Geo-Ecological Studies on Two Ultramafic Sites in Western Ireland

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Abstract Ultramafic soils are found in many sites around the world where they can vary from exceptionally barren to reasonably fertile. Two ultramafic sites in western Ireland were studied: grassland at Dawros, County Galway and grassy heath near the base of Croagh Patrick, County Mayo. Rock and soil chemistry was examined along with foliar nutrients (at Dawros only). Ellenberg reaction values of all plant species recorded were determined. Two bioassays were conducted to determine relative differences in fertility between ultramafic and adjacent non-ultramafic soils and to assess nutrient limitation in the Croagh Patrick soil. Both soils showed many of the chemical characteristics typical of other ultramafic sites including a moderately high nickel concentration; in general, soil metal concentrations were higher in Dawros soils. However, nitrogen, phosphorus and calcium (with a calcium:magnesium ratio c. 0.6) were all at high concentrations at Dawros leading to a fertile grassland with both calcicole and calcifuge species present spanning six Ellenberg reaction values. Foliar nutrient concentrations were not unusual although calcium:magnesium ratios were approximately double in non-ultramafic soils compared to ultramafic soils. Croagh Patrick soil had lower concentrations of most nutrients and presented a grassy heath vegetation with more acidic reaction values. The bioassays showed plant growth to be reduced in this soil relative to that at Dawros and to be clearly limited by phosphorus availability. Whilst these two Irish ultramafic sites do not show the extreme features associated with other sites across the world they indicate the global diversity of ultramafic ecologies.

Keywords: Connemara; edaphic variability; fertilisation; quartzite; serpentine

Introduction

The unique nature of soils derived from ultramafic rocks and the 'serpentine' plant communities inhabiting them has long been recognised (Proctor and Woodell 1975; Brady et al. 2005; Harrison and Rajakaruna 2011). Numerous hypotheses, including high concentrations of certain metals, calcium (Ca):magnesium (Mg) imbalances, essential plant nutrient deficiencies (especially phosphorus (P)), low water holding capacity and fire, have all been implicated in the 'serpentine syndrome' at various localities globally. The relative importance of these is likely to differ between sites and also on a species-by-species basis (Lazarus et al. 2011). It is clear, however, that not all outcrops of ultramafic soils support an edaphically distinct flora – why this might be could lead to further understanding of how more classically serpentine-mediated edaphic variants are formed and the relative importance of the factors noted above. For example, Johnston and Proctor (1979) described the Lime Hill serpentine site in central Scotland that had limited expression of floristic features associated with ultramafic soils and there are also many examples of densely forested communities on ultramafic soils (e.g. Horrill et al. 1975; D'Amico and Previtali 2012; van der Ent et al. 2016). Whilst there are numerous small outcrops of ultramafic rocks in Ireland (Rothstein 1957; Lemon 1966; Bremner and Leake 1981; Gallagher 1989; Chew 2001; O'Driscoll 2005), mainly in north-western Ireland, only two of these have been considered from an ecological perspective, namely Dawros (Dyos et al. 1991) and Croagh Patrick (Jeffrey 1992). However, both of these exhibit the serpentine syndrome to only a limited extent: the most notable feature is that the grassland and heathland plant communities contain a mix of calcicole and calcifuge plants over soils that are moderately fertile.

Examination of soil chemistry is standard practice in serpentine ecology given the challenging nature of the soil environment for plants and, therefore, the first part of this study presents extensive soil analyses of these two Irish ultramafic sites and compares these with adjacent non-ultramafic soils. This allows a determination of major plant nutrient and potentially toxic metal concentrations and an assessment of whether these may be leading to challenges for the vegetation of these areas. The serpentine plant communities are then described in a quantitative manner using Ellenberg's indicator values (Ellenberg et al. 1991) to compare them with respect to the positions of the niche of each species along an environmental gradient of soil acidity providing a quantitative measure of the relative importance of calcicoles and calcifuges in the two communities. Ellenberg indicator values have been used surprisingly little in serpentine plant ecology but, as examples, Marsili et al. (2009) described serpentine communities in Italy using this approach and Selvi et al. (2017) showed how pine invasion of serpentine soils led to the presence of ground vegetation with greater nutrient requirements (i.e. increased Ellenberg 'N' values). The examination of plant traits allows determination of strategies that plants might use to persist on 'stressful' soils and here foliar nutrient concentrations are used to assess plant strategies and differential selectivities for available nutrients. This is of relevance as serpentine plants often have preferential uptake of Ca over Mg when the soil Ca:Mg ratio is less than unity to maintain a stoichiometric balance between these two elements (e.g. O'Dell et al. 2006). To complete the study, two bioassay experiments and conducted to firstly determine the relative fertility of the soils from the two sites examined. Secondly, given that other experiments have shown ultramafic soils to be nutrient limited, often by P (e.g. Chiarucci et al. 1998; Brearley 2005; Chiarucci and Maccherini 2007), a range of nutrients are added to assess potential nutrient limitation in one of the soils in the second bioassay.

Materials and Methods

Study sites

The Croagh Patrick site is situated near Westport, County Mayo, western Ireland (53° 46' N; 9° 38' W). The geology is based on serpentinite contained within a mélange of various rock types known as the Deer Park Complex and is considered an extension of the Highland Boundary Fault in Scotland (Ryan et al. 1983; Max 1989). The small ultramafic area outcrops on the pilgrim's path to the summit of Croagh Patrick (Fig. 1a) at about 90 m altitude and the vegetation is a grassy heath; the non-ultramafic area sampled was at about 150 m altitude and based on a quartzite geology. The Dawros site is situated near Letterfrack, Connemara, County Galway, western Ireland (53° 34' N; 9° 58' W). It is underlain by peridotite and the geology has been described by Rothstein (1957), Leake (1964) and Hunt et al. (2012) among others. The vegetation is grazed grassland (Fig. 1b).

