Dalrymple, SE, Hopkins, J, Carter, SP and Slingsby, DR

Nutrient additions three decades on: potential interactions of nutrients and climate in the recovery of a high latitude serpentine system

http://researchonline.ljmu.ac.uk/id/eprint/12165/

Article

Citation (please note it is advisable to refer to the publisher's version if you intend to cite from this work)

Dalrymple, SE, Hopkins, J, Carter, SP and Slingsby, DR (2019) Nutrient additions three decades on: potential interactions of nutrients and climate in the recovery of a high latitude serpentine system. PLANT BIOSYSTEMS. ISSN 1126-3504

Nutrient additions three decades on: potential interactions of nutrients and climate in the recovery of a high latitude serpentine system

Sarah E. Dalrymple[a]*, John Hopkins, Stephen Carter[b] & David S. Slingsby[c]

[a] *School of Natural Sciences & Psychology, Liverpool John Moores University, Liverpool, United Kingdom.*

[b]*Headland Archaeology, Edinburgh, Scotland.* [c]*The Open University, United Kingdom.*

* School of Natural Sciences & Psychology, Liverpool John Moores University, Byrom Street, Liverpool L3 3AF. s.e.dalrymple@ljmu.ac.uk

Nutrient addition experiments initiated in 1980 on the Keen of Hamar, Shetland Isles, have produced a unique dataset of long-term vegetation response to amendments of major plant growth nutrients (N, P, NP, NPK and NPKCa). Previous studies have reported the notable impact of phosphorus on the ‘serpentine debris’ community, and the negligible effect of nitrogen. However, a survey in 2010 provided our first indication that the experimentally-induced phosphorus effect was weakening and this was consolidated by further surveys of vegetation cover and community composition. This community shift might have been different had the local climate acted synergistically with phosphorus additions: in the last few years of the study the Shetland Isles experienced particularly low spring rainfall - the dry spell may have been a well-timed environmental filter driving community recovery rather than a permanent change of state to heathland on an organic soil. The longevity of our investigation is a unique opportunity to explore vegetation response to the key drivers of global environmental change, namely climate change, eutrophication as a result of agricultural intensification, and the potential for invasion of species as new resource-rich niches become available.

Keywords: phosphorus limitation; arctic-alpine; fellfield; nitrogen; eutrophication; stable states

Introduction

Eutrophication of terrestrial systems by nitrogen (N) inputs has been widely blamed for plant community changes and species losses, but anthropogenic phosphorus (P) inputs are also increasingly demonstrated to be damaging (e.g. Wassen *et al.*, 2005). Elevated P inputs to terrestrial systems result from various anthropogenic activities such as agricultural fertilizer applications and manure deposition from cattle and these often far exceed natural inputs (Filippelli 2008). Consequently, most studies of community response to P inputs are concerned with agricultural systems in temperate regions and the subsequent impacts on aquatic systems that receive these inputs, whilst high latitude and high altitude systems have been relatively overlooked (Wu et al. 2013). Our limited understanding of P cycles in arctic and alpine regions suggests that they tend to be dominated by biochemical cycles where moisture availability enables the development of soils with relatively high organic matter content, but these cycles are replaced by geochemical processes in drier substrates with subsequent P limitation more likely to occur (Weintraub 2011). The drier fellfield systems fall into this latter category and include serpentine systems which, whilst not being limited to high latitude or high altitudes, are examples of nutrient-limited systems with low N, low P and both low N and P availability (Turitzin 1982). These properties, coupled with high plant endemism (Batianoff and Singh 2001) make serpentine regions of particular concern when identifying communities at risk of eutrophication-induced extinctions.

The loss of species resulting from eutrophication typically occurs through competitive exclusion (Wassen et al. 2005) when there are competitive species present that are able to rapidly exploit the available nutrients and outcompete the resident species that are adapted to low nutrient and often, very stressful conditions. Serpentine systems are usually resistant to colonisation by non-serpentine specialists due to high heavy metal concentrations, low organic matter and free-draining soils, but can be vulnerable to invasion when the normally restrictive growing conditions are ameliorated through increases in nutrients (Huenneke *et al.*, 1990; Vallano, Selmants and Zavaleta, 2012) and/or water availability (Schedlbauer 2015). However, the patterns of response are variable with some invasive species appearing to be N-limited and some P-limited, whilst others only need increased water availability to become established.

Although the potential for P limited sites to succumb to eutrophication and consequent species loss is well-established, there is a lack of consensus as to the relative importance of N versus P in driving species declines and community composition shift (Soons et al. 2017). This is particularly the case for high latitude and high altitude systems where nutrient addition experiments have been focused on a handful of sites (Weintraub 2011). Of the nutrient addition experiments that have been undertaken on high latitude or high altitude sites, there are no reports of recovery from the deliberate nutrient inputs suggesting that restoration of these systems will require substantial intervention and in some cases, reinstatement of typical soil conditions and vegetation composition may not be possible at all.

This paper reports on a nutrient addition experiment onto a serpentine fellfield system of which the monitoring spans more than 30 years. In addition to metrics of species richness and cover, we report on qualitative changes in community composition that evidence a shift in response to nutrient additions. We aim to demonstrate for the first time, that these systems are able to recover from anthropogenic inputs and that there may be an important role for climate in facilitating autonomous habitat restoration. Our investigation is an exceptional case study in how natural ecosystems might respond over the long-term to multiple threats and how the threats act simultaneously to exacerbate or weaken the impacts of others.

Study site

The Keen of Hamar is the largest area of serpentine debris in Europe (Scottish Natural Heritage 2010). It is situated on Unst, the most northerly of the Shetland Isles (Figure 1) and has long been of interest due to its unusual flora. The debris is formed of loose stones created from the underlying serpentine rock by a process of frost shattering. Serpentine, or ultramafic soils, are derived from igneous or metamorphic rocks, having less than 45% silica, high Mg, Cr, Fe, Co and Ni and low P, K and Ca (Proctor 2003) and on the Keen, form a montane-tundra soil (Spence 1970).

