

SURTSEY RESEARCH

13



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Website: www.surtsey.is

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Editors:

Borghór Magnússon, terrestrial biology (email: borgthor@ni.is)
Icelandic Institute of Natural History
P.O. Box 5320, Reykjavík, Iceland

Páll Einarsson, geology and geophysics (email: palli@hi.is)
Institute of Earth Sciences, University of Iceland
Sturlugata 7, Reykjavík, Iceland

Bjarni D. Sigurdsson, terrestrial biology (email: bjarni@lbhi.is)
Agricultural University of Iceland
Hvanneyri, Borgarnes, Iceland

Karl Gunnarsson, marine biology (email: karl@hafro.is)
Marine Research Institute
Skúlagata 4, Reykjavík, Iceland

Cover page: Pioneers colonizing tephra covered lava fields on southern slopes of Surtsey.
Photo: Sigurður H. Magnússon, July 18, 2012

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Introduction

The year 2013 marked the 50 years' anniversary of the start of the Surtsey eruption and the formation of an island. The eruption is one of the longest eruptions in historic times in Iceland and lasted from 14th of November 1963 to 5th of June 1967. The Surtsey 50th Anniversary Conference was held in Reykjavík, Iceland, 12-15 of August 2013 entitled: "Geological and Biological Development of Volcanic Islands". It was organised by the Surtsey Research Society in cooperation with the Icelandic Institute of Natural History, The University of Iceland, The Agricultural University of Iceland, The Marine Research Institute, The Environment Agency of Iceland and the South Iceland Nature Centre.

The organizing committee of the conference arranged for a special issue in the international scientific journal "Biogeosciences". The special issue had the same title as the conference "Geological and Biological Development of Volcanic Islands" (see http://www.biogeosciences.net/special_issue152.html). Handling editor for the special issue was Jens-Arne Subke and guest editors were: Bjarni D. Sigurdsson, Páll Einarsson, Borgþór Magnússon, Karl Gunnarsson, Henning Adersen, Steven Jewett, Timothy New, and Nemesio M. Pérez. Of the ten articles in the special issue, eight focus on research on Surtsey.

Numerous articles and books have been published on the island's development and one of the main aims of the Surtsey Research Society is to promote both scientific and popular publications from research and findings on the island. An important part of that has been the publication of a report series "Surtsey Research" with scientific findings from the island and related areas. The first report appeared fifty years ago, in 1965. Here the Surtsey Research Society publishes the 13th issue of the "Surtsey Research", which also is based on presentations from the 50 years anniversary conference (http://www.surtsey.is/afm_50/Surtsey_ProgrammeAbstracts.pdf). This new issue is published online only, not in print as the previous issues. It will be accessible on the home page of the Surtsey Research Society (http://www.surtsey.is/pp_ens/write_ref_2.htm).

Editors of this issue were: Borgþór Magnússon, Icelandic Institute of Natural History, Páll Einarsson, University of Iceland, Bjarni D. Sigurðsson, Agricultural University of Iceland and Karl Gunnarsson, Marine Research Institute of Iceland. On behalf of the Surtsey Research Society, I would like to thank the editors for their work.

The 50th anniversary of the island was also highlighted by the publication of the book "Surtsey in Focus" in 2014, from the authors Erling Ólafsson and Lovísa Ásbjörnsdóttir at the Icelandic Institute of Natural History. The book provides an exceptional opportunity to view the hidden world of Surtsey through numerous photographs and text.

Surtsey is a scientifically unique area. It offers an outstanding example of a virgin, volcanic island that is being actively created and shaped by geological, geomorphological and ecological processes. The Surtsey island immediately caught the interest of scientists as a singular opportunity to study geology in the making, as well as the settlement of life on a relatively sterile piece of land out in the ocean. In July 2008, the island of Surtsey and the surrounding sea was awarded a World Heritage Site status by the UNESCO's World Heritage Committee. In the committee's justification for this decision the scientific work that has continuously been carried out on the island from the start of the eruption was given as the main reason for Surtsey gaining this status. Furthermore, because the island and the surrounding sea were declared a nature reserve as early as 1965 and have thus been protected from human impact, as far as possible.

The aim of the Surtsey Research Society is to protect and raise the interest on scientific work related to Surtsey island. The anniversary conference was a success and we, the board of the society, trust that in the next 50 years, extensive research will continue on the island, and that there will be many opportunities for scientists to meet and publish results to increase the knowledge on the formation and development of volcanic islands.

Hallgrímur Jónasson,
Chairman Surtsey Research Society

BIOLOGY

Ecosystem CO₂ flux rates in relation to vegetation type and age of *Leymus arenarius* dunes on Surtsey

BJARNI D. SIGURDSSON AND GUÐRÚN STEFÁNSDÓTTIR

Agric. Univ. of Iceland, Hvanneyri, IS-311 Borgarnes, Iceland (bjarni@lbhi.is)

ABSTRACT

The primary succession on the 50 year old volcanic island of Surtsey, Iceland, has been intensively studied. Initial soil development and other belowground processes are important drivers of primary succession but frequently overseen. A *Leymus arenarius* and *Honckenya peploides* dominated plant community has formed a relatively stable successional sere on the island, where external inputs of nutrients remain low. These plants have had a stable <10% aboveground surface cover during the past 20 years, but less is known about their belowground development. We investigated the organic matter (carbon) output and input processes (soil respiration, ecosystem respiration and photosynthesis) of the community and how they were affected by soil temperature, soil water content, vegetation and age of *L. arenarius* dunes. We found that both soil respiration and root stocks have increased substantially from 1987, when an earlier study was conducted. The same pattern was found when different aged *L. arenarius* dunes were studied. *L. arenarius* had a stronger effect on the soil respiration fluxes than its surface cover might indicate, through its much higher photosynthesis rates than *H. peploides*. The study furthermore illustrated how water stress may temporally limit belowground processes in this coastal community.

INTRODUCTION

The study was conducted within the sparse *Leymus arenarius* and *Honckenya peploides* plant community that dominates the eastern part of Surtsey, where windblown tephra and sand have mostly levelled the underlying lava. This area is at present found at an earlier successional stage (sere) than areas which have received additional nutrient inputs from a dense seagull colony on the SW part of the island (Magnússon et al. 2014) or from organic matter washed upon the shore by the surf and possibly from a seal colony on the low ness (Figure 1). The eastern part was, however, the first area of the main (higher) island to be colonised by vascular plants, as *L. arenarius* and *H. peploides*, as well as *Mertensia maritima*, seedlings were found there in

1968 (Fridriksson et al. 1972). From this earliest colonisation, only *H. peploides* persisted, as the two other species did not successfully colonise until 1973 (Fridriksson 1978).

The plant species in this community are all commonly found in coastal habitats in Iceland (Magnússon et al. 2014) and most form smaller aboveground dense cushions (e.g. *H. peploides*) or dunes (*L. arenarius*) (Figure 2). The average plant surface cover in this area was 8.5% in 1987 (Fridriksson 1992) and the average surface cover of areas outside the seagull colony was found to be more or less unchanged in 2012, or only 7.1% (Magnússon et al. 2014), i.e. the aboveground vegetation succession has more or less halted after the initial colonisation phase.

The species-poor *Leymus-Honckenya* dominated community is probably maintained by low nitrogen inputs, or $0.7 \text{ kg ha}^{-1} \text{ year}^{-1}$ (Leblans et al. 2014), low water holding capacity (Sigurdsson 2009) and mechanical stress due to high sand abrasion that prevents other plants from colonising. The dominant plant species in this area have all large root:shoot ratios (R:S ratios), so in spite of the low surface cover, all the tephra sand soil has by now roots penetrating from the scattered cushions and dunes (Leblans et al. 2014, Stefánsdóttir et al. 2014). How this belowground colonisation has developed temporally is, however, less well known.

The present study took advantage of two previous research efforts: i) it re-measured ecosystem CO_2 fluxes on study plots with contrasting vegetation cover originally established in 1987 (Magnússon 1992) and ii) it compared CO_2 fluxes within and among *L. arenarius* dunes of different age used for studying age-related development of aboveground and belowground organic matter and nitrogen (N) stocks on the island (Stefansdóttir et al. 2014). By doing this we hoped to gain a better understanding of belowground organic matter processes in the *Leymus-Honckenya* dominated community on Surtsey.

MATERIAL AND METHODS

Site description

The measurements were done on already established research plots in the *Leymus-Honckenya* plant community on the eastern part of Surtsey (Figure 1), where two previous studies have taken place: a) On plots with contrasting vegetation cover (Magnússon 1992) and b) at three differently aged *L. arenarius* dunes (Stefansdóttir et al. 2014), as well as on control plots outside each dune.

The two Magnússon (1992) plots were termed “sand plot” (S) and “*Honckenya* plot” (H). The $15 \times 1 \text{ m}$ S-plot was in 1987 considered as a base-line reference area, with almost no aboveground plant cover (<1%) and no root biomass (Magnússon 1992). The $15 \times 1 \text{ m}$ H-plot in 1987 contained numerous mature *H. peploides* cushions and had then a surface cover of 13% and root biomass of 14.5 g m^{-2} in the top 20 cm of soil (Magnússon 1992). A third vegetation plot was placed across one of the two oldest *L. arenarius* dunes on Surtsey in 1987, developing from a plant that colonised in 1974 (no. 74-51; Fridriksson 1978). Then it had a total surface cover of 71% and

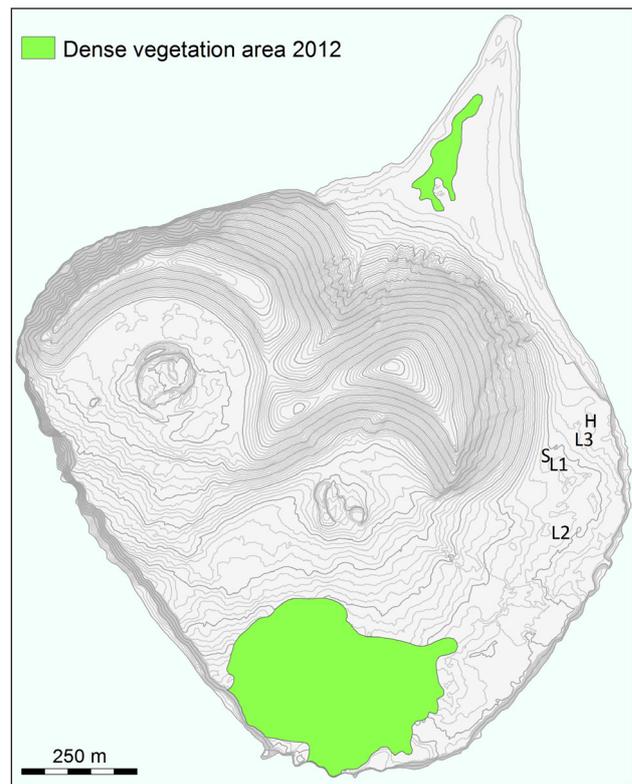


Figure 1. Location of the study plots on Surtsey. Plots L1, L2 and L3 were established in 2009-2010 on top of 17, 28 and 37 year old *Leymus arenarius* dunes, respectively. Plots S and H were established in 1987 on unvegetated sandy surface (S) and on a surface that contained relatively high *Honckenya peploides* cover (H). More densely vegetated surfaces on Surtsey in 2012 are shown in green color, but other areas at lower elevations are mainly covered by a *Honckenya-Leymus* dominated plant community. The elevation map and vegetation cover was derived from aerial and satellite images from 2012 by Anette Th. Meier at the Icelandic Institute of Natural History.

root biomass of 46 g m^{-2} (Magnússon 1992). The 74-51 dune has since then been partly degraded (Figure 2), probably because of disturbance and large N inputs from a breeding pair of great black-backed gulls (*Larus marinus*) that have used the dune as a nest site since the early 1980s. Because of this, we chose to establish a new *Leymus* plot (L3) in the second of the two oldest dunes on Surtsey, which originated from the plant no. 74-78. This dune was the tallest on Surtsey (Figure 2) and to our knowledge, gulls have not used it as a breeding site.

The Stefansdóttir et al. (2014) plots were located adjacent to and on top of three *L. arenarius* dunes which originated from plants that colonised 17, 28 and 37 years prior to the measurements that took place in 2010. The 17 year old dune was now found at the edge of the S plot and the 37 year old dune is



Figure 2. The two oldest *Leymus arenarius* dunes on Surtsey in July 2009; L3 (originating from plant 74-78) is in the foreground and the remains of the dune originating from plant 74-51 can be seen in the background (top). Dr Sturla Fridriksson surveys flowering on the L3 dune in July 2009 (bottom). Photos: BDS.

the L3 plot mentioned previously (plant no. 74-78), while the L2 dune was used in the Stefansdottir et al. (2014) study. In 2010 these three dunes were 0.3, 0.5 and 1.2 m tall and contained on average 134, 334, 471 g C m⁻² as soil organic matter (SOC) and 11, 20 and 42 g N m⁻² as soil organic nitrogen (SON) in the top 75 cm of soil, respectively. Their total plant cover, *L. arenarius* shoot density and R/S ratios did not vary significantly with age and were 28%, 44 shoots m⁻² and 20, respectively (Stefansdottir et al. 2014).

CO₂ flux measurements

Measurements of soil respiration (Rs; excluding aboveground biomass) or ecosystem respiration (Re; including aboveground biomass) and net ecosystem exchange (NEE) were conducted during two 5 day excursions in the middle of July in 2009 and 2010. An

EGM-4 infrared gas analyser and a CPY transparent CO₂ flux chamber (PP Systems, UK) were used to measure changes in atmospheric CO₂ concentrations in light (NEE) and dark (Rs and Re) and a linear regression was used to calculate the corresponding fluxes. Each measurement was made over 2 minutes or a 50 ppm change in atmospheric CO₂ concentration, whichever occurred earlier. By adding NEE to Re fluxes, the corresponding gross ecosystem photosynthetic rates (GPP) could be derived. This instrument also measures soil temperature (Ts) and irradiance (PAR).