Rocks

Rock samples collected in 2006 were pulverised in a Fritsch Pulverisette 6 and mixed in a ratio of 4.0 g rock to 0.6 g Fluxana Licowax C Micropowder PM (Hoechstwax); the subsequent mixture was pressed into a pellet using a Specac press at 10 tonnes pressure. Analysis of the pellets was carried out using a Spectro Analytical X-lab 2000 energy dispersive X-Ray fluorescence spectrometer under vacuum.

Soils

Five soil samples were collected from each of the ultramafic and non-ultramafic sites in 2006; they were air-dried, ground, and sieved to pass a 2 mm mesh. The moisture content of the air-dried soils was determined by heating c. 2 g sub-samples to 105º C for 24 hours. The same sub-samples were used to measure loss-on-ignition at 550º C for 5 hours in a muffle furnace. Soil pH was measured by adding 10 g of soil to 25 ml of distilled water; it was stirred and left to equilibrate for 1 h before measurement with a pH meter (pH 510, Eutech Instruments). Soil texture was determined by a hygrometer method: 50 g of homogenised soil from each of the four sites was added, in duplicate, to 25 ml of 4 % sodium hexametaphosphate (Calgon), made up to 1 litre of water and agitated vigorously for 10 min. Specific gravity at 45 seconds and 5 hours was recorded using a hygrometer to determine sand and clay content with silt calculated by subtraction; texture was then determined by reference to the USDA (1987) soil texture triangle. Total carbon (C) and nitrogen (N) were analysed on c. 0.2 g sub-samples using a LECO CNS-1000 elemental analyser. Delta^{15}N was measured in duplicate on a homogenised sample from each of the four sites using a ThermoFinnegan Delta^{plus} isotope ratio mass spectrometer interfaced with a CE Instruments 1112 Flash elemental analyser via a Conflo III. To determine total soil cation and metal concentrations, c. 1 g of soil was digested in 10 ml of concentrated nitric acid in a Milestone Ethos EZ Labstation microwave (with an initial 15 min ramp to 140º C, a 15 min additional ramp from 140º C to 180º C and then maintained for 10 min at 180º C under a power of 1000 Watts). Digests were subsequently diluted to 100 ml and analysed on a Thermo iCAP 6300 Duo inductively coupled plasma optical emission spectrometer (ICP-OES). Available P and potassium (K) were extracted from 2.5 g samples that were shaken with 25 ml of Mehlich 1 solution for ten minutes before being filtered and analysed by ICP-OES as above. Calcium and Mg were extracted from 2 g of soil with 20 ml of 1 M ammonium acetate by shaking for 2 hours, samples were then filtered and then analysed by ICP-OES as above. Available nickel (Ni) was extracted from 2.5 g samples with 25 ml of 0.5 M sodium-EDTA by shaking for one hour, filtered and analysed on a Varian SpectrAA 220FS atomic absorption spectrophotometer.

Plant species

The two sites were visited five times between 2005 and 2007 with all plant species present noted and added to those recorded by Dyos et al. (1991), Connolly (1992) and Jeffrey

(1992). In order to assess their preference for particular soil acidities (i.e. if they were calcicoles or calcifuges), the Ellenberg 'Reaction' (R) values were obtained for each species from the database of Hill et al. (1999); for plants only identified to genus (6 % of total), the mean value for all species within the genus was used.

Foliar nutrients

Foliar samples (and stem and flower samples of *Silene flos-cuculi*) were collected from plant species growing on and off ultramafic soils at Dawros in 2007 (in addition to *Asplenium adiantum-nigrum* found on ultramafic soil only). To assess nutrient concentrations, c. 75 mg of leaf material was digested in 2.5 ml concentrated sulphuric acid with a lithium sulphate/selenium (100:1) catalyst at 375° C for 4 hours, diluted to 50 ml with deionised water, and analysed on a Dionex ICS-5000+ Ion Chromatography System (N only) or a Thermo iCAP 6300 Duo ICP-OES (all other elements).

Bioassay #1

Seeds of perennial ryegrass (*Lolium perenne*) were planted into 7.6 cm diameter pots containing ultramafic or non-ultramafic soil from the two Irish sites in addition to soil from Meikle Kilrannoch alpine ultramafic site in Scotland (Proctor et al. 1991) and John Innes compost for comparative purposes. Pots were placed into a growth chamber with a 16 hour day and 8 hour night (both at 20° C) and watered on a regular basis. They were thinned to 10-15 seedlings per pot about half way through the experiment and the shoots of the ten largest seedlings were then harvested after 34 days, dried at 60° C for 48 hours before their dry weights were recorded. Nutrient concentrations of the plants grown in Irish ultramafic soils were assessed using a LECO TruSpec CN analyser for N (Dawros-grown plants only as there was insufficient material from Croagh Patrick-grown plants) or as above for all other elements.