The debris vegetation, whilst being characterised by very small plants and low vegetation cover (Figure 2), is typified by five taxa that are known as the ‘serpentine specialists’. These comprise *Cerastium arcticum*, formerly considered to be the endemic *C. nigrescens* ssp. *nigrescens*, the nationally rare *Arenaria norvegica* ssp. *norvegica*, *Arabis petraea*, local forms of *Cochlearia officianalis* and *Rubus saxatilis*. The Keen, as with other Scottish serpentine sites, has close phytosociological affinities with Icelandic and Faeroese fellfield communities, with most species typically being associated with very low vegetation cover (<10%) (Spence 1970). The serpentine creates particularly challenging conditions that prevent invasion from non-serpentine specialists occupying the patches of glacial drift soil that are interspersed with the debris habitat, and the debris flora appears to be a climax community as it has not been grazed for many years, if at all, yet has maintained its low coverage of plants over large areas. A feature of the grass- and *Calluna vulgaris*-dominated serpentine heath is the relatively high species richness with a variety of herbs; some of these are basicilous such as *Thymus polytrichus* and *Linum catharticum* and others, such as *Potentilla erecta*, are more commonly associated with *C. vulgaris* growing on acid soil.

Being high latitude but at sea level, the climate on Unst is classed as submontane-oceanic and climate records for Shetland indicate a general warming over recent decades (Kendon et al. 2018) that is projected to continue in keeping with global trends (IPCC 2014); for soils such as those on the Keen this is likely to exacerbate the lack of water holding capacity. The serpentine specialists appear to be vulnerable to warming (possibly directly, although the association is correlative; Slingsby et al. 2010) but have adaptations that may allow them to tolerate a certain amount of drought (i.e. low and compact growth forms, hairs, purple colouration).

Carter, Proctor and Slingsby (1987a) indicated that a large amount of P in Keen soils was inorganic and theorised that low P might interact with low water availability by restricting root growth and therefore making plants vulnerable to drought. In the early 1980s, a small part of the original extent of the serpentine debris was fertilised and seeded to create cattle pasture and a region of the site referred to as the Lower Keen was used for winter feeding receiving nutrient inputs in the form of manure. In response to this, Proctor & Slingsby initiated a nutrient addition trial in 1980 that showed that P and not N was the key element limiting plant growth on the debris (Carter et al. 1987a). Their P additions produced a marked increase in grass cover in only 5 years as well as promoting colonisation and growth of a handful of herbaceous species. The formation of a closed grass-dominated community was so rapid that Carter et al. (1987b) suggested that the effects of eutrophication were likely to persist indefinitely and that it posed a major threat to this habitat and its rare plant species.

The Keen is an ideal site for a nutrient addition study because low inputs of N from atmospheric pollution (some of the lowest in Europe; Air Pollution Information System 2018, http://www.apis.ac.uk/) mean that experimental nutrient additions are not confounded by elevated background levels of N deposition.

Methods

The present study made use of an existing long term dataset which has been collected from an experimental field site on the Keen of Hamar, Unst, Shetland, since 1980 (Carter et al. 1987b). The field site consists of permanent 1 m^2 quadrats, each receiving one of the following combinations of nutrients and Unst tap water: N, P, NP, NPK, CaNPK, and tap water alone (the control). The quadrats were arranged in a randomized block design, with one quadrat per block receiving each nutrient combination. Two blocks were established in the sparsely-vegetated debris on the Upper Keen (Figure 1), and a further two blocks were established in the moderately-vegetated debris in the middle debris patch. Nutrients were applied between 1980 and 1983, with NP quadrats receiving three applications and all other quadrats receiving two. N was applied as 10g N m^{-2} ammonium nitrate. P as 5g P m^{-2} dihydrogen phosphate. K was applied as 10g K m^{-2} potassium chloride. Ca was applied as 1.2 tonnes hectare ground limestone on the first application, then 100g Ca m^{-2} calcium carbonate. For full details of the experimental design see Carter et al. (1987b).

Community composition monitoring

In June, July or August of the seven survey years (1981, 1984, 1992, 1993, 2006, 2010 and 2013), point quadrats were used to ascertain the cover of each species present in the permanent quadrats. Within each quadrat 10 x 10 pins were evenly spaced in grid formation, giving a total of one hundred pins. Species cover estimates were generated from the number of ‘pin contacts’ i.e. where a pin came into contact with a species. Each species was only counted once per pin but where several species were in contact with the same pin, all species were recorded and cover totals for all species per plot of more than 100 were possible. Due to the very small size of many plants, some could only be identified confidently to genus level (*Agrostis*, *Festuca* and *Carex*).

Data analysis

Species richness and combined species cover (the sum total of pin contacts generated from pin frame quadrats) are presented without further analysis due to the very low of replication in the original study design (n=2 for each vegetation site), following

Weissgerber et al (2015) for small sample size studies we graphically present the data from each quadrat rather than summary statistics (as any ‘average’ would be based on ether n= 2 or 4). Community composition and abundance was ordinated using a Principle Components Analysis distinguishing between nutrient treatment, the debris type (sparsely- or moderately-vegetated) and the year of survey using PRIMER version 6.1.1.13. Centroids for each survey year were calculated as the mean co-ordinates for principal components 1 and 2 for plots grouped by debris type and whether the treatment contained P or not.

Results

Species richness shows a general increase over the study period to a maximum in 2010 for most treatments and the control in all four blocks. Although the pattern is variable, any treatments containing P result in higher numbers of species per plot than the control and N-only treatment (Figure 3). After 2010, the species richness generally decreases with the exception of the NP treatment in a sparsely-vegetated treatment block (Figure 3b) and the NPKCa treatment in one of the moderately-vegetated blocks (Figure 3d) which both continue to increase in species richness to 2013. Where species richness has declined, these have so far failed to return to the species numbers that were in the plots at the start of the study.

Combined species cover changed markedly over the study period in all four treatment blocks (Figure 4). All quadrats which received P additions, either alone or in combination with other nutrients achieved higher plant cover than the N addition and control. The maximum cover achieved was recorded in 2006 in both sparsely- and moderately-vegetated debris although the treatment blocks in the latter debris type generated higher plant cover totals than the former. Similarly, the moderately-colonised debris showed a greater difference between P treatments and non-P treated quadrats (N treatments and control).

After 2006 plant cover decreases in all P treatments closing the gap between P-present and P-absent treatments. The control and N treatment in Figure 3 indicate that the combined species cover increases were not limited to P-present treatments but that there were also increases in plant cover reaching maxima in 2006 or 2010. These peaks are much less pronounced than those produced by P addition (and arguably negligible in the treatment block represented by Figure 3b) but suggest that there may be some landscape-level process that is enhancing plant productivity that could have operated synergistically with P treatments.