In 2009 only the soil respiration (Rs) flux was measured across the oldest *Leymus* dune on Surtsey (L3). A 25m long tape was fitted in a SW-NE direction over the dune and its elevation was measured at 1 m intervals with a S90 GPS-unit (Garmin, KS, USA). Then Rs was measured at 1 m intervals. Soil temperature was recorded at a 10 cm depth with a probe placed adjacent to the respiration chamber, and the vegetation surface cover was recorded for each one m interval with the line intercept method as described by Magnússon and Magnússon (2000).

In 2010 both Re and Rs, as well as NEE, were measured repeatedly within four subplots placed at 4 (dune's edge), 5, 6 and 7 m (dune's top) along the 25 m transect on the 37 year old L3 dune, as well as at one subplot 4 m outside the dune. The same measurements were then repeated in two and four subplots within the 17 and 28 year old L1 and L2 dunes, as well as in one subplot 2 and 3 m outside them, respectively. Plant surface cover, Ts and PAR were recorded, as well as soil volumetric water content (SWC) in the top 5 cm of soil (Theta probe, Delta-T devices). In 2010 the Re, NEE and GPP were also measured in the S plot and the H plot of Magnússon (1992). There, flux measurements were done at five spots along each of the 15 x 1 m plots (1, 4, 8, 11 and 14 m from their E-end). Vegetation surface cover was also recorded under the flux chamber at each measurement spot, as well as PAR and Ts. Average vegetation surface cover within the whole vegetation plot was measured with the line intercept method as described by Magnússon and Magnússon (2000). For the third vegetation plot, the L3 plot, the previously described measurements from 4, 5, 6 and 7 m were used.

RESULTS AND DISCUSSION

CO₂ fluxes in the 1987 vegetation plots

The *H. peploides* and *L. arenarius* that dominated the H and L3 plots had 3.7 and 13 times higher ecosystem respiration (Re) rates in 2010 than the sparsely vegetated S plot and the differences were significant (Figure 3, bottom panel). This can be compared to 1.3 and 3.2 times higher rates in respiration activity between these plots in 1987, as reported by Magnusson (1992). It is, however, not straightforward to compare these two studies because of differences in the respiration measurement techniques (cf. Sigurdsson and Magnusson 2010). Still, the much larger relative differences in 2010 seem to support increased build-up of root biomass and SOC during the past 20 years, which will lead to increased soil respiration activities even if aboveground plant cover has not changed. In a recent chronosequence study of different aged *L. arenarius* dunes on Surtsey, such age-related patterns in SOC and root biomass build-up were indeed observed (Stefansdottir et al. 2014).

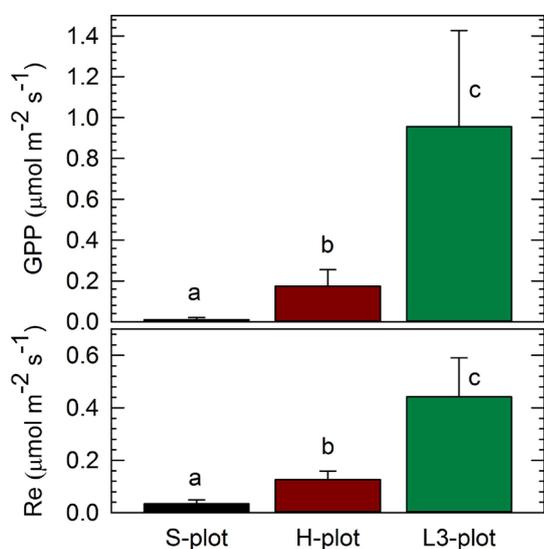


Figure 3. Mean gross photosynthetic rate \pm SE in (GPP; top panel) and ecosystem respiration (Re; bottom panel) in the three main surface types found outside the seagull colony on Surtsey: Sparsely vegetated plot with <2 % vegetation surface cover (S-plot), *Honckenya peploides* dominated plot (H-plot) with 14% \pm 6% cover and *Leymus arenarius* dune (L3-plot) with 27% \pm 11% vegetation surface cover. Letters above bars indicate significant differences ($P < 0.05$), tested with One-Way ANOVA and post hoc LSD tests. Mean irradiance (PAR) was 745 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ and mean soil temperature was 17.3 °C at 10 cm depth.

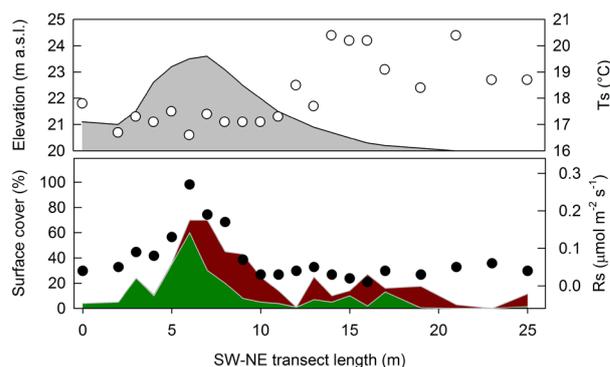


Figure 4. Soil temperature at 10 cm depth (open symbols) at 1-2 m intervals along a 25 m transect across the L3 dune (top panel) in July 2009. Surface cover of *Leymus arenarius* (green area) and *Honckenya peploides* (brown area) and soil respiration (Rs; black circles; bottom panel).

In July 2010, the CO₂ balance (NEE) was also measured in the three vegetation plots and their gross photosynthesis (GPP) input fluxes were derived (Figure 3, top panel). The relative differences in GPP were even larger than for respiration, or 17 and 96 times larger GPP at *Honckenya* and *Leymus* plots than at the sand plot, respectively. It was noteworthy that per unit surface cover in the flux subplots the GPP was 1.7 times higher in the *Leymus* dune than both in the *Honckenya* dominated H-plot and the sparsely vegetated S-plot (0.03 instead of 0.01 $\mu\text{mol CO}_2 \text{s}^{-1}$ per % plant surface cover). This illustrates a relatively higher photosynthetic capacity per unit leaf area of *L. arenarius* than *H. peploides*, a pattern also previously shown by Sigurdsson (2009). This might mean that even if *L. arenarius* has relatively less surface area or leaf area than *H. peploides* in the whole *Leymus-Honckenya* community (Magnusson 1992; del Moral and Magnússon 2014; Magnússon et al. 2014), then it may be more important in SOC buildup and CO₂ soil fluxes than its surface cover might indicate.

Spatial variation in Rs across the L3 dune

The lower panel of Figure 4 shows how Rs changed in 2009 across a 25 m long transect that crossed the second of the two oldest *L. arenarius* dunes on the island (L3; no. 74-78). The Rs peaked in the middle of the dune, where it was highest (oldest). Generally CO₂ surface efflux (respiration) increases exponentially with soil temperature (Ts; Chapin et al. 2002), a phenomenon also reported from Surtsey

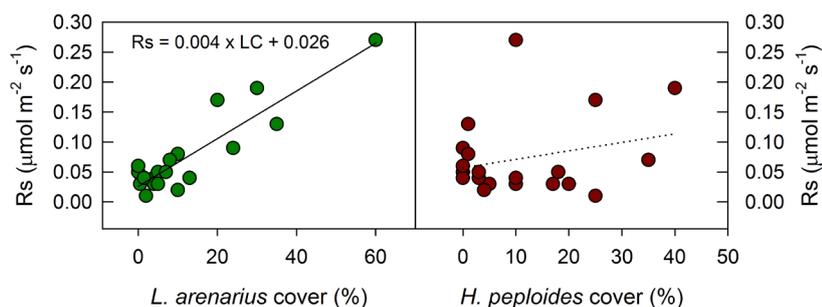


Figure 5. The relationship between a) *Leymus arenarius* surface cover (LC; right) and *Honckenya peploides* surface cover (left) and soil respiration (R_s ; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), shown in Fig. 3. The solid line indicates a significant regression relationship between LC and R_s ($P < 0.001$; normality and constant variance tests passed; $R^2 = 0.82$). The dotted line was not significant ($P = 0.25$; $R^2 = 0.07$).

(Sigurdsson and Magnusson 2010). Since T_s was actually ca. 2 °C lower where the vegetation cover and R_s were highest, the variation in T_s should actually have buffered the CO_2 fluxes there, not enhanced them. Therefore the spatial variation in the R_s should have mirrored spatial variability in respiration activity rather than soil temperature.

When the measured R_s rates were compared to *L. arenarius* and *H. peploides* surface cover in the same spots across the dune, *L. arenarius* surface cover showed a highly significant relationship with the measured R_s rates (Figure 5, left panel), while *H. peploides* cover (right panel) and total plant cover (data not shown) did not have a significant relationship. This further supports the earlier observation that *L. arenarius* is more important than *H. peploides* for carbon dynamics in the *Leymus-Honckenya* community on Surtsey.

Interannual variability in R_s

The strong relationship between R_s and *L. arenarius* cover shown in Figure 5 initiated the idea that it was not plant cover per se, but rather spatial variation in soil organic matter (SOC) and plant root distribution within and outside the dune that was the underlying cause for the observed differences. If so, then the follow-up question was raised whether surface CO_2 efflux (R_s or R_e) could be used as a proxy to survey differences in these belowground stocks. However, when the R_s measurements were repeated at the four subplots along the transect in July 2010, the measured R_s rates showed a very different pattern within the L3 dune; i.e. many of the measurements higher up in the dune showed very low R_s rates (data not shown). This was because of drier soil conditions in 2010 than 2009 within the dune, but a lack of soil moisture is known to reduce soil CO_2 fluxes (Chapin et al. 2002) and such a pattern has been found previously in the *Honckenya-Leymus* community on Surtsey (Sigurdsson 2009; Appendix A). Indeed, there

was a significant negative relationship ($P < 0.001$; $R^2 = 0.71$) between R_s and soil volumetric water content (SWC) in 2010 within the L3 dune:

$$R_s = 0.04 \times \text{SWC} - 0.10 \quad (1)$$

This explained the reversed spatial pattern in R_s observed in 2010. It is, however, important to note that SWC was low during this campaign in 2010, or ranged between only 2.1% to 9.7% at different spots within the dune. The relationship of Eq. 1 cannot be assumed to be valid when SWC increases above the relatively low range observed in 2010. The high inter-annual variability found means that R_s measurements over longer times at different soil moisture conditions (or T_s) cannot be directly used as a proxy to measure SOC status or amount of roots in the soil.

Changes in CO_2 fluxes between different aged *L. arenarius* dunes

However, we were still interested in investigating if R_s measurements could be used within a shorter time period when soil moisture and T_s conditions did not differ so much, as a proxy for SOM contents and/or root biomass in different aged *L. arenarius* dunes. When R_s fluxes measured only at spots with $>5\%$ SWC in 2010 were compared with sparsely vegetated areas 2-4 m outside *L. arenarius* dunes and within three 17, 28 and 37 year old dunes, a significant difference was found in R_s between all groups (Figure 6).

When compared across all groups shown in Figure 6, a linear regression relationship between R_s ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and root biomass (R ; g C m^{-2}) was highly significant ($P < 0.001$; $R^2 = 0.86$):

$$R_s = 2009.1 \times R + 92.3 \quad (2)$$

Hence, the root biomass which was obtained from Stefansdottir et al. (2014) explained 86% of the

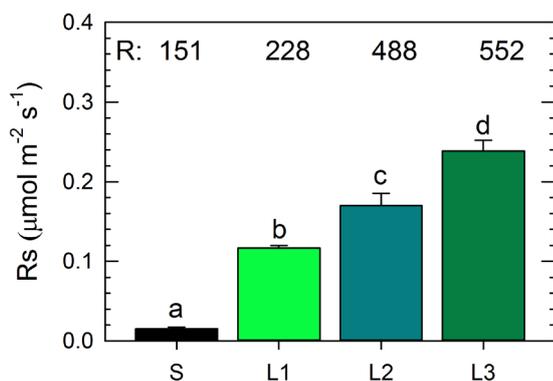


Figure 6. The average soil respiration flux \pm SE (Rs; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) at measurement spots with soil volumetric water content $>5\%$ in the top 5 cm layer, outside (S-plot) and inside a 17 (L1), a 28 (L2) and a 37 year old *L. arenarius* dune (L3-plot). The numbers shown at the top are the amount of root biomass (R; g C m^{-2}) in 75 cm deep soil for the exactly same measurement spots (data from Stefansdottir et al. 2014). Different letters above the bars indicate significant differences ($P < 0.05$) in Rs fluxes, tested with One-Way ANOVA and post hoc LSD tests. Mean soil temperature at 10 cm was 26.6 °C.

variability in Rs. The regression relationship between Rs and SOC (g C m^{-2}) was also significant ($P < 0.001$), but not as strong as with root biomass ($R^2 = 0.76$):

$$Rs = 1163.2 \times \text{SOC} + 59.6 \quad (3)$$

When, however, Rs measurements in spots with SWC $<5\%$ were also included in the 2010 analysis, the root biomass and SOC contents only explained 36% and 11% of the observed variability in Rs ($R^2 = 0.36$ and 0.11), respectively (data not shown). This clearly indicated a strong drought response of the soil and plant processes contributing to the soil respiration flux and that is why Rs does not necessarily scale with root biomass and SOC under such conditions.

CONCLUSION

The repeated Rs measurements in 2009 in the plots initially measured in 1987 by Magnússon (1992) indicated that both root biomass and SOC have increased substantially during the past 20 years, even if plant cover has remained relatively stable. Rs measurements can not be directly used as a proxy for soil organic matter, however, because of potential influences of variations in Ts and SWC on the fluxes during and between such surveys. However, when care was taken to compare only Rs measurements made under similar conditions, a highly significant

relationship was found between Rs fluxes and root biomass and to a lesser extent to SOC stocks in the *Leymus-Honckenya* plant community on Surtsey. The study illustrated how this plant community is characterised by belowground organic matter processes, which helps explain the surprisingly high activities of the soil fauna found (Ilieva-Makulec et al. 2014).