Bioassay #2

Seeds of lettuce (*Lactuca sativa* var. Marvel of Four Seasons) were planted into 5.6 cm diameter pots containing Croagh Patrick ultramafic soil. Pots were placed in a greenhouse (receiving up to 1200 μmol m^2 sec^{-1} irradiance), watered regularly and had their positions re-randomised weekly. Each pot was fertilised weekly with 10 ml of N, P, K or NPK solution (see Brearley 2005 for rates) or had $CaCO_3$ added at a rate of 0.25 g of $CaCO_3$ per pot. Initially, five seeds were planted and they were thinned to one after two weeks of growth. Shoots and roots were harvested after 37 days, separated and dried at 70° C for 70 hours before their dry weights were recorded. Final soil pH was measured by adding 5 g of soil to 10 ml of deionised water; it was stirred and left to equilibrate for 1 h before measurement with a Sartorius PB-11 pH meter.

Results

Rocks

The chemical composition of the rocks confirmed their ultramafic nature with low silicon (< 43 %) and high Mg (> 30 %) and iron (Fe) (> 6 %) concentrations (Table 1). Broadly speaking, the rock composition was similar for the top ten components but the rock from Dawros had greater concentrations of Fe, chromium (Cr), manganese (Mn) and lower concentrations of Ni than that from Croagh Patrick (Table 1).

Soils

Soils were silty loams and acidic, with pH ranging from 4.0 to 6.4; Croagh Patrick non-ultramafic soil (over quartzite) was significantly more acidic than the other sites by more than one pH unit (Table 1). Loss-on-ignition was significantly lower for the Croagh Patrick ultramafic soil and this was mirrored in the soil C concentrations. Soil N was, again, lowest in the Croagh Patrick ultramafic soil but also low in the Croagh Patrick non-ultramafic soil; this was supported by the $\delta^{15}N$ values (not replicated) that were less positive in Croagh Patrick soils relative to the Dawros soils. Carbon:nitrogen ratios were significantly higher in the Croagh Patrick non-ultramafic soil than all other sites (Table 2). Total soil P was greater at Dawros and greater in ultramafic than non-ultramafic soil at this site whereas the opposite pattern was seen at Croagh Patrick. Available soil P and K were at greater concentrations at Dawros and not different between ultramafic and non-ultramafic soils; they were lower at Croagh Patrick and lower (although not significantly for P) in ultramafic soil there (Table 2). Whilst exchangeable Ca and Mg were greater at Dawros, but not different between soil types due to high variability, the Ca:Mg ratio (on a molar basis) was greater both at Dawros and in non-ultramafic compared to ultramafic soils. Total soil metals (cobalt (Co), Cr, Fe, Mg, Mn, Ni) and extractable Ni were one to two orders of magnitude greater in the ultramafic soils; they were all found at greater concentrations at Dawros compared to Croagh Patrick. Total Ca was greater at Dawros but not different between soil types. Total copper (Cu) and zinc (Zn) were greater in ultramafic than on-ultramafic soil at Dawros but not Croagh Patrick. Potassium and sodium (Na) did not differ between sites or soil types (Table 2).

Plant species

The mean Ellenberg value was higher for Dawros species than Croagh Patrick species (4.99 ± s.e. 0.19 vs. 4.24 ± 0.28; $t = 2.21$, $p = 0.032$; Fig. 2) with an absence of any species scoring 7 at Croagh Patrick.

Foliar nutrients

All foliar nutrient concentrations differed significantly among species. Whilst foliar N, P and K did not differ between soil types, foliar Mg was higher in plants from ultramafic soil whereas Ca was lower (Table 3) leading to a mean Ca:Mg ratio of 1.28 ± s.e. 0.13 on ultramafic soil compared to 2.84 ± 0.32 on non-ultramafic soil. Foliar Co was less than 1.5 $\mu g\ g^{-1}$ and foliar Ni up to 90 $\mu g\ g^{-1}$ with both significantly greater in serpentine plants by an order of magnitude in many cases for Ni (notably for all three N-fixing legumes). Foliar Cr (< 7 $\mu g\ g^{-1}$), Cu (< 65 $\mu g\ g^{-1}$), Fe (< 185 $\mu g\ g^{-1}$) and Zn (< 190 $\mu g\ g^{-1}$) were not significantly different between soil types. For *Silene flos-cuculi*, soil effects broadly followed those described above with Co, Cr, Cu Mg and Ni at greater concentrations in plants on ultramafic soil. Potassium, Ca, Co and Ni did not differ between flowers and stems; Cr was lower in flowers, whereas N, P and a number of metallic elements (Cu, Fe, Mg and Zn) were greater in flowers (Table 3). As a serpentine specialist, foliar Ca of *Asplenium adiantum-nigrum* was notably lower than other species whilst its Ni concentration was among the highest (Table 3).

Bioassays

Biomass of ryegrass was about three-fold greater when grown in the Dawros soil (and was comparable to the John Innes compost) when compared with the Croagh Patrick soil (Fig. 3). In both cases, growth was actually greater in the ultramafic soils (although only significantly so in Croagh Patrick soil). This increased biomass was associated with greater foliar N concentrations (but not P or K) and foliar Ca that was greater in ryegrass grown in Dawros non-ultramafic soil compared to ultramafic soil; foliar Ca was lower when grown in Croagh Patrick soil but was not different between the two soil types (Table 4). Foliar Mg was greater when grown in ultramafic compared to non-ultramafic soils. Consequently the Ca:Mg ratio was greater than unity in Dawros non-ultramafic soil and less than unity for the ultramafic soils and the Croagh Patrick quartzite. Foliar Fe, Co, Ni and Cr were all greater in ultramafic compared to non-ultramafic soils (not significant for Ni) but foliar Cu and Zn did not differ between soils (Table 4).