The principal components analysis of community composition data generated eigenvalues of 444 for principal component 1 and 114 for principal component 2 explaining 85.8% of the variation in the dataset (68.3% for PC1 and 17.5% for PC2). Of the species recorded, the vast majority produce very low eigenvector values with both principal components 1 and 2 with the exception of *Festuca* spp. with an eigenvector coefficient of -0.872 and *Thymus polytrichus* generating a coefficient of -0.468 both against principal component 1, and *Agrostis* spp. which results in a coefficient of 0.988 with principal component 2. Figure 5 displays the PCA ordination of quadrats labelled by treatment with the control and N treatments concentrated in the bottom right quadrant of the ordination. The remainder of the treatments are spread in a triangular pattern that represents the dominant species as indicated by the eigenvectors above, namely *Festuca* ssp. and *Agrostis* ssp. in the bottom left and top right quadrants respectively. Figures 6a, 6b, 6c and 6d show centroids for each of the surveyed years for the plots by vegetation type and whether the treatments applied contained P (i.e. the four combinations arising from sparsely- *vs.* moderately-vegetated debris and with or without P). These ordinations indicate how the two debris types respond very differently to P treatments, especially in the first few years of the study, with the most marked shift in community composition resulting from P additions (alone or in combination with other treatments) to moderately-vegetated debris.

Discussion

A thirty yearlong manipulative experiment on serpentine soils is, as far as we are aware, unique in plant ecology. This makes it an important study although challenging to interpret due to the lack of replication. One way to view such data is that despite the lack of formal statistical tests of treatment effects, they can generate hypotheses for future experimental testing, both at this location and at other serpentine sites. However, we are not constrained to hypothesis generation because a key early prediction for this site was that the effects of eutrophication would be permanent and the pre-eutrophication vegetation *would not recover* (Carter et al, 1987b). This prediction enables us to use deductive (rather than inductive) logic and in such circumstances *replication is not required* – it is simply a case of observing if the prediction has been met (Oksanen, 2001). All four of the experimental blocks are now showing a return towards the original state – a result also seen in the PCA analysis – so these experiments can falsify this prediction.

Phosphorus limitation

Our study strongly suggests that P is a key nutrient limiting plant growth and increased availability enables plants to overcome some of the other significant constraints characteristic of serpentine. P addition provokes a shift from open debris vegetation to a closed community with a composition akin to heath-grassland (albeit with a lower stature than that of neighbouring vegetation patches on soils with higher organic matter). The nitrogen limitation identified in Californian serpentine grasslands (Going et al. 2009) was conspicuously absent in our study with P limitation being the more likely explanation for the low vegetation cover on the Keen.

The likely mechanism of P limitation is the lack of P in the soil parent material which means that inputs are low, in combination with depletion-driven P limitation where P in all forms is lost via leaching over long-timescales (Vitousek et al. 2010). Transactional P limitation, or the slow release of P in mineral forms, is also likely. This suggests that P is an ‘ultimate limiting nutrient’ according to Vitousek et al.’s (2010) definition of being “capable of transforming ecosystems, typically by driving a substantial and persistent change in ecosystem structure and/or species composition". For example, P additions to the Keen have caused net inputs of N and C by facilitating the increase in primary production in treatment areas where before there was little or no biomass, whereas additions of N did not cause the reciprocal effect. On the Keen, we can confidently conclude that P addition produces a novel niche space in this serpentine system that is evidenced by the increase in growth of non-debris species (MacDougall et al. 2009). However, this niche appears to be temporary as shown by the recent decline of non-serpentine specialists in P-treated plots.

Differential response based on debris type

The debris type mediated the community response to P addition resulting in rapid community change of moderately-vegetated debris with a more modest shift in community composition in sparsely-vegetated debris. Species richness and combined species cover are also slower to respond to the P additions (Figures 3 and 4). The marked shift in moderately-vegetated debris ordinated in Figure 5 (and with debris type differentiated in Figure 6) is principally explained by the rapid increase in *Agrostis* in the first few years of the experiment before a shift towards a *Festuca*-dominated community occurs over the following 22 years. It may be possible that serpentine ecotypes of *Agrostis* (identified by Marrs and Proctor, 1976), present in the moderately-vegetated debris were in an ideal position to exploit the added P but then could not compete when the *Festuca* took over. Regardless of this shift from one grass species to another, the presence of vegetation on the debris makes the community more responsive to P inputs due to the ability to exploit the sudden excess of this limiting resource. Once P has been taken up by plants it cycles very tightly between vegetation and soil (Filippelli 2008) so the greater abundance of vegetation retains a higher proportion of the initial P inputs as compared to the sparsely-vegetated debris.

Vegetation changes without P additions

Although this investigation has evidenced a substantial impact of P additions, there has also been a slight increase in species richness and to a lesser extent, combined species cover, in most of the control and N-treated plots peaking in 2006 and 2010. This indicates that there are site-wide changes that promoted plant colonisation and growth aside from those associated with P addition. Slingsby et al. (2010) showed that on the Keen the number of days in the growing season had increased by over 40 days over their study period 1976-2006, a pattern that has been demonstrated across northern latitude regions as increasing by > 6 days per decade since 2000 (Zeng et al. 2011) and this may explain the increased species richness and cover. In addition to an extended growing season, it is possible that the earlier start also increases water availability as the temperatures required for growth coincide with wetter times of the year and the growing season is not so tightly coupled to periods when droughting is likely to occur over the late spring and summer.

Where the control and N plots show an increase in combined species cover and species richness, there is then a marked decrease in these variables after 2006 or 2010 (depending on the plots). These decreases may be explained by a period of particularly low March rainfall for Shetland (Figure 7). The spring is a key time for plant growth in other serpentine systems (Blake Suttle and Thomsen 2007) and droughts at this time can have important implications for the success of vegetative growth and subsequent reproductive success. On the Keen, Spence (1957) noted that April-May was a critical time for resuming growth, but with the extended growing season, it can be assumed that March is now a key time for early growth. Over our study period, 12 of the last 13 years had rainfall below the mean value for March precipitation (117.3mm) and the last four years are particularly dry. The extremely stressful conditions during this important growth phase are a likely explanation for species loss and biomass decline for all treatments and control.