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Appendix A. Soil water content in the Sigurdsson (2009) plots.

In 2006 a pilot study was conducted where surface CO₂ fluxes from *Leymus arenarius* and *Honckenya peploides* patches were compared between “wet” and “dry” areas on Surtsey to ascertain whether water availability was a determining factor in plant and soil activity. It was a limitation of this study that the soil water contents were not directly determined, but a relatively high groundwater level at the “wet” plots and no visible groundwater in “dry” plots was used as a proxy for water availability.

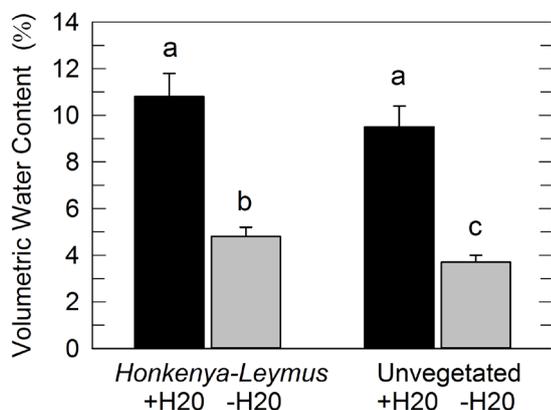


Fig. A1. Soil volumetric water content (%) in the top 5 cm of soil in vegetated *Leymus arenarius* and *Honckenya peploides* cushions and in the unvegetated soil surface in a moist area (+H2O) and a dry area (-H2O) on Surtsey in July 2010. These are the same plots as used for comparison of CO₂ fluxes under wet and dry conditions in Sigurdsson (2009). Means and SE of 8-12 measurements per site. Different letters above the bars indicate significant differences ($P < 0.05$) in Rs fluxes, tested with One-Way ANOVA and post-hoc LSD tests. Mean soil temperature at 10 cm was 26.6 °C.

In 2010, when a Theta Probe (Delta-T Instruments) was brought to the island, we measured the volumetric soil water contents (SWC) in the “wet” and “dry” plots used in Sigurdsson (2009). Those measurements are shown in Fig. A1. No difference in SWC was found between vegetated patches dominated by *L. arenarius* and *H. peploides* (data not shown). Therefore those two surface types were merged in the present analysis (the two left bars). Additionally we measured the SWC of unvegetated patches outside the 2006 plots (the two right bars).

The measurements confirmed the previous assumption made by Sigurdsson (2009) that there was a highly significant ($P < 0.001$) difference in SWC between the soil in the “wet” runoff area on the ness NE of the impermeable craters that are made out of palagonite tuff. Moreover, there was no significant difference in the SWC between vegetated and unvegetated patches on the “wet” ness ($P = 0.33$), while on the “dry” plots, which were located on the tephra sand on the S part of the island, the vegetation covered patches contained significantly more water in the top 5 cm of soil ($P = 0.03$). This might be caused either because of improved water holding capacity due to improved soil organic matter contents under the vegetated patches or by a “hydraulic lift”. Hydraulic lift is a process where water is transported from lower soil layers to higher by permeable plant roots that “irrigate” the topsoil as they transport the water to their aboveground parts (Chapin et al. 2002). Such processes can become very important in the dry sandy areas which do not receive runoff water.

ISSR analysis of two founding plant species on the volcanic island Surtsey, Iceland: grass versus shrub

AGNIESZKA SUTKOWSKA¹, KESARA ANAMTHAWAT-JÓNSSON^{2*}, BORGTHÓR MAGNÚSSON³, WOJCIECH BĄBA⁴
& JÓZEF R. MITKA⁵

¹Department of Plant Breeding and Seed Science, Agricultural University, Łobzowska 24, 31-140 Krakow, Poland.

²Institute of Life and Environmental Sciences, University of Iceland, Askja, Sturlugata 7, Reykjavík IS-101, Iceland.

Email: kesara@hi.is (corresponding author)

³Icelandic Institute of Natural History, Urridaholtsstraeti 6-8, Gardabaer IS-212, Iceland.

⁴Department of Plant Ecology, Institute of Botany, Jagiellonian University, Lubicz 46, 31-512 Krakow, Poland.

⁵Institute of Botany, Jagiellonian University, Kopernika 27, 31-501 Krakow, Poland.

ABSTRACT

Prior to the present study there was limited knowledge about the genetic basis of plant colonization on the 50-year-old island of Surtsey, South Iceland. The aim here was to compare genetic structure of two contrasting species, *Festuca rubra* (arctic fescue) and *Empetrum nigrum* (crowberry), which have colonized Surtsey since 1973 and 1993, respectively. Inter-simple sequence repeat (ISSR) markers were used to assess genetic diversity and population structure. Two census periods were compared: 1996-1997 and 2005-2006. Using six ISSR primers, we obtained 103 and 139 discernible DNA fragments from *F. rubra* and *E. nigrum* respectively. Although the two species displayed similarly high genetic diversity indices ($h = 0.238$ and 0.235 ; $I = 0.384$ and 0.380 , respectively), they differed significantly in their genetic profiles. *Festuca* was genetically structured at the subpopulation level ($F_{ST} = 0.034$, $p = 0.007$), whereas *Empetrum* showed a lack of genetic differentiation. A Bayesian STRUCTURE computation further revealed temporal and spatial genetic structure of the species. The early arrival grass *F. rubra* has expanded from a local genepool. The population was however initially established from different sources, forming a genetic melting pot on Surtsey. On the other hand, the late arrival shrub *E. nigrum* probably derived from a common source of immigrants.

Keywords: AMOVA, *Empetrum*, *Festuca*, founder effect, genetic diversity, island biogeography, ISSR, phenetic analysis

INTRODUCTION

Some theoretical and empirical studies seem to suggest that founder effects and bottlenecks can be both strong and frequent (Avice & Hamrick 1996) and can consequently determine the fate of species colonization in a new habitat (Barton & Charlesworth 1984; Carson & Templeton 1984). Studies on oceanic islands have often shown that colonizing plant species that experience these effects tend to show reduced genetic diversity (e.g. Westerbergh

& Saura 1994; Affre et al. 1997; Yamada & Maki 2012). Reduced variation within a population, due to inbreeding and increased homozygosity, often leads to loss of fitness or evolutionary potential and, in extreme cases, species depression and extinction (Charlesworth & Charlesworth 1987; Ellstrand & Elam 1993; Frankham 2005; Dostálek et al. 2009; Triantis et al. 2010). However, many invasive or introduced species seem either not to have gone through a genetic bottleneck or not to have suffered

much loss of fitness or evolutionary potential as a result of colonization (Hollingsworth & Bailey 2000; Sakai et al. 2001; Fernández-Mazuecos & Vargas 2011). In light of such consequential variability, the study of organisms which colonize recently formed islands could be an essential step towards a better understanding of the genetic behaviour of colonizing populations (Emerson 2002; Franks 2010).

Oceanic islands have long been thought of as natural laboratories for the study of evolutionary processes (MacArthur & Wilson 1967). The recent (1963) origin of the island of Surtsey just south of Iceland (lat. 63° 18' 22" N, long. 20° 36' 5" W) as well as the meticulously well-documented history of plant colonization on the island since its inception (Fridriksson 1966; Baldursson & Ingadóttir 2007; Magnússon et al. 2009, 2014) provide an unprecedented opportunity to study the colonization of a species in terms of its establishment, distribution and dispersal by natural means, devoid of all human influence. The place to actually see a founder effect in island archipelagos is in populations of newly established species, and in this context the young island of Surtsey provides an ideal study stage.

In this study, we investigate genetic diversity in populations of two plant species with different taxonomic statuses, life histories, modes of reproduction and histories of colonization on Surtsey: the arctic fescue, *Festuca rubra* L. subsp. *richardsonii* (Hook.) Hultén (Synonym: *Festuca rubra* subsp. *arctica* (Hack.) Govor., Poaceae), a grass species which was found on the island for the first time in 1973, only ten years after Surtsey was formed; and the crowberry, *Empetrum nigrum* L. (Empetraceae), an evergreen dwarf shrub which became established on the island 20 years later, in 1993. While arctic fescue has become one of the most common vascular plant species on the island (Magnússon et al. 2014), crowberry is still rare (authors' own observation). The creeping runner grass, *F. rubra*, is common and has a widespread distribution over all regions of Iceland (Kristinsson 2008) as well as on islands of the Vestmannaeyjar archipelago where it thrives on the fertile soils of seabird colonies (Fridriksson & Johnsen 1967; Magnússon et al. 2014). Based on flower/fruit and leaf morphology, the *E. nigrum* plants on Surtsey belong to the wind-pollinated, dioecious subspecies *nigrum*, which is found only in lowland areas of Iceland (Kristinsson 2005, 2008). The more common crowberry in Iceland belongs to

subspecies *hermaphroditum* (Basionym *Empetrum hermaphroditum* Hagerup), which has bisexual flowers and is found more inland and at higher altitudes than subspecies *nigrum* (Kristinsson 2005, 2008). The two subspecies are also distinctively different in their chromosome number: subspecies *nigrum* is diploid but subspecies *hermaphroditum* is tetraploid (Löve & Löve 1975; Suda et al. 2004) and this has been confirmed with material collected in Iceland using flow cytometry (Jacobsen 2005) and by direct chromosome counting (K. Ananthawat-Jónsson, unpublished).

Both *Festuca* and *Empetrum* species were genetically screened in the present study using the PCR-based fingerprinting method "inter-simple sequence repeat (ISSR, or anchored SSR)" originally described by Zietkiewicz et al. (1994), to detect variable sites in the microsatellite regions of the genome (Stepansky et al. 1999). The ISSR method has proven useful not only in detecting clonal and somaclonal diversity in crop plants as well as in the fingerprinting of closely related genotypes and cultivars (e.g. Li & Ge 2001; Bairu et al. 2011; Mukherjee et al. 2013), but also in resolving genetic relationships among related and hybridizing taxa in natural habitats (Chokchaichamnankit et al. 2008; Słomka et al. 2011, Sutkowska et al. 2013).

The aim of this study was to compare the genetic structure of the current populations of the grass *F. rubra* versus the shrub *E. nigrum* on the island in relation to previously collected data on species distribution dating to the timing of the species colonization of the island. The following questions were addressed: (1) are there genetic differences among populations at the temporal and spatial levels; and (2) what are the links between the multivariate-phenetic, Bayesian and population genetic characteristics of the species?

MATERIALS AND METHODS

Plant material and site description

The island of Surtsey, a UNESCO World Heritage Site since 2008, had an area above sea level of about 1.4 km² above sea level at that time (Baldursson & Ingadóttir 2007). In order to obtain material suitable for DNA analysis, fresh leaf samples, represented by 16 individual plants of *Festuca rubra* and 14 individuals of *Empetrum nigrum* (Fig. 1), were collected from the entire range of the two species distribution on the island of Surtsey during the month

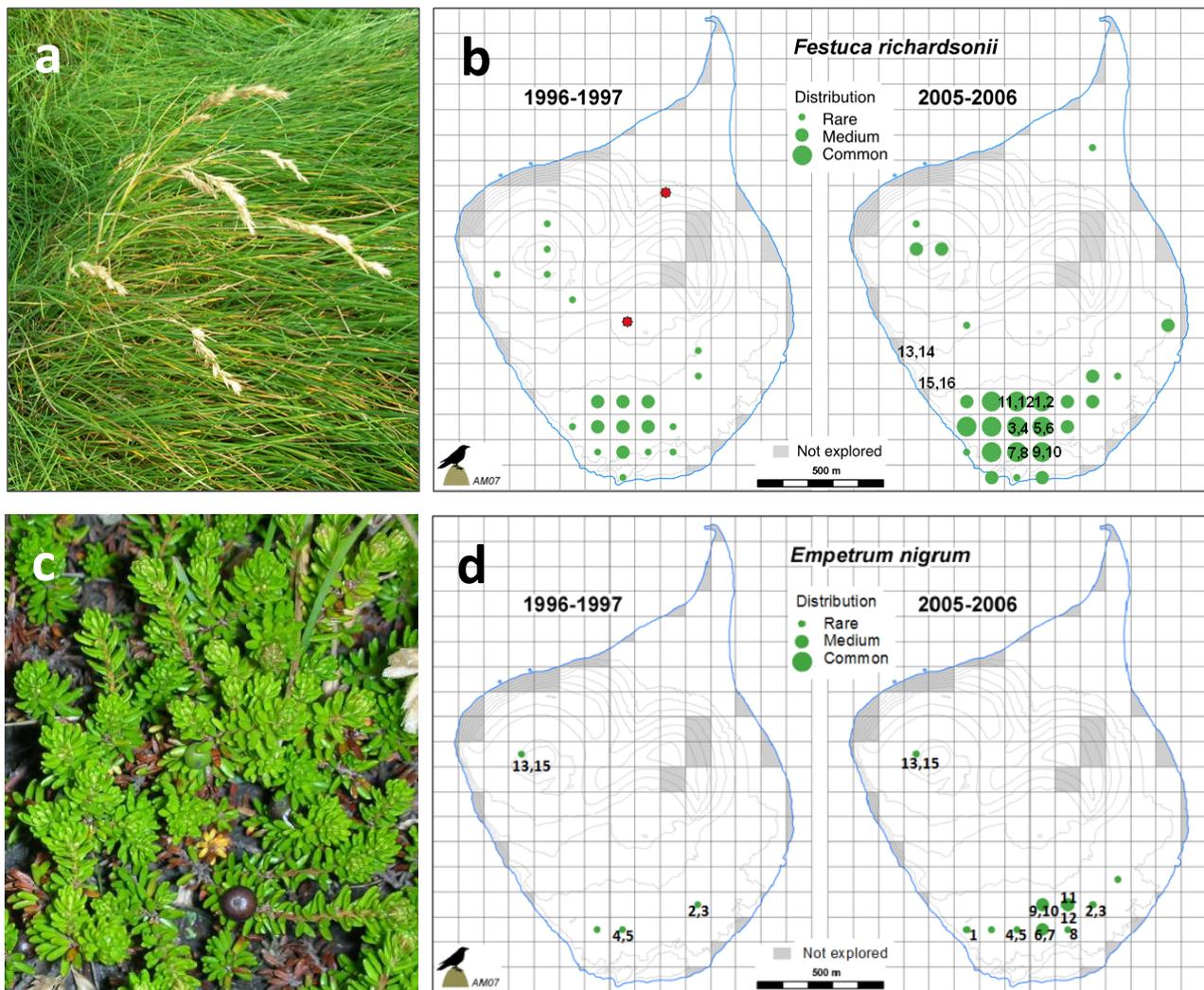


Figure 1. Distribution of *Festuca rubra* (a & b) and *Empetrum nigrum* (c & d) on the island of Surtsey. Photographs of *F. rubra* and *E. nigrum* plants (a & c), taken by author KAJ on 14 July 2010. Location of individual plants investigated (b & d), superimposed on the vegetation map showing distribution and abundance of the species in two different census periods: 1996-1997 and 2005-2006. Red dots indicate location of the first appearance on the island. The vegetation maps were kindly provided by Sigurdur H Magnússon from the Icelandic Institute of Natural History.