Suggestions of P limitation were confirmed by the second bioassay using lettuce in the Croagh Patrick soil that showed clear P limitation as root and shoot biomass both increased by a factor of at least 35 with P addition (Fig. 4). Addition of NPK further increased root and shoot biomass by at least 60 times relative to the control (Fig. 4). There was no influence of nutrient amendments on the root:shoot ratio that was quite variable with a mean value of 1.30 (s.e. 0.79). There was no significant change in soil pH with any of the nutrient amendments (mean = 5.98 ± s.e. 0.17), but Ca addition increased soil pH by about 0.6 pH units at the end of the experiment.

Discussion

The botanical and ecological literature on Irish ultramafic sites is still as sparse as when David Jeffrey asked 'Is there a serpentine flora in Ireland?' over 25 years ago (Jeffrey 1992). In this paper, more detailed descriptions of two Irish ultramafic sites are presented, neither of which has classic serpentine debris as found at, for example Meikle Kilrannoch or the Keen of Hamar in Scotland or many locations in California. Whilst there are clearly distinctive chemical compositions associated with the ultramafic rocks and soils, the weathering process has not lead to skeletal debris but to a more typical soil development.

Dyos et al. (1991) described the plant communities at Dawros from ten 1 m^2 quadrats and Jeffrey (1992) provided basic vegetation descriptions of the site at Croagh Patrick. Extending from their earlier work, it is confirmed that these two serpentine plant communities do not show any peculiarities other than a moderately high diversity due to the presence of both calcicoles and calcifuges. This was confirmed using a quantitative method showing that the species present ranged across six Ellenberg reaction values with the Croagh Patrick site more skewed towards acidic reactions as it was a grassy heath rather than a grassland. The use of Ellenberg values in other European serpentine plant communities would be valuable to compare the traits and physiological requirements of plants and may provide additional insights into plant strategies for survival in ultramafic soils.

The rock and soil analyses confirmed the ultramafic nature of the samples with soil metals at higher concentrations in the Dawros soil for the majority of those implicated in the serpentine syndrome. Soil Ni concentrations were moderately high at up to 1600 μg g^{-1} ('total' values). However, major plant nutrients (such as available P) and the soil C:N ratio showed a fertile soil, consistent with an organic matter rich grassland at Dawros. This fertility may also be linked to horse grazing that could transfer nutrients to the soil via faeces and promote vegetation growth – this would explain why this site has a more positive $\delta^{15}N$ (Peterson and Fry 1987). Furthermore, the exchangeable Ca:Mg ratio was about 0.6, also reflected in the foliar Ca:Mg ratio, which is not particularly large for ultramafic soils that can have a notable excess of Mg over Ca (Proctor and Woodell 1975). The Ca:Mg in the non-ultramafic soil was highly variable, ranging from 0.6 to 13, but about 5 on average indicating that Ca is abundant in these soils. So, whilst the metal concentrations were greater at Dawros than Croagh Patrick, this was not having a marked influence on the vegetation or on plant growth as shown in the first bioassay.

In the case of Croagh Patrick, soil metals were lower than at Dawros and soil P was particularly low. The second bioassay showed clear P limitation of plant growth (with a 30-fold increase in lettuce biomass with P addition) and no indication that Ca was deficient or influencing the availability of metallic elements. Other studies have shown P to be limiting in serpentine soils although rarely has the response been so marked as found in this experiment (e.g. Nagy and Proctor 1997; Chiarucci et al. 1998; Brearley 2005; Chiarucci and Maccherini 2007). It is notable that at Croagh Patrick, the adjacent quartzite soil studied for comparison was also poorly fertile, for example it was most acidic and had the highest C:N ratio. This is likely to be linked to the resistance of quartzite to weathering that therefore does not readily release rock-derived nutrients to support plant growth.

Foliar nutrients broadly represented the abundance of these elements in the soil and suggested that the plants require minimum stoichiometric balancing in the Dawros site. Differences between the field collected plant and the bioassay plants likely reflect species-specific differences as well as micro-site differences at the sampling sites. Phosphorus limitation is unlikely to be as important here as at Croagh Patrick. Calcium:magnesium interactions are clearly reflected in the foliar nutrient concentrations but also do not play a major role, as both calcicoles and calcifuges are present at the Dawros site. Previous experimental work suggested that serpentine plants may selectively take up more Ca and/or exclude or sequester Mg; for example, O'Dell et al. (2006) showed that serpentine shrubs had greater Ca:Mg ratios than non-serpentine shrubs. In the bioassay plants, foliar Ca:Mg was significantly higher in the quartzite soil at Croagh Patrick than the adjacent ultramafic soil indicating possible deficiencies of Ca in quartzite. Foliar metals important in ultramafic soils (Ni, Co, Cr) differed as expected. Foliar Ni was in close agreement with Dyos et al. (1991) for *Asplenium adiantum-nigrum* and *Thymus praecox*. It was notable that foliar Ni was markedly greater in N-fixing legumes agreeing with the work of Ho et al. (2013) in Taiwan and suggestive of a role of Ni in N-fixation. Similar with Lime Hill and a number of other serpentine sites in Scotland (Sleep 1985), is the presence of *A. adiantum-nigrum* of the serpentine variant (possibly *A. cuneifolium*: Scannell 1978). As a serpentine specialist, its foliar Ca was notably lower than other species and its foliar Ni was among the highest and comparable to that of Cornara et al. (2007) for *A. cuneifolium* who analysed ferns from serpentine sites in Italy where they found very low Ni in *Pteridium aquilinum*, also in agreement with this study. There were some similarities with the patterns of elemental allocation between leaves and flowers as shown by DeHart et al. (2014) with differences likely to be due to different species studied. Floral nutrient and metal concentrations deserve further study on ultramafic soils as they have the potential to influence pollinator behaviour and therefore lead to speciation over longer time frames. When compared with Croagh Patrick (D. W. Jeffrey and R. D. Reeves unpublished: Table 5), plants from the Dawros serpentine site were higher in P, K, Ca, Mg and Zn concentrations but not Cu or Ni (Co and Cr could not be compared directly due to relatively high detection limits of the Croagh Patrick analysis).