Interacting effects of phosphorus and water availability

Wassen et al. (2005) identified positive associations between the presence of endangered species and P limitation that have important implications for the conservation of rare plants. However, their study focussed on terrestrial wetlands and moist grasslands meaning that nutrient limitation could be analysed without the restrictions of water availability on species richness and productivity. In our study, the Keen is subject to periodic droughting due to the low soil water-holding capacity and an exploration of nutrient limitation and plant community response would be incomplete without investigating the potential of climate to influence community composition. In California and Australia, increased nutrients and water availability leads to greater abundance of species not normally found in those xerophytic communities (Eskelinen and Harrison 2014; Dwyer et al. 2015). Similarly, numbers of exotic species on Californian serpentine doubled in years of high rainfall (Gram *et al.* 2004). In the serpentine communities of the Keen, it seems likely that the impact of the P additions might be amplified by favourable climate change.

In one of the earliest reports on this study, Carter et al. (1987b) express the concern that P additions might bring about a permanent change in the Keen vegetation. Dwyer et al. (2015) presented a theoretical framework that would support this prediction and proceeded to identify such a phenomenon in their arid study system. Low P and low water availability impose a strong filter promoting only species that can tolerate such conditions, whereas the high P and water availability facilitate those species that can maximise growth under favourable resource availability. According to this framework, community change on the Keen could similarly be interpreted as following a directional trajectory from the ecologically specialised serpentine debris community typified by stress-tolerant species, to a qualitatively different heath or grassland assemblage dominated by more competitive species. However, the relatively recent decrease in species richness and cover, in conjunction with the community reversion shown in the PCA (Figure 5) strongly suggests that this prediction was incorrect. This is one of the most robust conclusions of this study, and of considerable conservation importance for such sites. We speculate that the community sampled in the final few years of the study was subject to strong environmental filtering from lack of water and the possible return of P-limitation.

Future survival of serpentine debris and resident flora

Bellard et al. (2013) suggest that climate change will present “restoration opportunities” in systems that have been colonised by invasive alien species and have extreme climates. Although Shetland falls in the boreo-temperate region which is not severely adverse to plant growth, the Keen is exceptional due to the wind exposure (Spence 1957) and lack of water-holding capacity in the soil. Consequently, this high latitude serpentine system is a good example of how invasive species might be constrained by climate change, in this case drought, rather than promoted. Whether the serpentine specialists can also tolerate climate change and benefit from the absence of competition is not known, but declines of serpentine species (Slingsby et al. 2010) suggest that they will eventually be lost from the site if droughts become longer.

Where communities have undergone substantive compositional shifts, the potential for reversing such changes is dependent on the initial status of the community, and whether the change initiated internal feedbacks that sustain the new stable state e.g. in arid grasslands (D'Odorico et al. 2012) but is generally thought to be possible only with significant management intervention if at all. On the Keen, serpentine soils with relatively low vegetation cover are able to retain P in internal cycles but do seem able to eventually shed P over relatively long-timescales. However, in other serpentine systems there are a number of factors which may slow the recovery down or prevent it altogether. Many serpentine sites are N-limited (Huenneke et al. 1990) but in areas of increasing N deposition, it is likely that the excess P can be exploited against a backdrop of elevated atmospheric N deposition, further increasing P retention. In addition, many serpentine sites have considerably higher vegetation cover than the Keen e.g. in Greece (Karataglis et al. 1982; Tsiripidis et al. 2010), Australia (Batianoff and Singh 2001) and Canada (Dearden 1979), meaning that P additions are likely to be conserved within a system that has the capacity to cycle the P in a plant-available form and recovery is unlikely without management. In fact, Vitousek et al. (2010) suggest that most incidences of P limitation (such as those identified by Elser et al., 2007) can be explained as “anthropogenic P limitation secondary to human alterations of the N cycle" rather than natural phenomena. The Keen therefore gives us important insights into the future maintenance of serpentine systems and P-limited habitats more widely: if the recovery of debris habitat is likely to take >30 years after one or two discrete applications of nutrients, then it seems unlikely that sustained P applications could be mitigated in this or other serpentine systems. This does not bode well for serpentine systems given the increasing P inputs to natural systems globally. In China for example, annual P inputs in 2013 matched those experimentally applied to the Keen (Lu and Tian 2017) but these are the peak in several decades of increasing P applications rather than one-off applications and the trend seems set to continue increasing. As a consequence, there is little hope that species dependent on low nutrient conditions for survival will persist through these global patterns of resource use.

The particular situation of serpentine systems presents further opportunities and challenges for their conservation. On the Keen, topsoil removal has been trialled and is probably necessary to reverse the soil development that has followed sustained nutrient input. Removing the topsoil restores the surface substrate to debris habitat and because harsh sites are less invaded (Zefferman et al. 2015) so debris restoration can reinstate stressful conditions preventing the encroachment of generalist species and minimising competition for the serpentine specialists. In other situations, vegetation and topsoil removal may not be so effective and it may be challenging to determine what level of soil removal is optimal. Soil removal may also take the soil seed bank and damage plant assemblages that are the source for new generations, and many serpentine regions are isolated and difficult to access presenting logistical constraints as well as ecological problems. Site managers may consequently feel that they have little scope to deal with the overriding threats of increasing P inputs and climate change.

Although this study is based on a single site and has very limited replication, the longevity of our investigation is a unique opportunity to explore theoretical predictions of the response of vegetation to some of the key drivers of global environmental change, namely climate change, eutrophication as a result of agricultural intensification, and the potential for invasion of species from other habitats as new resource-rich niches become available. The timescales allow us to observe the interacting effects of weather patterns and nutrient addition impacts against very low ambient pollution levels, but also at high latitude and under xeric conditions (at least with respect to soil water availability) where climate change is thought to be particularly exaggerated in its impacts. The presence and invasion of non-serpentine species adds a third axis to the pressures faced by the Keen rarities and together this system allows us to study processes of global environmental change in microcosm. Extrapolations from a site-based study are always limited but there is relevance to high latitude, high altitude, xeric, and naturally nutrient-poor systems which means the value of our study is much greater than the limited area might otherwise suggest.

Acknowledgements

The authors wish to thank Scottish Natural Heritage for access to the study site and the 2006 expedition team members from the University of Aberdeen, Samuel Green and Molly Toal for their contributions in data collation and analysis. Professor Dave Wilkinson provided valuable comments on a draft manuscript and insight into the interpretation of this data.

Disclosure statement

The authors declare no conflict of interest.

