total floristic species associated with *Euphrasia vigursii* from Detrended Correspondent Analysis of the ninety micro quadrats in Site 1, Site 2 and Site 3.

DISCUSSION

FLORISTIC COMMUNITY

The phytosociological analysis indicates that *E. vigursii* is a species associated with heath and acidic grassland communities typically containing *Ulex gallii*, *Agrostis curtisii*, *Calluna vulgaris* together with *Molinia caerulea* and *Potentilla erecta* mire. In all the sites there are external influences which reduce the plant communities' ability to transpose to successional community processes.

Colonisation in these communities by plants is limited to those species that are characteristically tolerant of environmental stresses, low nutrient availability and low soil pH (acidity), which in turn is associated with high Aluminium and Iron toxicity (Crawley 1997). Acidification of soil is a result of influences of the base substrate by mineral weathering, temperature, hydrology and leaching (Crawley 1997). Particular plant species can acidify the immediate edaphic environment, for example *Calluna* and *Ulex* species produce strong acidifying litter which rapidly reduces the pH of the soil beneath them (Grubb & Suter 1971).

ASSOCIATED FLORA OF *E. VIGURSII*

Germination of *E. vigursii* within the microenvironment was closely correlated with the presence of *A. curtisii* as opposed to its other known host species, *U. gallii*. Studies by Silverside (1999) however, indicate the opposite – i.e. *E. vigursii* apparently avoids the more open, species-poor areas dominated by *A. curtisii*. Silverside does mention, however, that *E. vigursii* is frequently reported as an associate.

The species that are associated with *E. vigursii* (Tables 1 and 3) have attributes, apart from *Carex flacca*, for counteracting low nutrient availability by the adoption of possessing VA mycorrhizals (Grime 1996). They therefore have the ability to use normally unavailable complex organic nitrogen sources, making them less dependant on mineralisation of organic matter (Aerts 1999). Nutrient-poor ecosystems are associated with low litter production and slow decomposition that leads to low rates of Nitrogen cycling; the ability to survive in such environments may prevent the invasion of highly competitive species dependant on high Nitrogen availability (Aerts 1999). *E. vigursii* does not possess symbiotic associations such as mycorrhizals but can, if resources are inadequate, parasitise other species, forming haustoria to obtain water, mineral nutrients and carbohydrates from the host's root system. (Lammi *et al.* 1999).

ENVIRONMENTAL VARIABLES

pH

Significant differences in pH were evident between macro and micro environments in sites 2 and 3 with levels ranging between 3·4 and 4·35. In Site 1 pH levels for both macro and micro samples were intermediate between these ranges and not significantly different, which suggests that in Site 1 any micro site would be suitable for germination in terms of pH preference. pH levels can be a good indicator of the nutrient availability to plants in a soil and previous work indicates that soils may show small scale heterogeneity in pH levels over small distances (Crawley 1997). This has been confirmed in this study.

Phosphorus

In Site 1 *E. vigursii* had germinated in a microsite significantly higher in Phosphorus than the macro environment (Fig. 3) suggesting a preference for Phosphorus levels that range from 0·26 mg/100 g to 19·01 mg/100 g. Phosphorus and Nitrogen are considered the two limiting factors which control plant growth and are geo-chemically complex (Zheng *et al.* 1999). There was a significant difference between the sites; in particular Site 1 had generally low levels of Phosphorus. In environments with low pH levels Phosphorus availability can be limited. However, if pH levels are increased Phosphorus utilisation improves more markedly than that of Potassium or Nitrogen (Rorison 1971). Low pH levels are associated with deficiency in Calcium, an element that renders phosphoric acid unavailable to plants and which might account for the lower levels observed. (Crawley 1997).

Potassium

E. vigursii germinated in a micro environment with Potassium levels ranging from 26·2 mg/100 g to 52·5 mg/100 g. Although differences between the macro and micro environment for each site were not statistically significant, in Site 1 the mean Potassium levels were slightly lower in the micro environment. There was a significant difference between the sites (Fig. 3) and the mean levels were higher in Site 1 than in Site 2 and Site 3, which could be the result of periodic swaling. Higher levels of Potassium have been reported in ash deposits following normal management fires although much is lost through leaching (Legg *et al.* 1992).