of June, 2010. The ID numbers from one to 12 were assigned to samples of both species collected from the most vegetated site on the island's south-western lava field known primarily as "the gull colony". This area, initially a barren lava field with sparse vegetation, became the nesting place for a few pairs of seagulls (*Larus* spp.) around 1985, and by 2008 the vegetation in this area had reached about 10 ha, providing the main nesting area for hundreds of pairs of gulls and other seabirds (Petersen 2009). The gull colony has been particularly important in the development of plant community on Surtsey, due to the positive effects of bird nesting on soil fertility (Sigurdsson & Magnússon 2010, Magnússon et al. 2014). Higher sample ID numbers represent the sampling areas

located furthest from the centre of the gull colony: *F. rubra* samples 13-16 were collected from newly established sites located near the western cliff of the island and *E. nigrum* samples 13 and 15 were collected from inside the crater *Surtungur*, at about 150 masl.

The island is visited every summer to record colonization and plant succession. Permanent plots (10x10 m²) were set up: the first five plots in 1990, additional 14 plots in 1994 and six plots in 1995 (Magnússon et al. 1996). Due to ground erosion or a revision of methods, a few plots were abandoned, new ones established, and by 2012 there were 25 plots operational on the island (Magnússon et al. 2014). Samples collected for the present study were

mostly from within the oldest area of vegetation, i.e. in the gull colony which is the location of the first ten permanent plots. Two floristic census periods, i.e. 1996-1997 and 2005-2007 (Fig. 1), were used in the present study to implement the molecular analysis of population structure on Surtsey.

DNA isolation and ISSR

Genomic DNA was isolated from dehydrated leaf tissue using Genomic Mini AX Plant extraction kit (A&A Biotechnology, Gdynia, Poland). Six (15-18 nucleotides) ISSR primers were used (Table 1). The primer sequences followed Stepansky et al. (1999). Amplification was carried out with a 25 µl reaction mixture, consisting of 2.5 µl 10-fold concentrated reaction buffer, 1.5 mM MgCl₂, 0.19 mM of each dNTP (Fermentas), 27 pmol primer, 100 ng template DNA and 1.4 units of Taq polymerase (Fermentas). Reactions were conducted in a 2720 thermal cycler (Applied Biosystems®). The annealing temperature for primers ISSR2, ISSR4 and ISSR7 was 44°C, but was 47°C for ISSR1, ISSR3 and ISSR6. Optimal conditions for the reaction were as follows: initial denaturation at 94°C 5 min; 42 amplification cycles of 94°C 59 s, 44°C (47°C) 59 s and 72°C 59 s; and final extension of 7 min at 72°C. A negative control reaction without DNA template was included in all amplifications. In order to confirm the results, 50% of the samples were amplified twice. ISSR reproducibility tests (Bonin et al. 2004) included within-plate (n=12) and between-plate (n=9) replicates. The products were subjected to electrophoresis in 1.5% agarose gel stained with ethidium bromide (50 µl/100 ml) at 100V for about 1.5 h. Bands were observed and digitized using an ImageMaster VDS (Amersham Pharmacia) and Liscap Capture version 1.0 software. For analysis of band patterns, GelScan software version 1.45 (Kucharczyk, Poland) was used. Molecular weight of the resulting amplification products was determined using a calibration curve based on the bend pattern of the length of the markers (GeneRuler TM 100 bp,

Fermentas).

Data analysis

All the analyses performed were based on the following assumptions: ISSR markers behaved as dominant markers; co-migrating fragments were considered homologous loci; and populations were at Hardy-Weinberg equilibrium, in which case allele frequencies were estimated from the square root of the frequency of the null (recessive) allele (Yeh et al. 1999) or Bayesian method with non-uniform prior distribution of allele frequencies, to calculate expected heterozygosity H_j (Vekemans 2002). The among-population diversity was estimated using Wright's fixation index F_{ST} (Wright 1965). Statistics of genetic diversity and population genetic structure were computed after estimating allele frequencies, including percentage of polymorphic bands (PPB) at 95% criterion and expected heterozygosity or Nei's gene diversity (h). The calculations were performed with AFLP-SURV (Vekemans 2002).

Additionally, Shannon's diversity index (I) was calculated to provide a relative estimate of the degree of genetic variation within each population using POPGENE version 1.31 (Yeh et al. 1999), based on the formula $I = -\sum P_i \log_2 P_i$, where P_i was the frequency of each ISSR band. As an additional diversity marker, the rarity index DW , corresponding to "frequency-down-weighted marker values" per individual (Schönswetter & Tribsch 2005) was computed using AFLPdat (Ehrich 2006). Fixed private fragments were searched for in all investigated individuals of each species (Schönswetter et al. 2002). Analysis of molecular variance (AMOVA, Excoffier et al. 1992) was carried out using the program Arlequin version 3.11 (Excoffier et al. 2005).

The genetic division among individuals in populations of both species was estimated by means of STRUCTURE, version 2.3.3 (Pritchard et al. 2000), applying a Bayesian model-based clustering algorithm for the use of dominant markers (Falush et al. 2003). The numbers of $K = 1-5$ groups were tested in ten replications per each K . A burn-in period 200 000 was applied, followed by a procedure using 1 million Markov chain Monte Carlo (MCMC) repetitions (Gilbert et al. 2012). Every individual collected (excluding one of *Festuca* with missing bands, plant ID no. F4) was included in the analysis and an admixture model with uncorrelated allele frequencies was applied. The dominant ISSR data

Table 1. Primers used in the PCR-ISSR reactions.

Primer	Primer sequence
ISSR1	(TC) ₈ C
ISSR2	(AG) ₈ T
ISSR3	(GGGTG) ₃
ISSR4	(ATG) ₆
ISSR6	(AC) ₈ G
ISSR7	(AC) ₈ T

were analysed by treating each class of genotypes as being, effectively, haploid alleles, according to the software documentation. The estimation of the optimal number of groups was based on the likelihood of partitions, estimates of posterior probability provided in STRUCTURE output, examined as a function of increasing K (Pritchard et al. 2000) and ΔK values, estimating the change in the likelihood function with respect to K and estimated as an indicator of the most reliable clustering structure (Evanno et al. 2005). Similarity between runs was estimated using the symmetric similarity coefficient (Nordborg et al. 2005) with the R-script Structure-sum-2011 (Ehrich et al. 2007). The function *Clones* in AFLPdat (Ehrich 2006) was used to check the clonality in the species. No clonal ramets within ISSR error rate 3-5% were found.

In the phenetic analyses, Dice distances (Nei & Li 1979) were obtained using PhylTools software (Buntjer 1997). The distance matrices were imported into the software package PHYLIP version 3.6 (Felsenstein 2005) to produce UPGMA trees using the NEIGHBOUR program. The bootstraps were then calculated in CONSENSE. The tree was displayed using MEGA version 5 (Tamura et al. 2011). Principal coordinates analysis (PCoA) was conducted to ordinate relationships among populations with Nei's distance matrix, and a minimum spanning tree (MST, Gower & Ross 1969) was calculated using NTSYS-pc version 2.11a (Rohlf 2002).

RESULTS

Festuca rubra

A total of 139 polymorphic ISSR markers were obtained from 16 plants using six primers (Table 1). These primers produced clear and reproducible fragments (error rate within 5%). Calculated from these fragments (Table 2), the polymorphism among all individuals, i.e. the percentage of polymorphic bands (PPB) for this species, was 99.3%. In four individuals that appeared after the later census period of 2005-2006, the PPB amounted to 51.8%, whereas in 12 individuals established earlier (from 1996-1997) the index reached 85.6%. At the species level, Nei's gene diversity h calculated over all loci was 0.238 and Shannon's diversity (I) index equalled 0.384. However, when comparing between the two periods the gene diversity indices (h and I) were generally lower in the recent, secondary population after 2005-2006 in comparison with the earlier period from 1996-1997, i.e. $h = 0.180$ vs. 0.231, and $I = 0.272$ vs. 0.365. The expected heterozygosity H_j was similar in both subpopulations and ranged within 0.271-0.275. Only the rarity index DW was almost the same (9.78-9.79) in the subpopulations from two periods of time.

The results of the Bayesian STRUCTURE (Fig. 2) indicated $K = 2$ as the most appropriate clustering of the individuals based on the mean $L(K)$ and ΔK criteria (the analysis is available upon request). The average similarity coefficient among runs for $K = 2$ was 0.992 (SD = 0.004). Other K values were characterized by lower similarity coefficients (from

Table 2. Genetic diversity of *Empetrum nigrum* and *Festuca rubra* on Surtsey Island. Abbreviations: n – sample size, PPB – percentage of polymorphic bands, I – Shannon's information index, h – Nei's gene diversity (POPGENE), H_j – Nei's gene diversity (AFLP-SURV), SD – standard deviation, and SE – standard error.

Species	<i>Festuca</i>		<i>Empetrum</i>	
	From 1996-1997	After 2005-2006	1996-1997	2005-2006
n	12	4	6	8
PPB	85.61	51.80	77.64	78.64
h (SD)	0.231 (0.160)	0.180 (0.192)	0.290 (0.179)	0.285 (0.175)
H_j (SE)	0.271 (0.012)	0.275 (0.016)	0.303 (0.013)	0.290 (0.014)
I (SD)	0.365 (0.219)	0.272 (0.278)	0.432 (0.252)	0.428 (0.246)
DW	9.789 (1.824)	9.777 (1.007)	5.760 (1.271)	4.669 (1.017)
	$F_{ST} = 0.034, p = 0.007$		$F_{ST} = -0.003, p = 0.913$	
Total	<i>Festuca</i>		<i>Empetrum</i>	
n	16		14	
PPB	99.28		94.17	
h (SD)	0.238 (0.146)		0.235 (0.136)	
I (SD)	0.384 (0.188)		0.380 (0.180)	
DW	9.786 (1.609)		5.214 (1.271)	

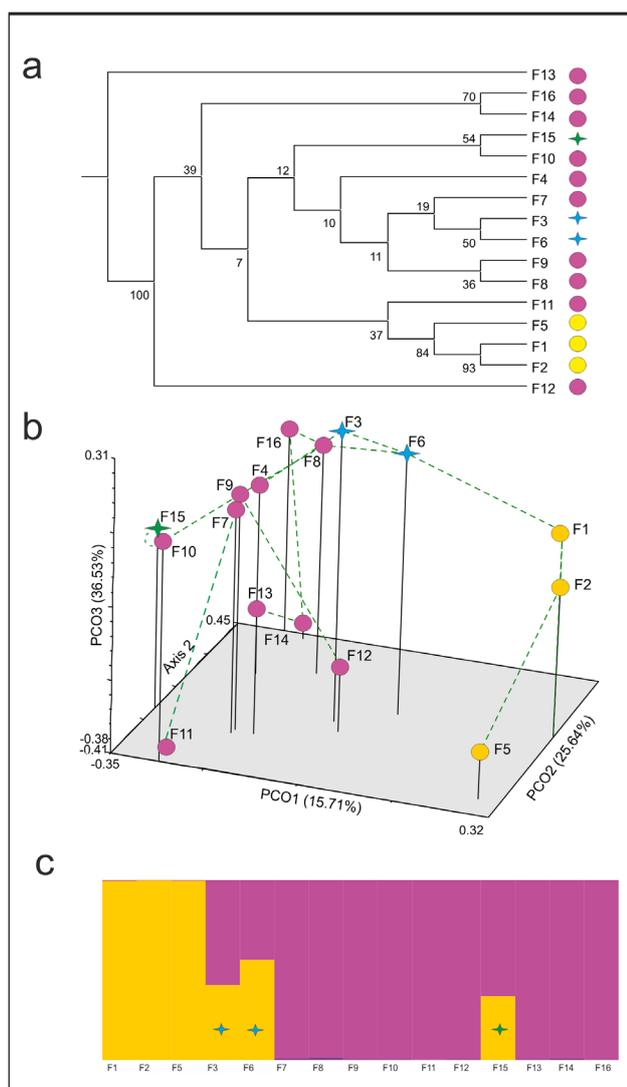


Figure 2. Phenetic and genetic variability of *Festuca rubra* (plant ID numbers F1-F16) based on ISSR data. (a) UPGMA clustering on Dice's distance matrix, bootstrap values based on 1000 runs. (b) PCoA ordination on Nei's distance matrix with Minimum Spanning Tree imposed. (c) Estimated population structure of 15 individuals (one individual removed due to missing bands) by STRUCTURE "admixture" model.