References

Batianoff GN, Singh S. 2001. Central Queensland serpentine landforms, plant ecology and endemism. S Afr J Sci. 97(11–12):495–499.

Bellard C, Thuiller W, Leroy B, Genovesi P, Bakkenes M, Courchamp F. 2013. Will climate change promote future invasions? Glob Chang Biol. 19(12):3740–3748.

Blake Suttle K, Thomsen MA. 2007. Climate change and grassland restoration in California: Lessons from six years of rainfall manipulation in a north coast grassland. Madroño. 54(3):225–233.

Carter SP, Proctor J, Slingsby DR. 1987. Soil and Vegetation of the Keen of Hamar serpentine, Shetland. J Ecol. 75(1):21–42.

Carter SP, Proctor J, Slingsby DR. 1987. The effects of fertilization on part of the Keen of Hamar Serpentine, Shetland. Trans Bot Soc Edinburgh. 45(2):97–105.

D’Odorico P, Okin GS, Bestelmeyer BT. 2012. A synthetic review of feedbacks and drivers of shrub encroachment in arid grasslands. Ecohydrology. 5(5):520–530.

Dearden P. 1979. Some factors influencing the composition and location of plant communities on a serpentine bedrock in western Newfoundland. J Biogeogr. 6(1):93–104.

Dwyer JM, Hobbs RJ, Wainwright CE, Mayfield MM. 2015. Climate moderates release from nutrient limitation in natural annual plant communities. Glob Ecol Biogeogr. 24(5):549–561.

Eskelinen A, Harrison S. 2014. Exotic plant invasions under enhanced rainfall are constrained by soil nutrients and competition. Ecology. 95(3):682–692.

Filippelli GM. 2008. The Global Phosphorus Cycle: Past, Present, and Future. Elements. 4:89–95.

Going BM, Hillerislambers J, Levine JM. 2009. Abiotic and biotic resistance to grass invasion in serpentine annual plant communities. Oecologia. 159(4):839–847.

Gram WK, Borer ET, Cottingham KL, Seabloom EW, Boucher VL, Goldwasser L, Micheli F, Kendall BE, Burton RS. 2004. Distribution of plants in a California serpentine grassland: Are rocky hummocks spatial refuges for native species? Plant Ecol. 172(2):159–171.

Huenneke LF, Hamburg SP, Koide R, Mooney HA, Vitousek PM. 1990. Effects of Soil Resources on Plant Invasion and Community Structure in Californian Serpentine Grassland. Ecology. 71(712):478–491.

IPCC. 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva, Switzerland.

Karataglis S, Babalonas D, Kabasakalis B. 1982. The Ecology of Plant Populations Growing on Serpentine Soils. Phyton (B Aires). 22:317–327.

Kendon M, McCarthy M, Jevrejeva S, Matthews A, Legg T. 2018. State of the UK climate 2017. Int J Climatol. 38(July):1–35.

Lu C, Tian H. 2017. Global nitrogen and phosphorus fertilizer use for agriculture production in the past half century: Shifted hot spots and nutrient imbalance. Earth Syst Sci Data. 9(1):181–192.

MacDougall AS, Gilbert B, Levine JM. 2009. Plant invasions and the niche. J Ecol. 97(4):609–615.

Marrs RH, Proctor J. 1976. The Response of Serpentine and Non-Serpentine Agrostis Stolonifera to Magnesium and Calcium. J Ecol. 64(3):953–964.

Met Office. 2018. UK Climate - Historic Station Data, Lerwick. [accessed 2018 Jul 26]. https://www.metoffice.gov.uk/pub/data/weather/uk/climate/stationdata/lerwickdata.txt.

Schedlbauer JL. 2015. Serpentine ecosystem responses to varying water availability and prescribed fire in the U.S. Mid-Atlantic region. Ecosphere. 6(7):art108.

Slingsby D, Hopkins J, Carter S, Dalrymple S, Slingsby A. 2010. Change and stability: monitoring the Keen of Hamar 1978-2006.

Soons MB, Hefting MM, Dorland E, Lamers LPM, Versteeg C, Bobbink R. 2017. Nitrogen effects on plant species richness in herbaceous communities are more widespread and stronger than those of phosphorus. Biol Conserv. 212:390–397.

Spence DHN. 1970. Scottish serpentine vegetation. Oikos. 21(1):22–31.

Tsiripidis I, Papaioannou A, Sapounidis V, Bergmeier E. 2010. Approaching the serpentine factor at a local scale-a study in an ultramafic area in Northern Greece. Plant Soil. 329(1):35–50.

Turitzin SN. 1982. Nutrient Limitations to Plant Growth in a California Serpentine Grassland. Am Midl Nat. 107(1):95–99.

Vallano DM, Selmants PC, Zavaleta ES. 2012. Simulated nitrogen deposition enhances the performance of an exotic grass relative to native serpentine grassland competitors. Plant Ecol. 213(6):1015–1026.

Vitousek PM, Porder S, Houlton BZ, Chadwick OA. 2010. Terrestrial phosphorus limitation: Mechanisms, implications, and nitrogen-phosphorus interactions. Ecol Appl. 20(1):5–15.

Wassen MJ, Venterink HO, Lapshina ED, Tanneberger F. 2005. Endangered plants persist under phosphorus limitation. Nature. 437(September):547–550.

Weintraub MN. 2011. Phosphorus in Action. Bünemann E, Oberson A, Frossard E, editors. Berlin, Heidelberg: Springer Berlin Heidelberg (Soil Biology).

Wu Y hong, Zhou J, Yu D, Sun S qin, Luo J, Bing H jian, Sun H yang. 2013. Phosphorus biogeochemical cycle research in mountainous ecosystems. J Mt Sci. 10(1):43–53.

Zefferman E, Stevens JT, Charles GK, Dunbar-irwin M, Emam T, Fick S, Morales L V, Wolf KM, Young DJN, Young TP. 2015. Plant communities in harsh sites are less invaded : a summary of observations and proposed explanations. :1–21.

Zeng H, Jia G, Epstein H. 2011. Recent changes in phenology over the northern high latitudes detected from multi-satellite data. Environ Res Lett. 6(4):045508.