Conclusions

In this study, the two Irish ultramafic sites examined are not very extreme when compared to many other localities globally, which can be attributed to their relative fertility. This is particularly the case at Dawros where there is fertilisation by grazing animals whereas the non-ultramafic comparison soil at Croagh Patrick is quartzite that does not weather readily and so forms poorly fertile soils. Despite having greater concentrations of metals in the soil, Dawros is more fertile than Croagh Patrick – likely due to greater N and P availability and forming a grassland rather than a grassy heath. Both sites are coastal and this may lead to input of cations via seaspray supporting the hypothesis of Ferreira (1963), which has received little attention, that coastal ultramafic sites may be less extreme than those further inland. To answer the question posed by Jeffrey (1992), 'is there a serpentine flora in

Ireland': there are certainly ultramafic soils with high concentrations of metals in Ireland but the relative fertility of these sites ameliorates the metallic influence and leads to a minimally expressed serpentine flora.

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Table 1: Chemical composition (%), including the top ten components in each sample, of a single rock sample from Dawros and Croagh Patrick ultramafic sites in western Ireland.

	Dawros	**Croagh Patrick**
SiO_2	40.9 ± 0.20	42.5 ± 0.19
MgO	31.8 ± 0.35	32.9 ± 0.31
Fe_2O_3	13.0 ± 0.02	6.98 ± 0.013
Cr_2O_3	0.85 ± 0.002	0.39 ± 0.001
Na_2O	< 0.34	< 0.29
NiO	0.26 ± 0.002	0.33 ± 0.002
MnO	0.16 ± 0.001	0.047 ± 0.0004
CaO	0.087 ± 0.002	< 0.014
Al_2O_3	< 0.052	0.57 ± 0.039
CoO	0.028 ± 0.003	0.025 ± 0.002
P_2O_5	0.026 ± 0.004	0.031 ± 0.003

Table 2: Characteristics of soils from Dawros and Croagh Patrick ultramafic and adjacent non-ultramafic sites in western Ireland. All values are mean ± standard error; letters indicate significant differences according to Tukey's tests with $P < 0.05$.

	Dawros Ultramafic	**Dawros Non-ultramafic**	**Croagh Patrick Ultramafic**	**Croagh Patrick Non-ultramafic**
pH	5.51 ± 0.28 a	5.57 ± 0.35 a	5.17 ± 0.20 a	4.07 ± 0.07 b
Loss-on-ignition (%)	27.0 ± 1.9 ab	36.9 ± 6.4 a	8.7 ± 3.0 b	42.6 ± 7.7 a
Texture	Silt loam	Silt loam	Silt loam	Silt loam
C (%)	12.1 ± 0.9 ab	22.7 ± 5.5 a	3.6 ± 1.1 b	19.8 ± 3.3 a
N (%)	1.17 a	1.40 a	0.27 b	0.88 ab
$\delta^{15}N$ (‰)	6.00	4.45	3.99	3.46
C:N	10.4 ± 0.50 a	15.6 ± 0.96 a	13.6 ± 1.17 a	23. 9 ± 2.77 b
Available P ($\mu g\ g^{-1}$)	36.1 ± 11.5 a	38.2 ± 8.31 a	7.10 ± 2.34 b	15.3 ± 3.70 ab
Total P ($\mu g\ g^{-1}$)	1930 ± 330 a	1290 ± 178 a	250 ± 60.2 b	427 ± 74.5 b
Available K ($\mu g\ g^{-1}$)	241 ± 44.5 a	196 ± 55.7 a	35.9 ± 9.61 b	103 ± 18.3 ab
Total K ($\mu g\ g^{-1}$)	2290 ± 440 a	3040 ± 673 a	2110 ± 170 a	1810 ± 329 a
Total Na ($\mu g\ g^{-1}$)	437 ± 22.6 a	1540 ± 1010 a	347 ± 75.2 a	453 ± 49.6 a
Exchangeable Ca ($cmol_c\ kg^{-1}$)	5.72 ± 1.46 a	13.8 ± 4.76 a	0.90 ± 0.21 b	1.25 ± 0.26 b
Exchangeable Mg ($cmol_c\ kg^{-1}$)	10.2 ± 2.06 a	6.70 ± 3.65 ab	3.15 ± 0.64 ab	2.82 ± 0.60 b
Exchangeable Ca:Mg	0.61 ± 0.15 b	4.77 ± 2.43 a	0.33 ± 0.07 b	0.44 ± 0.01 b
Total Ca (%)	0.46 ± 0.07 a	1.20 ± 0.50 a	0.10 ± 0.03 b	0.11 ± 0.03 b
Total Mg (%)	4.17 ± 0.95 a	0.62 ± 0.17 b	2.84 ± 0.93 a	0.14 ± 0.02 c
Total Co ($\mu g\ g^{-1}$)	160 ± 52.4 a	5.58 ± 1.57 b	61.0 ± 24.6 a	1.14 ± 0.15 b
Total Cr ($\mu g\ g^{-1}$)	2000 ± 427 a	54.7 ± 13.2 b	712 ± 274 a	63.1 ± 33.5 b
Total Cu ($\mu g\ g^{-1}$)	58.4 ± 24.8 a	13.6 ± 4.15 b	7.43 ± 2.04 b	6.71 ± 1.99 b
Total Fe (%)	13.4 ± 3.31 a	3.24 ± 0.83 ab	6.41 ± 2.36 a	1.42 ± 1.02 b
Total Mn ($\mu g\ g^{-1}$)	2330 ± 772 a	178 ± 61.1 b	921 ± 538 ab	13.8 ± 3.20 c
Extractable Ni ($\mu g\ g^{-1}$)	147 ± 39.0 a	22.9 ± 2.04 ab	31.0 ± 10.8 ab	4.27 ± 1.91 b
Total Ni ($\mu g\ g^{-1}$)	784 ± 254 a	38.4 ± 9.38 b	401 ± 157 a	12.7 ± 3.71 b
Total Zn ($\mu g\ g^{-1}$)	84.0 ± 23.7 a	8.19 ± 7.40 b	18.2 ± 9.47 b	7.76 ± 4.81 b