Nitrogen

No significant differences between Nitrogen supply at macro and microsite level were evident at any of the sites, but there was a definite trend for increased levels where *E. vigursii* had germinated. There were significantly higher Nitrogen levels in Site 1, possibly linked to the grazing regimes in place. Nitrogen levels in grazed swards fluctuate with patterns of defoliation and severity of grazing determines the relative importance of the two Nitrogen recycling pathways: internal recycling – remobilization from senescent leaves; and external recycling – via animal intake and urine and faeces return (Lemaire & Chapman 1996). The former process is subject to leaching and gaseous loss, increasing the stock rates within grazing systems and thus leading to lower of Nitrogen utilisation efficiency by vegetation when uptake rates are lower than input rates. (Lemaire & Chapman 1996).

Spatial distribution of E. vigursii

The position in a habitat of an individual plant is determined by its capability for colonisation, competition and longevity and that is dependent initially on its immediate spatial separation from neighbours (Ross & Harper 1972; Tilman 1994).

E. vigursii has to recognise, after the arrival of a seed in a micro site, the location of a potential host species which is an important factor in determining its survival; it does not have a persistent seed bank (Grime 1996). Studies on species of *Euphrasia* in cultivation indicate that when a seed is planted 2·5 cm from a host, it establishes a week earlier than those spaced 4 5 cm and two weeks earlier than those spaced 6·5 cm apart; the latter also result in lower percentage survival (Yeo 1964). In addition the seeds are very small (<1 mm) and wind dispersed (Stace 1999) and upon landing are subjected to a highly heterogeneous micro soil surface. As a result they may require a particular morphological dispersal site in order to establish (Harper *et al.* 1965).