0.285 to 0.809). The first cluster included three individuals F1, F2 and F5 (Fig. 2c: genetic group 1, colour code yellow) while the second contained nine individuals F7-F16 (genetic group 2, colour code purple). Three individuals, i.e. F3, F6 and F15, could be regarded as genetic hybrids. The phenetic analyses (Figs. 2a and 2b) also showed individuals F3 and F6 as intermediates between the two genetic groups. In the UPGMA clustering, the group of putative hybrids is supported with 50% bootstrap analysis. One of their parental genotypes could be F8 (PCoA, Fig. 2b). Also, individual F15 could be of hybridogenous origin and one of its parental individuals could be F10 (UPGMA, 54% support, Figs. 2a and 2b).

The individuals F1, F2 and F5 (genetic group 1) had one fixed private band, whereas all individuals in the genetic group 2 had two fixed private bands (Table S1). The four newly established individuals in the second genetic group, F13-F16, had two additional private bands (Table S1).

The level of genetic differentiation among temporal subpopulations is low but statistically significant, as reflected in the fixation F_{ST} index of 0.034 for *Festuca* (Table 2). The AMOVA analysis contributed a statistically significant 10.53% of the total variance to the among-population component, i.e. between the two census periods (Table 3).

Empetrum nigrum

A total of 103 polymorphic ISSR markers were obtained from 14 plants with six primers (Table 1). These primers produced clear and reproducible fragments (error rate 3%). Calculated from these bands (Table 2), the percentage of polymorphic bands (PPB) for this species was 94.2%. There were no clear differences between the two subpopulations from the first (1996-1997) and second census period (2005-2006), in terms of the percentage of

Table 3. Analysis of molecular variance (AMOVA) of *Festuca rubra* and *Empetrum nigrum* on Surtsey Island. The population level includes the species occurrence in two periods: 1996-1997 and 2005-2006.

Source of variation	d.f.	Sum of squares	Variance components	Percentage variation	p
<i>Festuca rubra</i>					
Among populations	1	37.180	2.589	10.53	0.002
Within populations	13	285.886	21.991	89.47	
Total	14	323.067	24.580		
<i>Empetrum nigrum</i>					
Among populations	1	16.089	0.279	1.93	0.208
Within populations	12	170.125	14.177	98.07	
Total	13	186.214	14.456		

polymorphic bands PPB (77.7 vs. 78.6), the expected heterozygosity h and H_j (0.290 vs. 0.285 and 0.303 vs. 0.290) and Shannon's diversity index I (0.432 vs. 0.428), respectively. The rarity index DW was slightly lower in 2005-2006 subpopulation and amounted to 4.67, as compared to 5.76 in the earlier period.

The results of the Bayesian STRUCTURE (Fig. 3) indicated $K = 3$ as the most appropriate clustering of the individuals based on the mean $L(K)$ and ΔK criteria (the analysis is available upon request). The average similarity coefficient among runs for $K = 3$ was 0.996 (SD = 0.001). Other K values were characterized by lower similarity coefficients (from 0.64 to 0.96) and higher SD values. Of the three genetic groups, the first group (colour code purple)

included four individuals EN1-EN4 and one putative hybridogenous EN5 (Fig. 3c). However, only EN1 and EN3 were highly supported with 97% bootstrap values (Fig. 3a). The putative hybrid EN5 was genetically close to EN12 and EN15 (54% support), but also to EN4 (Fig. 3a). The next two groups (colour codes green and yellow) consisted of genetically pure individuals with a negligible admixture of alien alleles (Fig. 3c). The phenetic analyses UPGMA (Fig. 3a) and PCoA (Fig. 3b) pointed to weak genetic signals as some individuals (EN4, EN8, EN9) were intermingled within different genetic groups, however with a weak support (30-37%). Two individuals from inside the crater far from the main vegetated gull area, EN13 and EN15, belonged to the same genetic group (Fig. 3c).

There were no fixed private bands in the three genetic groups, but two individuals EN4 and EN5 shared one private band (Table S2). These two samples represented the population established early, i.e. at least in 1996-1997. The AMOVA analysis (Table 3) showed only 1.93% and statistically insignificant ($p = 0.208$) part of the total genetic variance that was attributed to among-population diversity.

DISCUSSION

Genetic structure of the grass Festuca rubra on Surtsey

The results of Bayesian analysis (STRUCTURE) of the grass species on the island of Surtsey are in accordance with its temporal and spatial organization. Two genetic groups from genetically different stocks were distinguished. The spatial and temporal subdivision of the population was supported by AMOVA analysis and F_{ST} index. The results also indicated hybridization between genetic groups. Significant population subdivision and the presence of some unique ISSR bands are in general attributed to selfing (Culley & Wolfe 2001). But for the wind-pollinated *Festuca* the subdivision is more likely to be associated with the founder effect from various genetic pools, and in this case from sources outside the island.

The first genetic group can be attributed to the early colonization phase, i.e. before 1996-1997, and the individuals in this group (F1, F2 and F5) were actually from the area of the earliest successful colonization of the species (Fridriksson 1978), the area which was part of the permanent plot no. 1

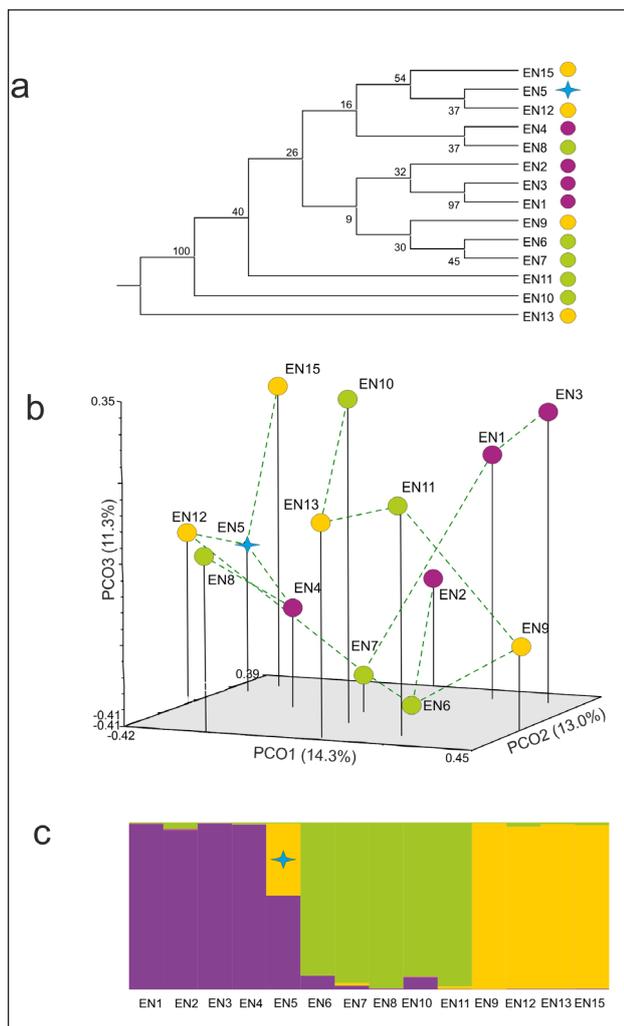


Figure 3. Phenetic and genetic variability of *Empetrum nigrum* (plant ID numbers EN1-EN15) based on ISSR data. (a) UPGMA clustering on Dice's distance matrix, bootstrap values based on 1000 runs. (b) PCoA ordination on Nei's distance matrix with Minimum Spanning Tree imposed. (c) Estimated population structure of 14 individuals by STRUCTURE "no admixture" model. Plant ID number EN14 did not exist.

established in 1990 (Magnússon et al. 1996). The second and more extensive genetic group consists of individuals from both inside and outside the vegetated gull area. The samples from the marginal habitat outside the gull area (F13-F15) were collected from small and newly established (after the census period 2005-2006) but spatially separated (at least 20m apart) individual clusters of *F. rubra* scattering over almost barren lava by the sea. The STRUCTURE analysis indicated that this marginal subgroup most probably originated *in situ* (on the island) from the older and denser population in the gull area. The newly established group showed lower values of the genetic diversity indices, and especially the percentage of polymorphic bands PPB, than the earlier group, but no difference in the rarity index *DW* was found. This reduced genetic diversity is a clear sign of the genetic bottleneck effect occurring on the island.

According to the vegetation monitoring records, the spread of *Festuca* coincided with the expanding range of sea gulls nesting in the area, especially in the period 1985-1994 defined in Baldursson & Ingadóttir (2007) as “new wave of colonization and succession facilitated by breeding gulls” as opposed to the earlier period (1965-1974) of “the invasion of coastal species on the empty island”. Initially the ground substrate in this gull area was barren lava with some tephra sand, but the architecture of lava sheets is believed to have provided shelter for nesting of the first breeding pairs of sea gulls (Magnússon et al. 1996). Although *Festuca* was spotted on the island as early as 1973, the founders during the first six years were only very few seedlings, most of which did not survive in the following years, either due to the windy and cold conditions or the first gulls gathering all of the grass for use as nesting material (Fridriksson 1982). It was not until 1978 that the *Festuca* population became established and began flowering on the island. However, what followed was still a slow progress of vegetation development, possibly due to the lack of essential soil nutrients. But as the gull colony increased drastically in size from ten nests in 1986 to 180 nests by the summer of 1990, new founders as well as old survivors became established and the grass expanded into dense turfs. The vegetation cover on Surtsey was found to be strongly related to density of gull nests, driven by the significant increase in soil respiration, soil carbon, nitrogen and the C: N ratio (Sigurdsson & Magnússon 2010, Magnússon et al.

2014). The first census period shown in the present study (1995-1996) reflects the rapid expansion of *Festuca* from the initial phase of colonization inside the gull area. The population then became dense in the second period (2005-2006), after which *F. rubra* had spread out of the gull area and colonized marginal habitats.

Studies of *Festuca* species from subarctic-alpine regions show highly variable levels of genetic diversity. Average gene diversity *h* based on AFLP analysis of 81 local populations and cultivars of *F. pratensis* from Norway and Lithuania varied from as low as 0.090 in a population near agricultural fields with active gene flow from meadows to a high level of 0.254 in an isolated population in a wooded area (Fjellheim et al. 2009). At the species level, the population of *Festuca* on Surtsey falls in the upper limit of the genetic diversity index ($h = 0.180 - 0.231$). The study of *F. pratensis* growing on the islands of Lake Onega, Russia (Fedorenko et al. 2009), reveals lower levels of genetic diversity based on 64 RAPD loci ($h = 0.093$) than those found in *F. rubra* on Surtsey and much less loci polymorphism (PPB only 30% vs. 51.8 - 85.6% for Surtsey). Although it is not ideal to compare levels of genetic diversity among populations based on different methodology and marker types, there is a clear indication that genetic diversity of *Festuca* in the Surtsey populations is on the higher end of the spectrum. A recent study on spatial genetic diversity of the coastal plant species, *Honckenya peploides*, in relation to populations from a nearby island and from the southern coast of Iceland revealed a high level of gene diversity on Surtsey compared to its source populations (Árnason et al. 2014). Together with the Bayesian analysis of the species, the authors have interpreted the results as an indication of multiple origins of immigrants and active colonization especially during the early stage of population establishment on an empty island. This may be the case for *Festuca* as well, particularly regarding the early colonization and establishment on Surtsey. Successful invaders, especially grasses and herbaceous weeds, can be characterized as “gap grabbers” (early germinators with fast initial growth), competitors (for resources) and survivors (Sakai et al. 2001). *Festuca rubra* has been spreading relatively fast on Surtsey, especially in the nutrient-rich gull area.

Colonization of the late arrival shrub Empetrum nigrum on Surtsey

Empetrum nigrum was found on the island for the first time in 1993, right at the end of the period known as “gull invasion and vegetation enhancement” and at the beginning of the period “secondary plant colonization and first breeding of land birds” with other shrubs such as *Salix* species following suite (Fridriksson 2000; Magnússon et al. 2009). At the time of the sampling for the present study in 2010, only one *E. nigrum* individual (EN7) produced berries for the first time on the island. All individuals on the island found that year were therefore first generation immigrants.

The genetic diversity of *E. nigrum* on Surtsey was generally high ($h = 0.235$) and to some extent comparable to the range of the grass *F. rubra*. But unlike *Festuca*, almost 100% of the genetic variability of this evergreen shrub species was attributed to the within-population genetic component, a feature characteristic of highly out-crossing, wind- or mixed-wind pollinated, late-successional and long-lived perennials (Hamrick & Godt 1989). Populations of *E. nigrum* subsp. *hermaphroditum* in northern Sweden also showed high levels of genetic variation (Szmidt et al. 2002). The percent of polymorphic loci and diversity indices were the highest in the youngest population (c. 150 year-old), with the clonal fraction also being the lowest there. This, along with the large number of unique genotypes observed, indicated that clonal propagation had minor significance in comparison to seedling recruitment in the initial colonization. In other early successional communities, rapid population expansion of *Empetrum* from seedling recruitment has been documented (Boudreau et al. 2010). But island colonization of Japanese crowberry (*E. nigrum* subsp. *japonicum*) showed the opposite, i.e. very low gene diversity (Chung et al. 2013), a typical situation of genetic depauperation expected among isolated oceanic islands when compared with their mainland conspecifics (Wright 1940; Whittaker et al. 2008). As for the case of Surtsey reported here, *Empetrum* had just begun its sexual propagation on the island and therefore nearly all of its genetic diversity should be similar to that of the source population(s), therefore not depauperated. Indeed the level of gene diversity in *E. nigrum* on Surtsey is similar to, or even higher, not lower, than that found by Jacobsen (2005) for populations on mainland Iceland or elsewhere across

the North Atlantic regions. Furthermore, the history of colonization on Surtsey was so short for this long-lived perennial, merely 17 years, that the species had not as yet experienced any founder or bottleneck effects, selection or adaptation. *Empetrum* is a slow-growing plant and in boreal forest ecosystems both sexual and asexual propagation allow colonization of vacant sites, though it can be 100 years or more before it dominates the site (Szmidt et al. 2002).