Table 3: Foliar nutrient concentration of plant species from the Dawros ultramafic and adjacent non-ultramafic site, in western Ireland. All values are mean ± standard error; asterisks significant differences according to a two-way ANOVA: ns = non-significant, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

Species (Plant part)	Soil type	N (mg g^{-1})	P (mg g^{-1})	K (mg g^{-1})	Ca (mg g^{-1})	Mg (mg g^{-1})	Co (µg g^{-1})	Cr (µg g^{-1})	Cu (µg g^{-1})	Fe (µg g^{-1})	Ni (µg g^{-1})	Zn (µg g^{-1})
Calluna vulgaris	Ultramafic	19.8 ± 0.85	1.10 ± 0.16	4.43 ± 0.46	4.22 ± 0.30	2.61 ± 0.07	0.19 ± 18	1.66 ± 1.05	7.60 ± 1.83	51.8 ± 12.8	0.01 ± 0.01	14.6 ± 2.52
	Non-ultramafic	16.7 ± 1.06	0.88 ± 0.07	5.09 ± 0.28	3.75 ± 0.35	2.11 ± 0.12	0.13 ± 0.3	0.21 ± 0.17	7.07 ± 1.54	82.8 ± 21.2	0 ± 0	18.6 ± 2.33
Carex sp.	Ultramafic	43.6 ± 7.94	1.94 ± 0.26	9.62 ± 2.46	1.58 ± 0.60	2.15 ± 0.29	0.16 ± 0.10	1.30 ± 1.30	4.98 ± 1.29	40.2 ± 5.16	1.27 ± 0.65	52.0 ± 11.3
	Non-ultramafic	35.5 ± 3.43	1.28 ± 0.17	7.60 ± 1.99	3.92 ± 1.39	2.87 ± 0.70	0.07 ± 0.04	0 ± 0	4.66 ± 1.10	43.6 ± 4.12	0.73 ± 0.35	38.4 ± 8.17
Erica cinerea	Ultramafic	24.0 ± 1.67	0.91 ± 0.04	5.45 ± 0.42	2.89 ± 0.01	2.21 ± 0.08	0.18 ± 0.03	0 ± 0	5.83 ± 1.29	38.4 ± 1.42	5.04 ± 0.27	13.9 ± 1.37
	Non-ultramafic	26.2 ± 2.05	0.92 ± 0.06	5.16 ± 0.29	4.50 ± 0.23	2.24 ± 0.05	0.04 ± 0.02	0.88 ± 0.83	4.97 ± 0.36	43.5 ± 4.59	0.47 ± 0.47	14.9 ± 0.23
Lotus corniculatus	Ultramafic	65.1 ± 3.69	2.15 ± 0.31	25.9 ± 3.22	6.52 ± 1.19	7.95 ± 1.19	0.69 ± 0.20	0.36 ± 0.25	5.34 ± 1.44	85.6 ± 14.6	39.5 ± 12.6	31.0 ± 6.62
	Non-ultramafic	57.8 ± 4.84	2.00 ± 0.48	14.3 ± 4.89	12.9 ± 2.98	3.61 ± 0.37	0.36 ± 0.07	1.10 ± 0.63	5.53 ± 0.72	87.9 ± 18.5	5.60 ± 2.42	26.3 ± 6.16
Pteridium aquilinum	Ultramafic	26.8 ± 1.37	1.51 ± 0.12	20.9 ± 0.66	1.85 ± 0.12	1.91 ± 0.37	0.36 ± 0.23	0.55 ± 0.27	6.59 ± 0.46	50.1 ± 2.73	1.24 ± 1.24	22.0 ± 4.62
	Non-ultramafic	30.1 ± 2.28	2.08 ± 0.22	17.2 ± 1.81	2.09 ± 0.28	1.54 ± 0.10	0.27 ± 0.10	0.64 ± 0.20	6.58 ± 0.65	55.7 ± 2.52	0 ± 0	28.6 ± 2.65
Thymus praecox	Ultramafic	22.5 ± 1.11	0.89 ± 0.07	15.5 ± 1.59	5.43 ± 0.68	5.92 ± 0.32	0.44 ± 0.12	1.49 ± 0.85	8.15 ± 1.58	93.2 ± 23.4	17.7 ± 4.26	60.5 ± 15.8
	Non-ultramafic	25.8 ± 1.83	1.35 ± 0.07	22.9 ± 3.03	10.6 ± 1.63	2.79 ± 0.16	0.09 ± 0.04	0 ± 0	9.75 ± 2.00	54.1 ± 13.8	1.82 ± 0.60	39.1 ± 2.20
Trifolium pratense	Ultramafic	27.7 ± 3.25	1.77 ± 0.31	13.0 ± 5.73	9.32 ± 1.55	6.19 ± 1.10	0.56 ± 0.09	0.99 ± 0.50	6.24 ± 0.77	54.3 ± 5.76	24.4 ± 5.91	17.5 ± 2.75
	Non-ultramafic	19.6 ± 1.18	0.88 ± 0.13	14.0 ± 3.62	11.4 ± 0.79	2.90 ± 0.75	0.22 ± 0.07	0.73 ± 0.39	7.39 ± 0.50	34.3 ± 4.31	2.54 ± 1.24	16.4 ± 2.25
Trifolium repens	Ultramafic	40.0 ± 3.36	2.90 ± 0.19	20.2 ± 4.01	8.86 ± 1.11	3.69 ± 0.44	0.60 ± 0.18	2.79 ± 1.23	20.2 ± 10.9	65.4 ± 3.60	30.3 ± 10.6	58.4 ± 31.9
	Non-ultramafic	50.2 ± 4.21	2.86 ± 0.22	22.3 ± 2.23	11.6 ± 1.96	3.45 ± 0.41	0.50 ± 0.22	2.75 ± 1.05	13.9 ± 2.59	68.8 ± 5.51	5.45 ± 3.38	38.9 ± 3.97
Soil		ns	ns	ns	***	***	**	ns	ns	ns	***	ns
Species		***	***	***	***	***	**	*	***	***	***	***
Silene flos-cuculi (Stem)	Ultramafic	9.13 ± 0.56	1.72 + 0.56	20.6 ± 2.33	4.08 ± 0.45	3.73 ± 0.45	0.73 ± 0.17	2.13 ± 0.34	5.02 ± 1.48	58.0 ± 11.8	10.4 ± 1.28	12.8 ± 2.99
	Non-ultramafic	7.70 ± 0.90	0.84 ± 0.15	34.0 ± 4.14	4.98 ± 0.53	1.55 ± 0.17	0.21 ± 0.09	1.23 ± 0.35	3.66 ± 0.42	38.8 ± 5.39	3.32 ± 0.24	15.2 ± 2.78
Silene flos-cuculi (Flowers)	Ultramafic	28.7 ± 1.47	4.44 ± 0.52	27.9 ± 1.88	4.77 ± 0.63	4.40 ± 0.41	1.16 ± 0.23	1.26 ± 0.38	9.58 ± 0.62	110 ± 5.66	20.8 ± 3.02	38.6 ± 26.6
	Non-ultramafic	27.0 ± 3.07	3.86 ± 0.53	25.4 ± 2.62	5.46 ± 0.35	2.88 ± 0.29	0.23 ± 0.06	0.25 ± 0.10	5.74 ± 0.98	106 ±6.20	1.72 ± 0.45	38.9 ± 5.26
Soil		ns	ns	ns	ns	**	***	**	*	ns	***	ns
Plant part		***	***	ns	ns	***	ns	**	**	***	ns	***
Asplenium adiantum-nigrum	Ultramafic	47.7 ± 2.96	2.21 ± 0.15	24. 8 ± 1.63	1.65 ± 0.57	3.05 ± 0.65	0.16 ± 0.03	1.17 ± 1.68	7.73 ± 1.15	44.2 ± 2.21	42.1 ± 4.58	24.9 ± 0.74