The soil solution contains dissolved substances that can affect germination, in

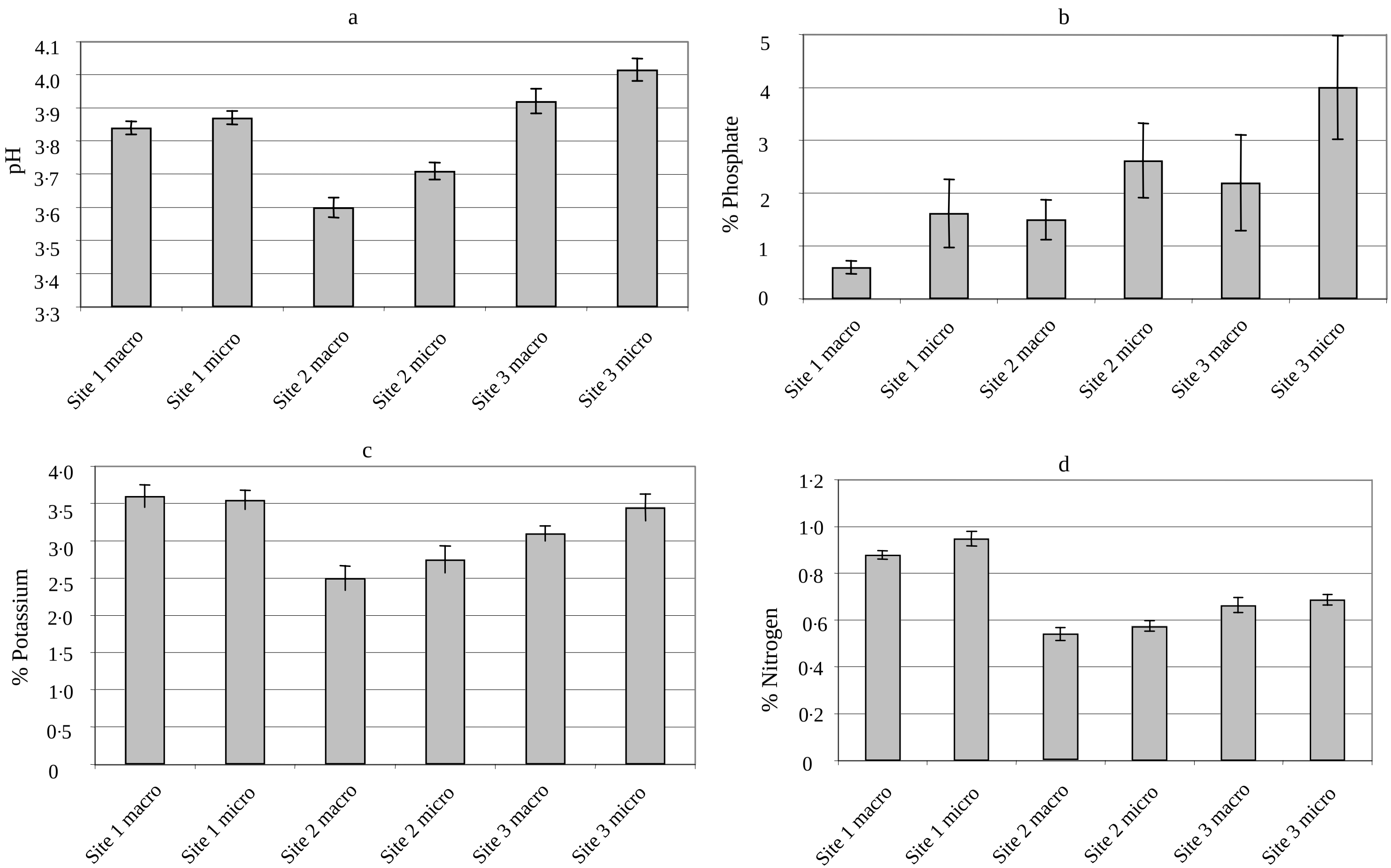

FIGURE 3 (a) Soil pH, (b) Phosphorus, (c) Potassium and (d) Nitrogen values in Macro and Micro Quadrats in Site 1, Site 2 and Site 3. Vertical bar = ± standard deviation.

particular allelochemicals that inhibit germination; but the host plants of parasitic angiosperms produce chemical signals that stimulate germination of the parasitic seeds and allelochemicals at low concentrations may also be stimulatory (Karssen & Hilhorst 1992). It is possible that nutrient and pH levels may also indicate the spatial position in relation to a host species.

The subsurface of the edaphic environment contains a matrix of root systems and although in this study *E. vigursii* has been found to be closely associated with *A. curtisii*, it remains possible that new young plants of *Ulex gallii* were also forming but were not detected above ground level. *Euphrasia* species show a particular preference for Leguminosae over Gramineae because of increased Nitrogen fixation (Yeo 1964).

Competition

The species associated with *E. vigursii* are predominately of low or retarded growth, either because they have an ascending growth form or their vigour is kept in check by grazing or abiotic influences. A separate study by Dartmoor National Park (Norman Baldock, Ecologist Dartmoor National Park; unpublished data 1997) targeted a 10 m × 10 m grazing exclusion site close to Site 1. This reported that over a seven year period shrubby species such as *Ulex* and *Calluna* formed a dense canopy reducing the frequency and abundance of low herb species. Heathland communities are a direct result of disturbance by natural stochastic events or anthropogenic management regimes and are considered an essential resource for seasonal grazing of livestock by farmers. Disturbance of heath and grassland communities by fire and grazing blocks succession to dominant competitive species (Smith & Rushton 1994). Selective grazing produces a patchy distribution of vegetation and irregular edges, creating gaps (Hearn 1995; Bullock *et al.* 1994) which can be utilised by species which require high light availability and are poor competitors. This is considered an essential factor in successful colonisation of *E. vigursii* (Yeo 1964).