In *E. nigrum* virtually no clear differences in genetic diversity indices were found in either the temporal or spatial population subdivisions. Neither the results of AMOVA analysis nor F_{ST} index were statistically significant. The spatial genetic structure of *Empetrum* population on Surtsey appeared to be more uniform when compared to *Festuca*. Although the admixture analysis produced three main genetic subpopulations from *Empetrum* samples, this genetic division based on Bayesian inference was not supported by the genetic analysis of variance, as the among-population differentiation revealed only 1.93% of the total variance, in contrast to the highly significant 10.53% variation among *Festuca* subpopulations. Even so, it is an indication that the genetic groups derived from different colonization episodes. The first colonization episodes (seen in the census period 1996-1997) involved two spatially separated genetic groups. One of these groups includes individuals from inside the western crater about 600 m northwest of the gull area where all other *Empetrum* samples in this study were taken. An enigma is the appearance of a hybrid or a mixed type (EN5) before the arrival of one of the putative parental groups (the third group, which appeared in the period 2005-2006). The hybridisation must have taken place in the original, source population. As the spatial subdivision of the population on the island into the older and younger subpopulations was not statistically supported, the existence of the genetic groups can only be a relic of the source population(s). Thus, no founder effect was found.

The most likely source locations are along the southern part of Iceland as well as from the nearby island of Heimaey. This dioecious subspecies of *E. nigrum* is common in lowland and coastal areas, especially in the south of Iceland (Kristinsson 2005). Surtsey is only 30 km away from the nearest point of the southern coast of mainland Iceland. This plant is believed to have colonized Surtsey by means of seed dispersal most probably via ingestion by birds such

as snow buntings and ravens (passerines), which became more common among breeding birds during the secondary phase of plant colonization on the island (Petersen 2009). The AFLP analysis of bird-dispersed *E. nigrum* by Jacobsen (2005) indicated that the species colonized Svalbard in the first place from East Greenland, which in turn was colonized from West Siberia source populations. Popp et al. (2011) used molecular tools to demonstrate that long-distance dispersal by birds (i.e. from northwest N-America to the southern hemisphere) could explain the extreme bipolar disjunction in *Empetrum*. Seed dispersal by birds is highly effective and can reach farther than previously thought.

Grass versus shrub

Both *Festuca rubra* and *Empetrum nigrum* probably colonized Surtsey via bird-facilitated seed dispersal, directly (bird as seed carrier) or indirectly (site amelioration by breeding gulls), and the initial seedling (sexual) recruitments seem to have been highly successful. About 75% of the plant species colonizing Surtsey were brought to the island by birds, the rest by sea currents and wind (Magnússon et al. 2009, 2014). As a result of colonization and rapid expansion on the island of Surtsey, although at different time periods, both species are genetically divergent at the species level. At the time of study the grass species *Festuca* had formed a genetic melting pot, i.e. a place where various genetic lineages met, whereas the shrub *Empetrum* could be characterized as near-panmictic populations, however still reflecting the genetic structure of the source population.

No signs of reduced genetic variability are found in the two species under study apart from the secondary subpopulation of *Festuca* deriving from the *in situ* genetic material. The limited sample size and the lack of reference materials do not allow a conclusive statement to be made regarding genetic diversity in the source populations, which are presumably from mainland Iceland and other islands in the Vestmannaeyjar archipelago. It should be noted that *Festuca* is a dominant species on all islands of the archipelago, whereas *Empetrum* is only found on Surtsey and the largest island, Heimaey (Magnússon et al. 2014). In any case, it may be reasonable to assume that genetic diversity of both *Festuca* and *Empetrum* on Surtsey is not depleted when compared to the source populations, a case similar to that which was found for the early colonizing coastal species

Honckenya peploides on Surtsey (Árnason et al. 2014). Active colonization of a species, i.e. by multiple or repeated introductions of genetic material, is thought to be one of the main factors ameliorating losses of gene diversity in founding populations (Dlugosch & Parker 2008). But in the case of the long-lived shrub species *Empetrum*, the relatively high level of genetic diversity discovered in the present study is clearly a relic of the gene diversity brought by the initial immigrants. Due to Surtsey's small size, young age and fast-eroding nature (Jakobsson & Gudmundsson 2003), we predict that the species will in the near future suffer from reductions in genetic diversity and adaptive potential. Both physical dimensions and biological characteristics are important factors influencing levels of genetic variation in plant species found on oceanic islands (Whittaker et al. 2008; Stuessy et al. 2014). The present study shows that genetic diversity is already drastically reduced in the secondary subpopulation of the grass *Festuca*, due to founder and bottleneck effects.

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Appendix

Table S1. Block-structure of ISSR bands across genetic groups delimited by STRUCTURE in *Festuca rubra*.

population	2 1 5	7 3 6 9 0 1 8 2	1 1 1	1 1 1 1
band no.		X X		X
76	* * *	* *		* *
127	* * *	* * *		*
124	* * *	* *		*
48	* * *	*		* *
52	* * *			
55		* * * * * * * *		* * * * *
53		* * * * * * * *		* * * * *
33		* * * * *		*
47		* * *		* * *
30		* * *		* * *
114			* * *	* * *
121			*	* * *
50				* *
111				* *
39		* * * * *		
120		* * *		*
29		* * *		*
131		*		*
102				* * * *
69				* * * *

Table S2. Block-structure of ISSR bands across genetic groups delimited by STRUCTURE in *Empetrum nigrum*.

	1 1 1	4 5 1 3 2	1 1
	9 3 2 5 8	X	6 7 1 0
3 5		* *	
3 3		* * *	
2 8	* *		
4 2	* *		
5 8	* * * *	*	
1 4	* * * *		
9 9	* * * *	* * *	* *
7 3	* *	* * *	* *
2	* *	* * *	* *
5 2	* *	* *	*
8 7	* * * *	* * *	* *
1 0 2	*	* * * *	
1 0 0	*	* * * *	*
3	*	* * *	
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Colonization, succession and conservation: the invertebrates of Anak Krakatau, Indonesia, and contrast with Surtsey

TIM R. NEW

Department of Zoology

La Trobe University

Victoria, Australia 3086

E-mail: t.new@latrobe.edu.au

ABSTRACT

Surveys of selected terrestrial invertebrates on Anak Krakatau, Indonesia, during the 1980s/1990s exemplify the variety of colonization and successional processes contributing to foundation of new ecological communities. Both aeolian and vegetation-based successions are important, but interpretation is hampered by lack of knowledge of the fauna of species-rich source areas in this tropical environment. Major disturbances from increased visitor numbers contaminate the natural processes, and volcanic activity is an ever-present influence. The monitoring and inventory studies needed to provide a sound basis for ecological management and conservation of this unique island, despite wide acknowledgement of its interest and significance, will be difficult to assure. The scenarios for documenting and conserving terrestrial invertebrates on Anak Krakatau and Surtsey are briefly compared.

INTRODUCTION

The processes of island colonization and early successions hold immense interest for ecologists, in helping to understand how complex interacting systems may be founded, and develop. Nowhere can these processes be demonstrated better than from studying those on newly formed volcanic islands, where there can be no debate about survival of organisms from previous periods and where those processes can be traced from their earliest pioneer stages. Parallels in successions and community development on isolated new volcanic islands have been discussed extensively, with several commentators (including Fridriksson & Magnusson 1992, New, 2008, Thornton 1996, 2007) focusing on the similarities and differences between the ecological scenarios presented by Surtsey (subarctic: cool

temperate) and Anak Krakatau ('Child of Krakatau', tropical). Reflecting these very different climates, these two small islands are likely to reach markedly different climax points. Anak Krakatau could potentially achieve tropical rainforest conditions, should time and absence of volcanic activity permit. The two islands show remarkable parallels in size (both around 2.5 km² in area), topography (both around 200 m high during major survey periods, but with Anak Krakatau now considerably higher), ecological age, and distances from source biota - but, of course, also differ substantially in climate, the richness and knowledge levels of the source areas that may provide biota, the rates and extents of possible changes through succession, and the political and practical environments through which they can be protected and studied.

These contrasting islands are fascinating and informative natural laboratories in which to explore some fundamental ecological themes, and in which speciation processes of resident populations have not yet developed. As a slight caveat to this, possible hybridization on the Krakatau archipelago of distinctive parental strains (such as of a few butterflies with distinct ‘forms’ either side of the Sunda Strait) from Sumatra and Java, the two main source areas, has led to consideration of this, and several putative ‘subspecies’ have been named. However, in reality in studying Anak Krakatau we are restricted to dealing with rapid recent ecological change rather than any longer term evolutionary changes or speciation. This is also so for the considerably less rich fauna on Surtsey, but there with the advantage that the potential donor faunas are well documented and of limited richness. The identities and likely origins of most invertebrates on Surtsey are unambiguous. Relative intensity of collecting on the Krakatau archipelago has perhaps disproportionately inflated impressions of endemism, because of lack of equivalent attention to progressively degraded source areas. Simply that particular taxa have been found only on one or more Krakatau islands is, perhaps, far more likely to reflect undercollecting elsewhere than endemism. In contrast, for example, the far older examples of the Hawaiian archipelago have generated enormous numbers of radiative taxa from founder colonizers, to constitute complex and wholly endemic suites of invertebrates and others. Hawaii is also a potent warning of the impacts of people, and of invasive species, on such isolated biotas, as a widespread context of conservation concern.

Invertebrates are the major components of animal diversity. They encompass enormous taxonomic and ecological variety, and govern many key ecosystem processes. Invertebrates are also major tools in leading to understanding of how such systems establish, become sustaining, and also vulnerable. This short overview draws on published information from selected invertebrate surveys on the Krakatau archipelago in the 1980s-1990s to indicate their values in documenting and interpreting early successional processes.

ANAK KRAKATAU

Following the massive eruption of Krakatau in August 1883, submarine volcanic activity continued in the caldera between the three residual islands

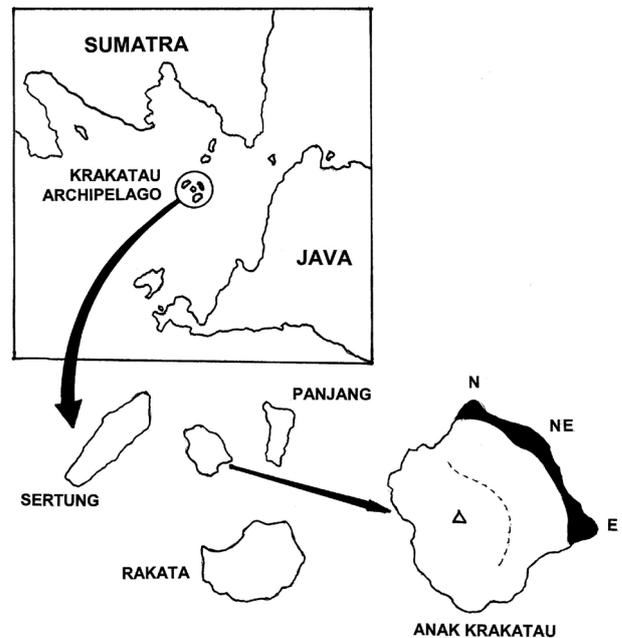


Figure 1. The Krakatau Archipelago, showing position in the Sunda Strait, the position of Anak Krakatau in the caldera surrounded by the three older islands left from the 1883 eruption (Sertung, Panjang, Rakata), and major features of Anak Krakatau ca 1990 (black, extent of vegetation along eastern coast with three main seral areas (Eastern Foreland, Northeastern Headland and Northern Foreland indicated by initial letters; dashed line, rim of outer crater; triangle, active crater).

of Rakata, Sertung and Panjang. Anak Krakatau emerged first from the sea in the centre of the caldera of the Krakatau archipelago, Sunda Strait, in 1927, but stabilised above water only in 1930 (Fig. 1). It has continued to increase in size, and is actively eruptive to the present.

There is continuing controversy over whether the whole communities there were truly extirpated by volcanic activity in 1952-1953 and damaged severely again in 1972 (van Borssum-Waalkes 1960, Partomihardjo et al. 1993, Whittaker et al., 1989, 1992), and Fosberg (1985) noted that the 1952 and 1972 eruptions were ‘two total or almost total sterilizations of Anak Krakatau’. Subsequent ecological studies have widely adopted that premise, and focused on successions since 1953, and the extent and ways in which they have been deflected by volcanic activity. In contrast, the vegetation on the three older islands (only 2-4 km distant) has proceeded for more than a century without such disruption. Unfortunately, however, and in marked contrast to the initiatives shown for Surtsey, Dammerman’s (1948) plea that ecological developments on Anak Krakatau should

be monitored carefully (so in part compensating for lack of such earlier systematic survey efforts for Krakatau from 1883) has not been adopted. No such coordination was possible, and information has accrued mainly through efforts of several independent research groups only from the early 1980s on. That work was facilitated immensely by the support of the Indonesian Institute of Science (LIPI: Lembaga Ilmu Pengetahuan Indonesia) in seeking to mark the centenary of the 1883 eruption. Outcomes of work by teams of scientists from Japan, the United Kingdom and Australia working with Indonesian scientists were partially assembled by Thornton (1992, 1996) and Tagawa (2005), with successional processes on the islands a predominant research theme. The general appearance of Anak Krakatau around that period is shown in Fig. 2. Despite the attractiveness of the concept that Anak Krakatau exhibits succession that closely parallels that occurring earlier on the other islands, this proposition remains controversial, because of the highly changed nature of source areas. Development on Anak Krakatau can draw from the well-developed communities on the nearby older islands, as well as from Sumatra and Java.