Table 4: Foliar nutrient concentration of *Lolium perenne* plants grown in a bioassay experiment using soils from two ultramafic and adjacent non-ultramafic sites in western Ireland. All values are mean ± standard error; letters indicate significant differences according to Tukey's tests with $P < 0.05$.

	Dawros Ultramafic	**Dawros Non-ultramafic**	**Croagh Patrick Ultramafic**	**Croagh Patrick Non-ultramafic**
N (mg g^{-1})	30.3 ± 0.92 b	43.2 ± 1.70 a	-	-
P (mg g^{-1})	1.64 ± 0.26 a	1.69 ± 0.16 a	1.34 ± 0.28 a	1.05 ± 0.05 a
K (mg g^{-1})	34.6 ± 6.00 a	25.2 ± 2.10 a	20.2 ± 1.30 a	22.4 ± 1.59 a
Ca (mg g^{-1})	3.66 ± 0.67 b	7.25 ± 0.76 a	1.55 ± 0.10 c	1.10 ± 0.12 c
Mg (mg g^{-1})	5.78 ± 0.93 a	3.42 ± 0.17 b	5.43 ± 0.48 ab	3.03 ± 0.42 b
Ca:Mg	0.62 ± 0.02 b	2.10 ± 0.12 a	0.29 ± 0.01 d	0.37 ± 0.01 c
Co (μg g^{-1})	5.98 ± 1.58 a	0.21 ± 0.08 b	8.71 ± 0.93 a	0.20 ± 0.20 b
Cr (μg g^{-1})	16.3 ± 6.13 a	2.05 ± 0.77 b	11.9 ± 3.33 ab	6.50 ± 4.34 ab
Cu (μg g^{-1})	11.0 ± 2.83 a	8.22 ± 0.71 a	13.5 ± 3.41 a	5.21 ± 1.58 a
Fe (μg g^{-1})	481 ± 133 ab	233 ± 7.61 b	699 ± 174 a	320 ± 88.8 ab
Ni (μg g^{-1})	48.7 ± 7.00 a	18.0 ± 8.24 a	40.6 ± 12.9 a	12.3 ± 5.89 a
Zn (μg g^{-1})	41.7 ± 7.87 a	43.6 ± 6.82 a	44.0 ± 9.59 a	33.5 ± 8.65 a