The main associate with *E. vigursii* is *Agrostis curtisii*, which can be found in a number of important heathland communities where it can form dense patches and is considered unpalatable to herbivores. It is highly competitive with other Poaceae species, not by its ability to compete for light but its ability to reduce possible establishment sites for other Poaceae species due to its dense sward; it is also known to become especially abundant after burning (Rodwell 1992) together with *Ulex* species (Grime 1996). *Euphrasia* species and rare species in general and are considered superior competitors to common grasses (Rabinowitz 1981). *Potentilla erecta* can have either a prostrate or ascending growth form which reduces the damage caused by trampling and is not as readily grazed, affording a competitive advantage in grazed situations (Hearn 1995). Similarly *E. vigursii* also overcomes possible competitive interactions with other low growing species by forming dense clusters of individual plants (Yeo 1964). Inter and intra-specific interactions between individuals may occur in *E. vigursii*, as Yeo also reports that *Euphrasia* species can parasitise more than one host at a time – for example *Carex curta*, *Poa annua* and *Trifolium pratense*, and also members of its own species.

Many endangered endemic species have low population numbers, together with small geographical ranges and narrow habitat specificity which can cause natural selection to favour traits which offset the disadvantages of small local population size (Rabinowitz 1981). However, natural selection can also reinforce narrow habitat selection imposing further distribution restrictions (Rosenzweig & Lomolino 1997). *E. vigursii* is able to coexist with species that have adapted to benefit from an environment that is otherwise hostile to many of the common competitive species and its habitat preference and choice is a result of evolutionary habitat selection (Bazaz 1991).

Within this study it has become evident that there are differences in environmental variables at the areas where *E. vigursii* has germinated and those where it has not and that there are significant spatial associations with particular plant species not normally closely associated. Significantly, variation in the environmental parameters may reflect the present management regimes within the of the Dartmoor sites. The evidence from these sites indicates that management within preferred habitats should continue to maintain gaps and habitat heterogeneity, but further research is required into temporal affects of management, influences of grazing and fire regimes on edaphic factors and also the key floristic species which associate with *E. vigursii*.

REFERENCES

AERTS, R. (1999). Interspecific competition in natural plant communities: mechanisms, trade-offs and plant-soil feedbacks. *Journal of Experimental Botany* **50**: 29–37.

BAZAZ, F. A. (1991). Habitat selection in plants. *The American Naturalist* **137** (Supplement): S116–S130

BULLOCK, J. M., HILL, B., DALE, M. P. & SILVERTOWN, J. (1994). An experimental study of the effects of sheep grazing on vegetation change in a species-poor grassland and the role of seedling recruitment into gaps. *Journal of Applied Ecology* **31**: 493–507.

CHEFFINGS, C. M. & FARRELL, L. eds. (2005). *The Vascular Plant Red Data List for Great Britain. Species Status* **7**: 1–116. Joint Nature Conservation Committee, Peterborough.

CRAWLEY, M. J. (1997). Life History and Environment, in M. J CRAWLEY ed. *Plant Ecology*, 2nd Edition. Blackwell Science.

DAVEY, A. J. & JEFFERIES, R. L. (1981). Approaches to the monitoring of rare plant populations, in *The biological aspects of rare plant conservation*. John Wiley & Sons.

DINSDALE, J., DALE, P. & KENT, M. (1997).The biogeography and historical ecology of *Lobelia urens* L. (the heath lobelia) in Southern England. *Journal of Biogeography* **24**: 153–175.

FITTER, R., FITTER, A. & FARRER, A. (1995). *Grasses, sedges, rushes, and ferns of Britain and Northern Europe*. HarperCollins, Hong Kong.

FRENCH, C. N., MURPHY, R. J. & ATKINSON, M. G. C. (1999). *Flora of Cornwall. Atlas of the flowering plants and ferns of Cornwall.* Wheal Seton Press, Camborne.

GRIME, J. P. HODGSON, J. G. & HUNT, R. (1996). *Comparative Plant Ecology: A functional approach to common British species*. Chapman & Hall, London.

GRUBB, P. J. & SUTER, M. B. (1971). The mechanism of acidification of soil by *Calluna* and *Ulex* and the significance for conservation, in E. DUFFEY & A. S. WATT eds. *The Scientific Management of Animal and Plant Communities for Conservation*. Blackwell Scientific Publications, Edinburgh.

HARPER, J. L., WILLIAMS, J. T. & SAGAR, G. R. (1965). The behaviour of seeds in soil. 1. The heterogeneity of soil surfaces and its role in determining the establishment of plants from seed. *Journal of Ecology* **53**: 273–286.