No systematic zoological surveys were made on Anak Krakatau for almost 30 years from 1952, so that critical early stages of colonization and succession have not been recorded. Since the mid-1990s, more recent work by visiting biologists has become infrequent because of political difficulties and continuing volcanic activity. The ecological validity of surveys is also being distorted because the island is subjected to largely uncontrolled visitation by tourists and others, despite formal need for permits for landing access. The major data on successions and invertebrates have thus come largely



Figure 2. Anak Krakatau, from the east in 1985, looking on to developing *Casuarina* forest on the Eastern Foreland (Sertung in background).

from work up to the early 1990s, by which time considerable anthropogenic disturbance was already evident. This ‘ad hoc’ accumulation of information differs fundamentally from the thorough systematic approach for Surtsey, but nevertheless illustrates some important and complex ecological themes based on temporal and spatial mosaics of vegetation, the variety of successional processes, and the trajectories being influenced by unpredictable disturbances.

SUCCESSIONAL PROCESSES

The major arrival and post-arrival processes relevant for invertebrate community development on Anak Krakatau are themselves diverse, and have been discussed extensively elsewhere, together with the likely filter effects that have occurred for some groups (New & Thornton 1992, Thornton, 1996, 2007) – as examples, termites found there are wood nesters likely to have arrived in driftwood, and soil nesting taxa had not been found (Abe 1994); and most of the aculeate Hymenoptera recorded are not swarm movers, but disperse as solitary individuals (Yamane et al. 1992). Relatively informative analyses of Anak Krakatau terrestrial invertebrates in the context of those on the three older islands nearby and the mainland faunas are few, but encompass three main themes:

- (1) inventories of particular taxonomic groups, notably terrestrial molluscs, soil nematodes, and a variety of arthropod orders of particular interest to individual expeditioners;
- (2) the biases of modes of arrival and early succession; and
- (3) progressive changes and development of assemblages and communities as succession proceeds, and placed in the wider context of vegetational development, vertebrate influences, and integration of mutualistic or other specific ecological associations.

These broad themes can be indicated using invertebrates, mainly insects, as examples to illustrate some of the more general findings and resulting concerns. In particular the transition from emphasising inventory surveys undertaken simply to enumerate taxa to clarifying faunal changes in relation to ecological processes and integration has wider importance in considering development and restoration. These processes are, however, founded in correlations of diversity, heterogeneity and turnover.

Whilst turnover (involving losses of species) on Anak Krakatau is largely due to succession, more drastic losses may occur from volcanic activity. In contrast, losses from Surtsey may occur from progressive erosion (Svavarsdottir & Walker 2009).

The major foci on natural processes involve (1) aeolian succession, with predators/scavengers depending on aerial fall-out for their food, and (2) the trajectories derived from initial colonizations of vegetation by herbivores as the foundation of foodwebs. They are augmented, and confused, by (3) anthropogenic influences and introductions that are extremely difficult to detect, monitor and differentiate from natural arrivals. Direct short visitations by tourists (both individuals and larger groups, such as from cruise ships), pumice-gatherers, fishermen and those seeking shelter from storms are frequent, and the debris from one of the world's busiest shipping lanes and from both Java and Sumatra assures continuing beach deposition of wood and other organic materials of unknown provenance. The major components that have been studied on Anak Krakatau over similar periods and are thus complementary in contributing to inventory listings, are:

- (1) aeolian communities in bare ash and lava, with the predominant scavenger/predator being a small flightless cricket (*Pteronemobius krakatau*) and trapping demonstrating that at least several million arthropods are deposited as aerial fallout on the island each day (New & Thornton 1988, Thornton et al. 1988);
- (2) invertebrates associated with *Saccharum* clumps extending progressively as the pioneer colonizer of bare ash, and acting both as interception traps for aerial drift and foci for colonization as litter accumulates (Turner 1992);
- (3) the invertebrate richness and biomass on *Casuarina* trees of different ages, as a temporal sequence from east (oldest) to north (youngest) along the coast, together with changes in some insect groups along this temporal sequence (Turner 1997); and
- (4) the progressive development of mutualisms between figs (*Ficus* spp.) and fig wasps (Agaonidae) as the initial stages of secondary forest are reached (Compton et al., 1988).

All have been documented, as cited above, with wider synthesis by Thornton (1996), but none has

been followed beyond these important initial stages to determine their later fate.

The general importance of prevegetation successions involving invertebrates feeding on allochthonous aeolian fallout is still novel to many ecologists, despite it being widespread on many kinds of substrate. Indeed, Hodkinson et al. (2002) proposed that it may be a general rule in primary community assembly, with roles including nutrient conservation and facilitating establishment of green plants through which more 'conventional' successions may proceed. The two main processes occur together on Anak Krakatau and, whilst largely separated in space, the participants are brought together by, for example, *Saccharum* tussocks. As elsewhere, the basic information was derived initially from surveys to collect, diagnose and enumerate the species present, using a variety of sampling techniques, but with surveys necessarily limited in duration and seasonal coverage. Interpretation has inevitably been uneven – as in many (most!) invertebrate surveys from the tropics, only selected groups can be appraised realistically at the species (or morphospecies) level. Attempts to sample the founder faunas on either side of the Sunda Strait and on the three older islands of the archipelago have been valiant but, again, are highly incomplete. Likewise, the roles of the island of Sebesi, to the north, as a 'stepping stone' for colonisation have been suggested repeatedly. It is also generally unknown whether colonists arrived from the older islands or from further afield, and how their incidence may be facilitated by the very short distances involved. One instructive example is the antlion *Myrmeleon frontalis* (Neuroptera, Myrmeleontidae), found on the three older islands, but not Anak Krakatau in the early 1980s (New & Sudarman 1988). It was found there in 1986, initially under the shelter of the small coastal hut built in that year, from where it expanded to frequent clumps of wild sugarcane (*Saccharum spontaneum*) on the adjacent ash cone (Turner 1992).

Perhaps the most informative data have come from the fact that the seral vegetation stages on Anak Krakatau are well-defined, with the major vegetated areas over the main sampling periods comprising three distinct but intergrading seral ages following a similar trajectory along the east-north shoreline. These, termed the Eastern Foreland (oldest), Northeastern Headland (intermediate) and Northern Foreland (youngest) could thus be considered

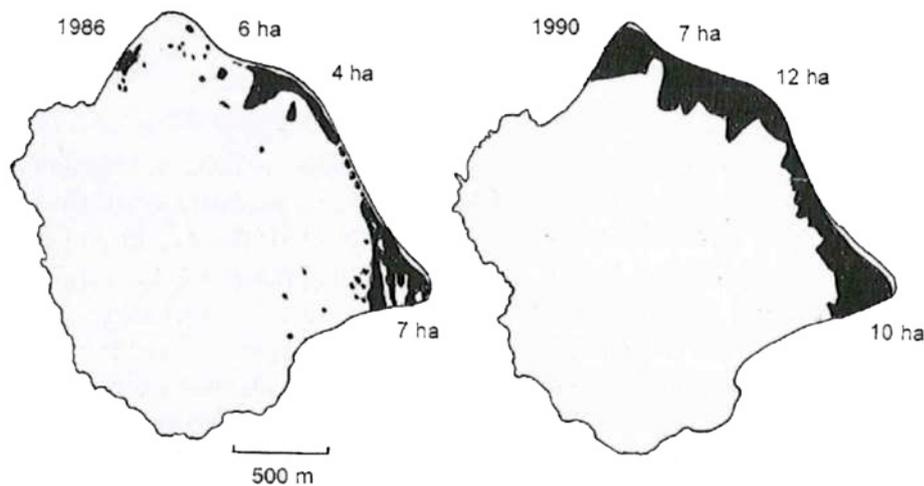


Figure 3. Changes in extent and continuity of vegetation from 1986 to 1990: vegetation in black, approximate areas given in hectares (from Thornton et al. 1992).

separately, but as a temporal sequence of decreasing variety and complexity. This enables the presence of successional mosaics, and probably originated from the differentially damaging eruptions of 1972/1973 (Thornton 1996). Nevertheless, changes were rapid (Fig. 3). In 1984, little vegetation occurred on the Northern Foreland, and the most advanced *Casuarina equisetifolia* woodland on the Eastern Foreland, was open with substantial pioneer *Ischaemum* and *Ipomoea* understorey. By 1990, the latter area was far more mature, and *Casuarina* also well-established to the north. The transition from sparse *Saccharum* grassland to definable *Casuarina* forest

was described by Suzuki et al. (1995). *Saccharum* grass clumps extended progressively up the outer ash cone as the major pioneer species away from the coast (Fig. 4). At the time of our work in the 1980s, the vegetated area of Anak Krakatau was only about 17 ha of the total island area of about 235 ha, and the coastal length available for arrivals by sea was 7-8 km. Rafting has clearly been important for such arrivals, with seeds of numerous plants (propagules of 66 taxa in 1990-91, with only 30 of these known from elsewhere in the archipelago: Partomihardjo et al. 1993) found in strand surveys, and logs and large complex mats of vegetation a clearly viable vehicle



Figure 4. The spread of *Saccharum spontaneum* tussocks up the bare volcanic slope above the Eastern Foreland, 1993.

for a variety of biota to arrive – one vegetation mat noted during our visits extended to around 20m² and included 3-4 m high palm trees with green foliage.

These seral vegetation changes can be correlated with changes in some invertebrate groups. Of the better-documented herbivore groups, the butterflies (with most taxa recognizable consistently, and a relatively strong regional picture of distribution and biology), are by far the most comprehensively surveyed and have been enumerated by most expeditions. Richness correlated strongly with vegetation life forms. Of the 44 species recorded in 1990, 18 had apparently arrived since 1986 (New & Thornton 1992a,b), and several were unknown from the older three islands. The greatest richness (31 species, of which 26 were considered locally resident: New 2008) occurred on the most mature East Foreland area, with progressive attenuation northward.

Whilst study of some groups of invertebrates (such as molluscs and soil nematodes: Smith & Djajasmita 1988, Winoto Suatmadji et al. 1988) implies that the Anak Krakatau fauna is an impoverished subset of those taxa found on the older islands, Anak has also yielded numerous species that are (1) not known from the older islands or (2) may now depend on early successional stages, such as open grasslands, not now present there, so constituting an ‘ecological rescue’ effect. Several grassland butterflies, for example, can be supported only on Anak Krakatau where these environments occur. Some of those species were found in earlier surveys on other parts of the archipelago, where their requirements are no longer available. As demonstrated on the older islands, the trajectories on Anak Krakatau, if undisturbed, are likely to engender forest environments of greater complexity and richness within a few decades. In part, this will reflect greater opportunities for interactions with the biota of those islands, with the Anak environment progressively more hospitable to such local colonizers and, perhaps, the ‘filter effect’ for arrivals reducing as the islands converge in character.

Developments on Surtsey are rather more constrained but also have been monitored more intensively from the earliest stages, so that changes are documented well. Studies of Surtsey invertebrates commenced in 1965 and proceeded through regular surveys until 1984. After a more irregular period, yearly visits re-commenced in 2002 (Olafsson & Ingimarsdottir 2009), concentrating on a standard

season of four days in July. One valuable clue to understanding has been to include trapping close to access points, to attempt to detect human impacts. Visitors to Anak Krakatau also have limited access sites. These are mainly on the eastern beaches adjacent to the most complex vegetation systems, with a few access tracks facilitating tourist walks to the interior and, for many people, a scramble to the rim of the outer cone or the summit area. No regular surveys that parallel those on Surtsey have been formalized on Anak Krakatau, and traits such as the entry of the antlion noted earlier are found fortuitously. Another artifact for some years was a small concrete-lined rainwater-gathering trough constructed near the main landing beach of Anak Krakatau, which was the foundation for the only freshwater community on the island (Thornton & New 1988b).

In essence, invertebrate surveys on Anak Krakatau have been sporadic, opportunistic and almost wholly by non-Indonesian scientists.

DISCUSSION

The basic successions noted above, and the relatively low species diversity across a variety of taxonomic and trophic invertebrate groups on Anak Krakatau, presented a substantial opportunity to elucidate some key elements of tropical ecology. The chances of undertaking those studies properly as undisturbed natural processes, probably already past, depend on continued monitoring and effective conservation through control of human interference and impacts. This seems unlikely to occur. The chances of effective conservation of Anak Krakatau at levels approaching those in place for Surtsey, are very low.

At one level, Anak Krakatau is regarded as important, a source of wonder, pride – and tempered with trepidation of what it might portend. As a designated World Heritage Site (from 1992) a duty of care is mandated, but without dedicated personnel and greater controls on tourism and other visitations, this is difficult to pursue. Likewise, the regular systematic surveys needed to follow further the ecological trajectories so far discerned are unlikely to come primarily from within Indonesia.

Many visitors to the island during our surveys were motivated by the volcano and the ‘romanticism’ of ‘Krakatau’. Some had little appreciation of the wider environmental significance of Anak Krakatau, and did not hesitate to leave litter and debris. It

seems that without greater awareness and regulation of access, any conservation is unlikely to proceed beyond 'paper commitment'. Recent nomination of Anak Krakatau to become a UNESCO Geopark (2012), by the Lampung Provincial Administration (Sumatra), is motivated strongly by desire to increase tourism for Lampung, following the submission guideline that such a park should be 'a large enough area for it to secure local economic and cultural development (particularly through tourism).' Strong community support and local involvement are integral to the assessment criteria. Clearly, increased tourism and visitations are anticipated, and likely to be encouraged, to the substantial benefit of local economies.