Table 5: Foliar nutrient concentrations (μg g^{-1}) of plant species collected by David Jeffrey and Ray Specht in May 1990 from Croagh Patrick and analysed by Roger Reeves. Samples were washed in deionised water, ashed at 500° C, taken up in 2 M hydrochloric acid and analysed on an ARL 34000 inductively coupled plasma optical emission spectrometer.

	Al	B	Ca	Co	Cr	Cu	Fe	K	Mg	Mn	Na	Ni	P	Sr	Zn
Ultramafic															
Blechnum spicant	43	20	922	<1	1	7.9	66	20909	3469	16	1610	9.0	929	11.2	16.2
Calluna vulgaris	59	16	2883	<1	<1	5.3	58	3096	1566	273	812	9.4	687	10.7	12.1
Carex pilulifera	118	6	803	<1	4	3.8	183	4596	2363	75	555	31.2	616	15.6	15.7
Erica cinerea	18	18	3331	<1	<1	6.4	35	4489	2042	66	2205	6.1	821	7.7	12.0
Nardus stricta	4	1	917	<1	<1	2.3	35	7694	1145	33	353	35.6	1238	3.7	17.9
Non-ultramafic															
Agrostis cf. *capillaris*	15	65	1363	<2	<1	6.1	42	21050	1120	200	1853	<1.5	1311	11.8	22.7
Agrostis cf. *capillari*s	18	16	1512	<1	<1	4.6	43	19442	1108	119	957	<0.8	1184	12.7	27.4
Calluna vulgaris	84	28	2652	<1	<1	7.6	55	4385	1598	337	1405	<0.8	1018	11.7	17.4
Calluna vulgaris	162	37	4720	<1	<1	7.1	106	2986	2129	226	1024	<0.9	635	20.3	20.2
Carex viridula cf. subsp. *brachyrhyncha*	20	29	940	<1	<1	10.2	45	17412	1136	92	911	<0.7	1175	10.8	31.2
Carex panacea	28	51	1282	<1	<1	15.9	67	17139	1550	138	1323	0.9	1166	11.2	30.0
Eleocharis palustris	6	15	977	<1	<1	8.6	38	12836	926	63	940	<0.8	1066	3.3	33.5
Empetrum nigrum	52	23	3257	<1	<1	7.0	47	6030	1312	213	842	<0.8	804	10.3	13.2
Erica cinerea	66	17	2918	<1	<1	6.7	60	3984	1528	379	1535	0.9	498	6.5	15.5
Erica tetralix	106	26	4375	<1	<1	8.5	78	3899	1633	265	1331	<0.7	566	8.7	18.9
Festuca ovina	24	6	1200	<2	<2	5.5	45	6276	573	280	517	3.2	658	7.6	30.1
Festuca rubra	17	22	1008	<1	<1	5.4	36	15969	866	110	937	<1.1	1421	5.5	26.0
Juncus squarrosus	5	26	729	<1	<1	4.0	33	14984	1146	58	1671	<0.8	1613	2.9	74.4
Juncus squarrosus	17	27	683	<1	<1	6.3	35	12096	840	107	133	<0.7	1043	2.8	28.0
Nardus stricta	44	9	653	<1	<1	2.2	74	8361	742	101	604	<0.8	904	4.1	22.4
Pedicularis palustris	55	59	4721	<1	<1	18.7	63	23501	3778	849	4914	1.4	2530	22.8	45.7
Potentilla erecta	10	79	4773	<1	<1	7.3	41	15986	4069	420	1944	<0.7	2280	57.3	65.2
Potentilla erecta	35	49	5802	<1	<1	7.8	80	12736	4465	489	2640	<0.9	1564	80.2	78.6
Vaccinium myrtillus	42	43	5971	<1	<1	8.3	40	5591	1541	645	857	<0.8	1383	10.5	18.1

Figure 1: Two ultramafic sites in western Ireland: (a) Serpentinite outcrop on the path to the summit of Croagh Patrick, County Mayo, Ireland, and (b) grassland over peridotite at Dawros, County Galway, Ireland.

Figure 2: Frequency distribution of Ellenberg 'Reaction' values (modified by Hill et al. 1999) of plant species found at Dawros and Croagh Patrick ultramafic sites in western Ireland. Lower values indicate species associated with more acidic soils (calcifuges) while higher values indicate species associated with more alkaline soils (calcicoles).

Figure 3: Mean (± standard error) above-ground biomass of *Lolium perenne* grown in a bioassay experiment in various ultramafic (grey) and non-ultramafic (white) soils for 34 days. Letters indicate significant differences according to a Tukey's test with $P < 0.05$.

Figure 4: Mean (± standard error) (a) shoot and (b) root biomass of *Lactuca sativa* grown in a bioassay experiment using soil from the Croagh Patrick ultramafic site in western Ireland with various nutrient amendments for 37 days (note logarithmic scale). Letters indicate significant differences according to Tukey's tests with $P < 0.05$. The bottom panel (c) shows typical plants from each treatment.