HEARN, K. A. (1995). Stock grazing of semi-natural habitats on National Trust Land. The National Trust and nature conservation 100 years on. *Biological Journal of the Linnean Society* **56**: (Supplement) 25–37.

HMSO (1995). *Biodiversity: the UK Steering Group Report 1995*. Volume 2. Action Plans. HMSO, London.

HUBBARD, C. E. (1985). *Grasses: A guide to their structure, identification, uses and distribution in the British Isles*. Penguin Books, London.

KARSSEN, C. M. & HILHORST, H. W. M. (1992). Effect of chemical environment on seed germination, in M. FENNER ed. *Seeds: The Ecology of Regeneration in Plant Communities*. C.A.B. International, Wallingford, Oxford.

LAMMI, A., PIRKKO, S. & SALONEN, V. (1999). The role of local adaptation in the relationship between an endangered root parasite *Euphrasia rostkoviana* and its host *Agrostis capillaris*. *Ecography* **22**:145–152.

LEMAIRE, G. & CHAPMAN, D. (1996). Tissue flows in grazed plant communities, in J. HODGSON & A. W. ILLIUS eds. *The Ecology and management of grazing systems*. C.A.B. International, Wallingford, Oxford.

LEGG, C. S., MALTBY, E. & PROCTOR, M. C. F. (1992). The ecology of severe moorland fire on the Yorkshire Moors: Seed distribution and seedling establishment of *Calluna vulgaris*. *Journal of Ecology* **80**: 737–752.

PALMER, M. E. (1987). A critical look at rare plant monitoring in the United States. *Biological Conservation* **39**: 113–127

PANKHURST, R. J. (1977). The identification of the British species of *Euphrasia* L. (Eyebrights) (experimental draft). Pankhurst, R. J., London.

RABINOWITZ, D. (1981). Seven forms of rarity, in H. SYNGE ed. *The Biological Aspects of Rare Plant Conservation*. John Wiley & Sons Ltd., Bognor Regis.

RORISON, I. H. (1971. The use of nutrients in the control of floristic composition of Grassland, in E. DUFFEY & A. S. WATT eds. *The Scientific Management of Animal and Plant Communities for Conservation*. Blackwell Scientific Publications, Edinburgh.

ROSENZWEIG, M. L. & LOMOLINO, M. V. (1997). Who gets the short bits of the broken stick? in W. E. KUNIN & K. J. GASTON eds. *The Biology of Rarity*. Chapman & Hall, London.

ROSS, M. A. & HARPER J. L. (1972). Occupation of biological space during seedling establishment. *Journal of Ecology* **60**: 77–88.

SCHEMSKE, D. W., HUSBAND, B. C., RUCKLESHAUS, M. H., GOODWILLIE, C., PARKER, I. M. & BISHOP, J. G. (1974). Evaluating approaches to the conservation of rare and endangered plants. *Ecology* **75**: 584–606.

SHAFFER, M. L. (1981). Minimum population sizes for species conservation. *BioScience* **31**: 131–143.

SILVERSIDE, A. J. (1999). *Euphrasia*, in M. WIGGINGTON ed. *British Red Data Books. 1. Vascular Plants 3rd Edition*. Joint Nature Conservation Committee, Peterborough.

SMITH, R. S., RUSHTON, S. P. (1994). The effects of grazing management on the vegetation of mesotrophic (meadow) grassland in Northern England. *Journal of Applied Ecology* **32**:13–24.

STACE, C. A. (1999). *Field flora of the British Isles*. Cambridge University Press, Cambridge.
TILMAN, D. (1994). Competition and biodiversity in spatially structured habitats. *Ecology* **75**: 2–16.
YEO, P. F. (1964). The growth of *Euphrasia* in cultivation. *Watsonia* **6**: 1–24.
ZHENG, D. W., AGREN, G. I. & BENHGTSSON, J. (1999). How do soil organisms affect total organic nitrogen storage and substrate nitrogen to carbon ratio in soils? A theoretical analysis. *Oikos* **86**: 430–442.

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