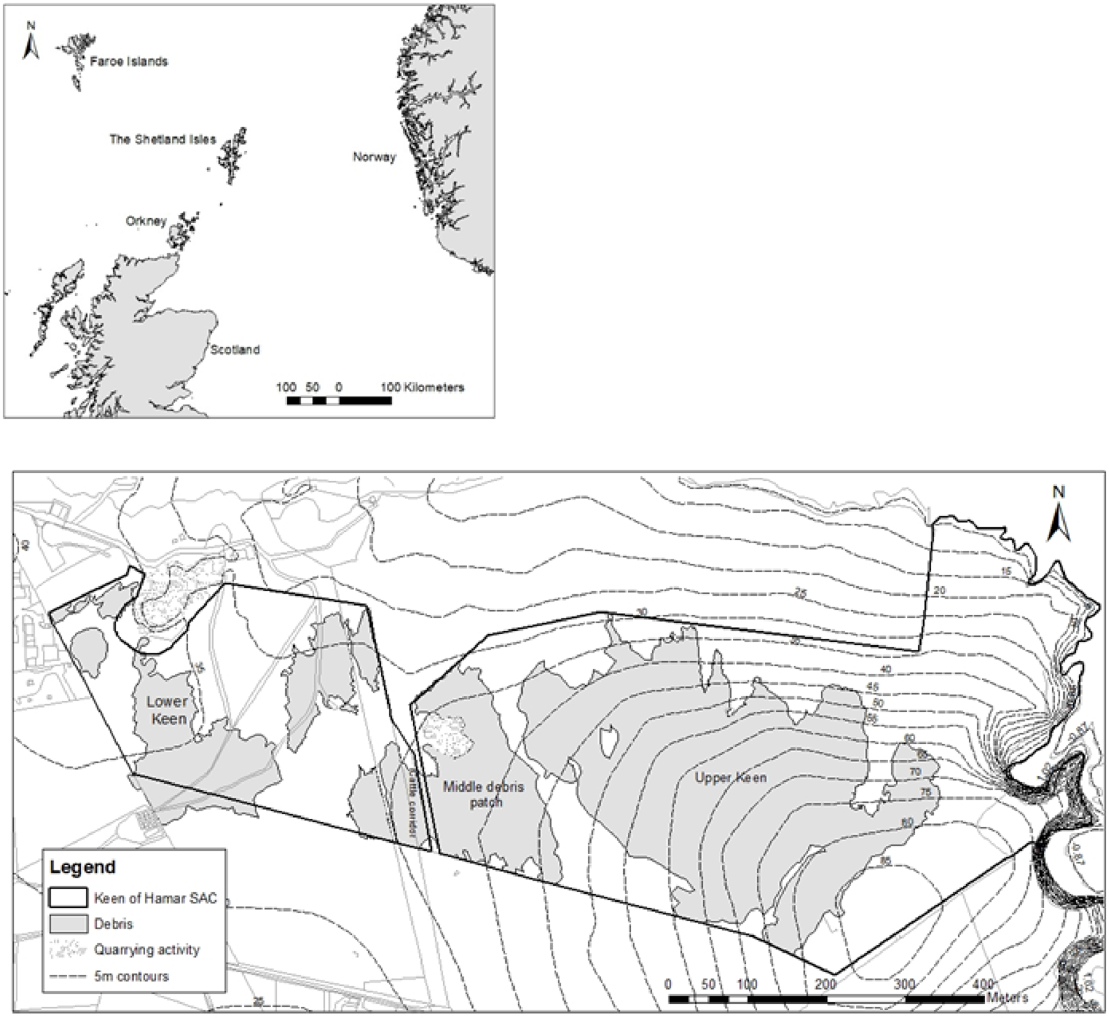


Figure 1. Position of the Shetland Isles relative to British and Norwegian landmasses (a). The Keen of Hamar is on Unst, the most northerly of the Shetland Isles. (b) Distribution of debris habitat on the Keen of Hamar, Unst. Mapping imagery in this document belongs to and was derived from © Crown Copyright Ordnance Survey. An EDINA Digimap/ JISC supplied service. All ESRI screen shots and imagery belong to and were derived from © Environmental Systems Research Institute, Inc.

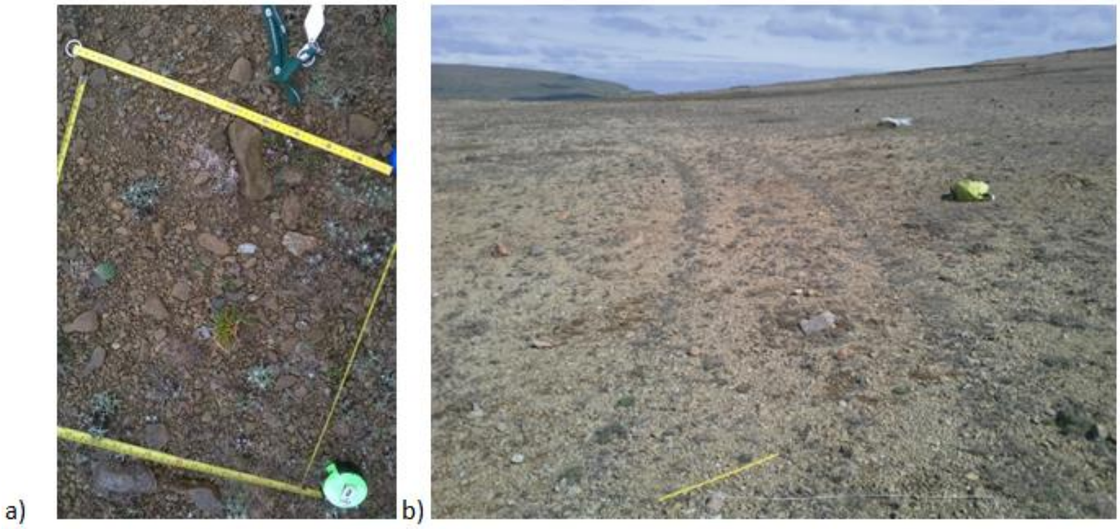


Figure 2. Typical vegetation on the middle debris patch in (a) wet conditions (50 x 50 cm quadrat marked) and (b) the same debris patch on the following day; note the difference in colour between wet and dry conditions indicating the speed at which the upper soil layer dries out. Also visible are wheel ruts from long abandoned mineral extraction work – these slight depressions are made more visible by higher vegetation cover than the surrounding debris.

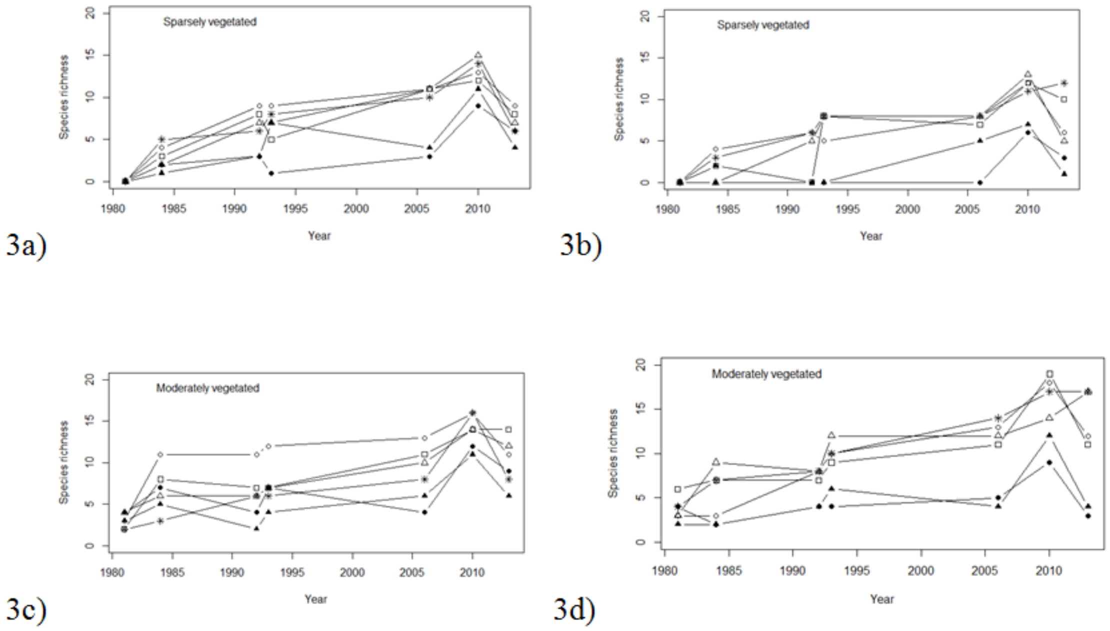
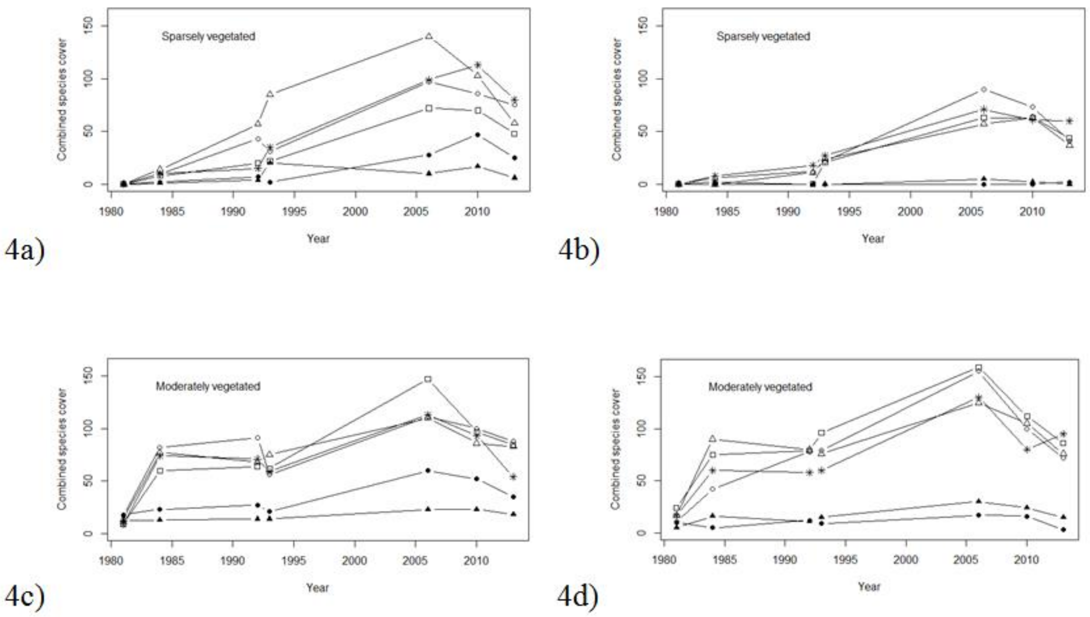


Figure 3**.** Species richness m^{-2} in each of the four treatment blocks, two of which were positioned in sparsely-vegetated debris (Figures 2a and 2b) and two in moderately-vegetated debris (Figures 2c and 2d) over the time period 1981-2013. Treatments consist of five nutrient additions and a control, control = black circles, N = filled triangles, P = open circles, NP = stars, NPK = unfilled squares, NPKCa = open triangles.



4a) 4b) 4c) 4d)

Figure 4. Combined species cover m^{-2} in each of the four treatment blocks, two of which were positioned in sparsely-vegetated debris (Figures 4a and 4b) and two in moderately-vegetated debris (Figures 4c and 4d) over the time period 1981-2013. Treatments consist of five nutrient additions and a control, control = black circles, N = filled triangles, P = open circles, NP = stars, NPK = unfilled squares, NPKCa = open triangles.

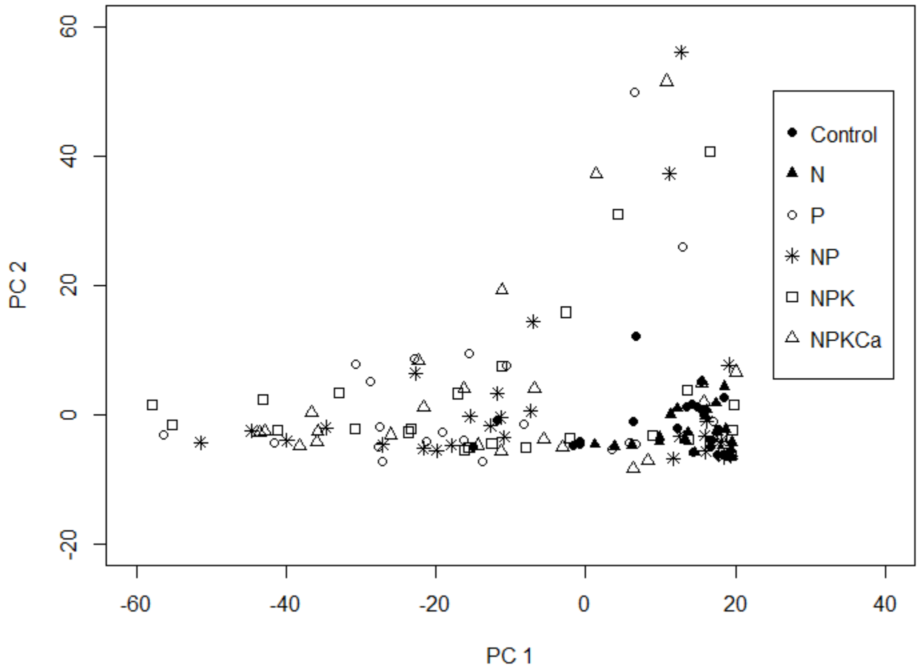


Figure 5. Principal components analysis of all species and their relative abundances in four treatment blocks on the Keen of Hamar, Shetland. Points are labelled according to nutrient treatment and include all surveys between 1981 and 2013.

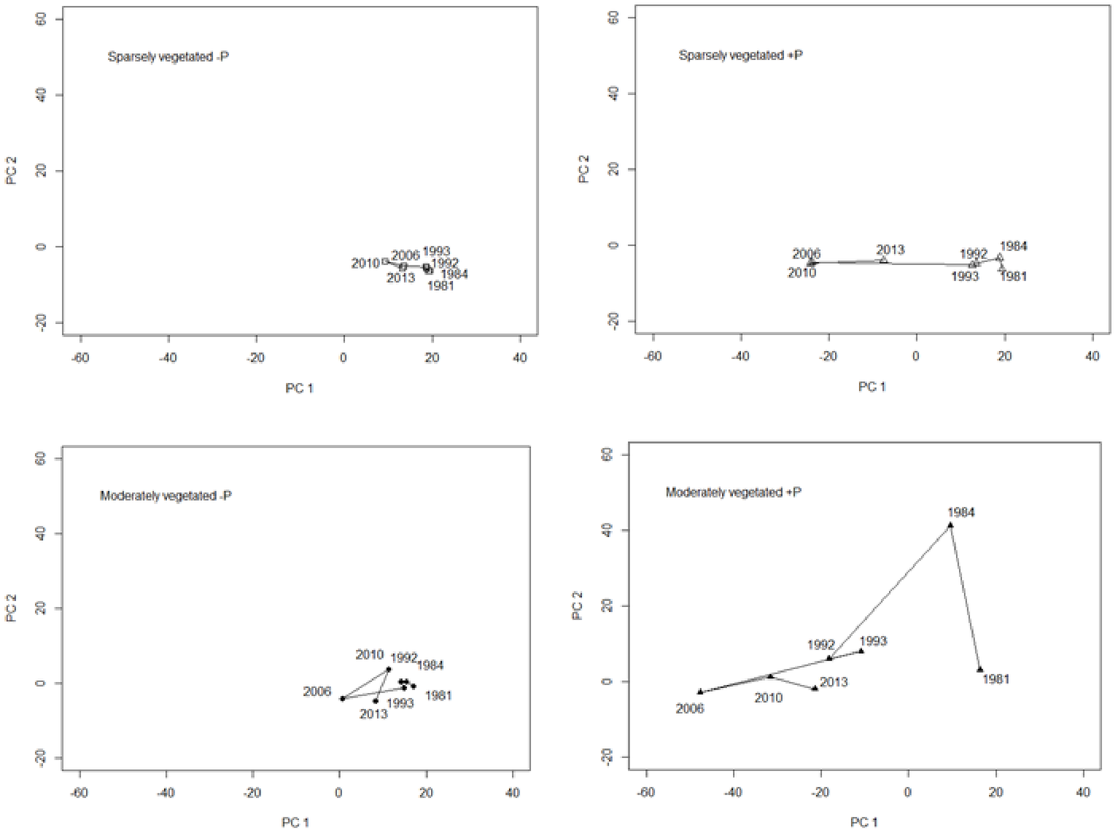


Figure 6. Centroids for survey years separated by vegetation cover at start of investigation (sparsely-vegetated debris in Figures 6a and b, moderately-vegetated debris in Figures 6c and d) and whether treatments contained P (Figures 6a and c) or did not contain P (Figures 6b and d). Centroids for these groupings all derived from the same PCA presented in Figure 5.

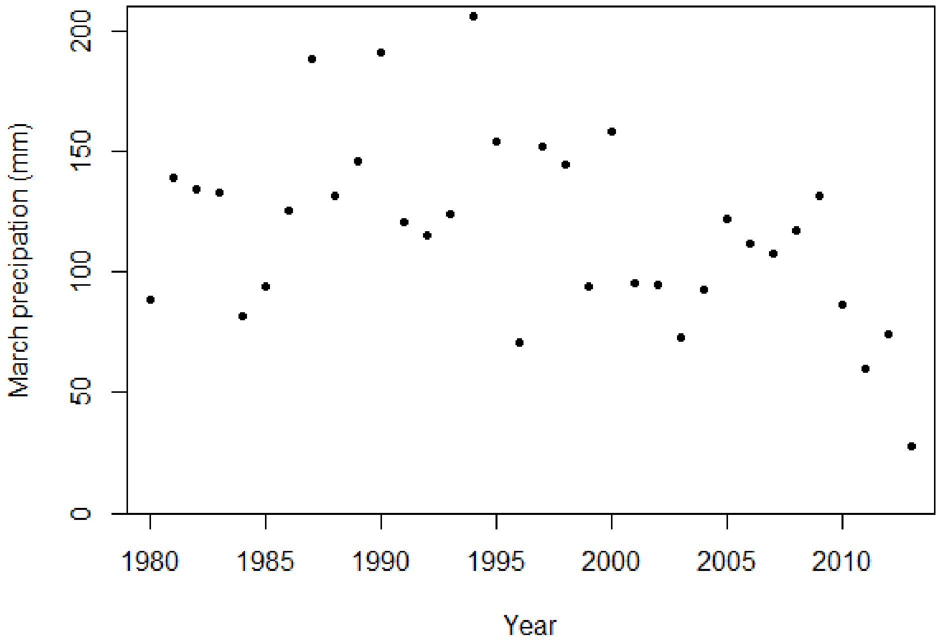


Figure 7. March precipitation (mm) for the study period 1980-2013 according to weather station records from Lerwick (Met Office 2018).