However, 'restricted access is extremely valuable in the study of primary succession', and one of the greatest advantages for Surtsey is simply this restricted and regulated visitation, emphasized by Svavarsdottir & Walker (2009, as in the above quotation). Even on Surtsey, they noted that any visit causes some disturbance. On Anak Krakatau, disturbance is frequent, unpredictable but certain, varied and with largely undocumented impacts. Unlike Surtsey, where ecological progression under regulated and monitored conditions seems assured and Hawaii, with more complex environments heavily contaminated by alien species and resident human populations, Anak Krakatau is to some extent a self-generating environment where a progressively complex suite of temporal mosaic substrates and

vegetation continues to be generated. Each has its future at the whim of continuing volcanism (Fig. 5), and potential for planning its practical long-term conservation has limits. The underlying desirability of facilitating chances of natural development and evolution depends on minimizing human intrusions and disturbance, but also assuring sufficient monitoring and survey to interpret changes sensibly. Permanent survey plots, so important in successional interpretations (del Moral 2009), have not been established on Anak Krakatau. Such plots were, however, established on the three older Krakatau islands in 1989 and have yielded valuable information on changes in vegetation (Whittaker et al. 1999).

Volcanic activity may be both a great benefit and a severe threat to the biota present. In the short term, low level activity is a deterrent to some visitation and may thus be a considerable protection against human disturbance with little impact on other biota. In the longer term, increased volcanic activity may destroy all that is present. It is believed by some that Anak Krakatau's recent sustained activity may be a prelude to a far more devastating eruption – perhaps within the next few decades, and possibly equivalent to the 1883 episode in intensity and impact. Information on the island's ecology will then become of historical interest but may also constitute a comparative template for some future equivalent study, much as information in Dammerman (1948) on the colonization of the older Krakatau islands post-1883 stimulated considerable debate.



Figure 5. Interruption of vegetation between Northeastern Headland and Northern Foreland by volcanic lava flow of 1993.

More broadly, the current lack of attention to development of the unique environment of Anak Krakatau reflects considerations of wider protected areas in Indonesia. The impressive declared Protected Areas system of Indonesia, with its considerable extent and variety, does not extend fully from paper to practice. Most National Parks receive little practical protection, even when inhabited by charismatic large mammals, and most such areas on the densely populated islands of Java and Sumatra continue to be exploited by forest clearance and kebun gardening systems – leading to predictions such as Sumatra being likely to lose all of its lowland primary forest (Jepson et al. 2001). The only more secure areas are likely to be those that are either at high elevations or otherwise remote, and are difficult to access. Mainland Ujung Kulon (as relatively remote) falls into this ‘lower risk’ category whilst, in contrast, the Krakatau archipelago (previously part of the same National Park) appears increasingly vulnerable.

Whatever basic ecological information can be gleaned, the scientific case for effective conservation of the Krakatau archipelago rests largely on its unique status as ‘... an example of the natural recovery of lowland tropical forest from the most extreme natural disturbances’ (Thornton 1996), even as nearby forests either side of the Sunda Strait succumb to human pressures. Understanding successions, based on sound documentation of changes in composition and diversity of invertebrate assemblages, and protecting their capacity for continued ecological and evolutionary development, is fundamental to that case.

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Observations on seals on the island of Surtsey in the period 1980-2012

ERLINGUR HAUSSON

Vör Marine Research Center at Breiðafjörður

erlingur@sjavarrannsoknir.is

ABSTRACT

Grey seals (*Halichoerus grypus* Fabricius) and harbour seals (*Phoca vitulina* L.) have been surveyed on the coasts of Iceland since 1980. During the period 1980-2012, both seal species have declined markedly in numbers at the Icelandic coast. The grey seal has established a considerable breeding site on the northern spit of the Surtsey island. This is at present one of the biggest grey seal rookeries on the southern shores of Iceland, with estimated about 60 pups born there in the autumn of 2012. On the other hand, the harbour seal has not been numerous on Surtsey during breeding time in the summer. Breeding sites of harbour seals on the south coast of Iceland closest to Surtsey are in the estuaries of the glacial rivers Ölfusá, Þjórsá, Markarfljót and Kúðaflljót. Harbour seals, however, haul-out in great numbers on the northern shores of Surtsey during the winter, presumably using the island as a resting place after foraging in the adjacent waters.

INTRODUCTION

Harbour and grey seal numbers have been surveyed on the coasts of Iceland since 1980 (Hauksson 2008; Hauksson 2010; Granquist et al. 2011; Hauksson et al. 2014). Seals visited the island the first time shortly after it had formed, and used it as a resting place. Constant changes of the shore seem to have hindered seals in breeding there until first year 1983 (http://www.surtsey.is/pp_isl/lifsj_4.htm). Fridriksson (1994) noted that that grey seal breed regularly on the island but harbour seals only sporadically. Hauksson (2009) presented information from surveys on seals in Surtsey until the year 2005. New information, from the period 2006-2012, is here and discussed on context with previous work.

MATERIAL AND METHODS

The present work summarizes seal sightings on Surtsey island from year 1980 to 2012. Information on the survey methods and basic data analysis in

the grey seal pups surveys have been published in (Hauksson 2007) and the harbour seal aerial census is described in (Hauksson 2010). Further analyses of data and estimation of the grey seal breeding O-give is described in (Hauksson 2007).

RESULTS

Only a few harbour seals have ever been observed in Surtsey during August (Table 1), and hardly any during the grey seal surveys in the autumn months.

The first time the author observed grey seals in Surtsey from the air, was in August 1980, and grey seals have been regularly seen there since (Table 2). In 1989 estimated pup-production on the breeding site there was at least 38 pups and in 2012 a total of 62 pups were born (Table 3). In the period 1989 – 2012 the medium breeding date was the 12 October (Table 3). Pup-production was increasing from 1989 to 2008 and probably did decline in 2012 (Table 3).

Table 1. Observations on seals in Surtsey and vicinity from aerial surveys during the summer, aimed for harbour seals. Information about time of counting, time of midday, weather, tide and time of low tide, are included in the table for comparisons with future data. These factors can influence the number of harbour seals counted hauling out (see Hauksson 2010).

Day	Time of counting	Harbour seals	Grey seals	Time of midday	Weather	Tide	Time of low tide
11 Aug 1980	14:01	20	1	13:33	Wind force 1-2, cloudy	Spring tide	12:09
22 Jul 1985	14:57	4	3	13:34	NW-breeze, lightly cloudy	Spring tide	15:30
11 Jul 1988	12:18	0	6	13:33	N-4, lightly cloudy	Spring tide	16:11
9 May 1989	17:30	9	0	13:24	S-4, lightly cloudy	-	14:00
12 Aug 1990	16:40	18	0	13:33	S-breeze	Spring tide	15:27
12 Aug 1992	12:53	0	27	13:26	No wind cloudy	Increasing tide	11:17
23 Aug 1995	11:15	6	0	13:30	SV-4, cloudy	Neap tide	11:00
6 Aug 2003	20:57	2	1	13:26	NV-4, lightly cloudy	Neap tide	18:23
16 Aug 2006	16:40	0	0	13:24	NV-4, lightly cloudy	Neap tide	17:12
16 Jul 2011	12:05	0	0	13:27	NA-4, lightly cloudy	Spring tide	12:24

Table 2. Observations on grey seals in Surtsey and vicinity from aerial surveys during the autumn. Environmental factors not given because they do not influence significantly the number of pups seen

Day	Time of counting	Pups	Adults	Notes
8 Oct 1982	15:45	0	0	
19 Oct 1986	13:14	34	16	Estimated minimal pup-production in 1986; $34 \times 1.25^1 = 42$
9 Oct 1988	10:30	1	1	
21 Nov 1988	11:30	15	11	Estimated minimal pup-production in 1988; $16 \times 1.25^1 = 20$
25 Nov 1989	11:05	3	1	
21 Nov 1989	10:55	35	0	
13 Dec 1989	12:00	73	0	Three white pups 70 grey weaned pups
3 Nov 1990	11:00	23	-	Estimated minimal pup-production in 1990; $23 \times 1.25^1 = 29$
2 Nov 1992	10:30	25	10	Estimated minimal pup-production in 1992; $25 \times 1.25^1 = 31$
19 Oct 1995	16:10	39	-	Estimated minimal pup-production in 1995; $39 \times 1.25^1 = 49$
15 Oct 1998	-	30	-	Karl Gunnarsson counted on foot (personal communication)
16 Oct 2002	11:36	22	-	
6 Nov 2002	12:55	35	-	Estimated minimal pup-production in 2002; $35 \times 1.25^1 = 44$
17 Sep 2003	-	3	-	
8 Oct 2003	-	23	-	
29 Oct 2003	-	37	-	
21 Nov 2003	-	8	-	
9 Dec 2003	-	5	-	
24 Sep 2005	10:45	10	-	
20 Oct 2005	13:00	34	-	
11 Nov 2005	10:30	29	-	
25 Nov 2005	12:50	66	-	Six white pups, 60 weaned pups
25 Sep 2008	10:50	24	$\cong 10$	
18 Oct 2008	11:49	9	-	Additionally 34 weaned pups counted
21 Nov 2008	11:13	13	-	Additionally 69 weaned pups and juveniles counted
19 Sep 2012	10:34	8	-	One dead pup probably, motionless and gulls standing by it
1 Oct 2012	10:36	45	-	
5 Oct 2012	15:30	41	-	
17 Oct 2012	11:49	55	-	
11 Nov 2012	-	54	-	

¹ From (Hauksson 2007).

DISCUSSION

It is not known why the peak birthing date of grey seals on the island was about month earlier in year 2003 compared with year 1989. However, the

birthing O-give in 1989 was only based on three non-negative counts, which is the absolute minimum for fitting a normal distribution to it, so it was not as sound as the O-give in 2003, which was based on

Table 3. Peek birthing date and 90% confidence interval births for the grey seal herd in Surtsey and information for estimation of the relationship between pup counts on breeding sites (n), estimated pup production and correction factor to correct pup counts.

Date	Max count (n)	Breeding (Time interval for 90% births)	Pup-production (p)	p/n	The distribution that gave best fit (log likelihood value)
14 Sep – 13 Dec 1989	35	19 Nov (7 Nov – 1 Dec)	38	1.09	Normal (-129.36)
17 Sep - 11 Dec 2003	37	20 Oct (25 Sep – 26 Nov)	54	1.46	Gamma (-230.98)
24 Sep – 25 Nov 2005	34	24 Oct (28 Sep – 13 Nov)	63	1.85	Weibull (-241.41)
25 Sep – 21 Nov 2008	24	13 Oct (5 Oct – 21 Oct)	88	inconclusive	Lognormal (-310.28)
19 Sep – 17 Oct 2012	55	4 Oct (12 Sep – 26 Oct)	62	1.13	Loglogistic (-222.24)
Median (min – max)	35 (24 – 55)	12 Oct (12 Sep – 1 Dec)	62 (38 – 88)	1.46 (1.09 – 1.85)	

five counts. But there is evidence for different peek birthing dates in same rookery in different years in Breidafjord, W-Iceland, but the reason for it is only speculative (Hauksson 2007).

The grey seal has established a sizeable breeding site on the northern spit of Surtsey, which is now one of the biggest rookeries on the southern shores of Iceland. It was of similar size in 1989 to 2008 in spite of considerable decrease in the Icelandic grey seal population (Hauksson 2010). All hunting is prohibited in Surtsey and only researchers are allowed to visit and stay on the island, so it can truly be said that the grey seal rookery is protected in Surtsey. In spite of that it has not increased markedly since 1989, probably because pups born there have died, as juveniles and adults, elsewhere along the Icelandic coast. Gill-nets are especially dangerous for juvenile grey seals, as if they get caught they easily drown. Juvenile grey seals have been found to undertake extensive trips as marked weaned pups have been recaptured far away from the site where they were marked (Einarsson 1993).

The harbour seals are not numerous in Surtsey during breeding in the summer. Their main breeding sites on the south coast of Iceland closest to Surtsey are in the estuaries of the glacial rivers Ölfusá, Þjórsá, Markarfljót and Kúðaflljót (Hauksson 2010). They, however, haul-out in great numbers on the shores of Surtsey during the wintertime, when feeding. Therefore, Surtsey seems not as important for breeding of harbour seals as it is for the breeding of grey seals. There is also evidence for grey seals driving harbour seals a way from places they have colonized (Hauksson and Ólafsdóttir 2004).

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Pattern and process of vegetation change (succession) on two northern New Zealand island volcanoes

BRUCE D. CLARKSON¹, BEVERLEY R. CLARKSON² AND JAMES O. JUVIK³

¹Environmental Research Institute, University of Waikato, Private Bag 3105, Hamilton, New Zealand, (b.clarkson@waikato.ac.nz),

²Landcare Research, Private Bag 3127, Hamilton, New Zealand, (clarksonb@landcareresearch.co.nz)

³Geography and Environmental Studies, University of Hawai'i–Hilo, Hawaii 96720 USA, (jjuvik@hawaii.edu)

ABSTRACT

Pattern and process of vegetation change (succession) were compared on two northern North Island volcanoes: Whakaari (White Island) and Rangitoto Island where the endemic woody tree *Metrosideros excelsa* is the primary colonizer of raw volcanic substrates. Quantitative data from our previous publications (see References) and the references therein illustrate sequences of vegetation succession following significant volcanic eruptions. New information on Rangitoto Island *M. excelsa* patch dynamics and updated vascular species statistics for Whakaari have also been included. We also draw on supporting data from *M. excelsa* forest on the mainland and long-inactive volcanic islands in the Bay of Plenty, to provide a context for understanding the vegetation dynamics on Whakaari and Rangitoto Island. Species facilitation, light availability, humidity, substrate and disturbance history are all key determinants of vegetation succession across these volcanic landscapes.

INTRODUCTION

Volcanic activity (including lava flows, debris flows and tephra eruptions) has been a regular feature of many northern New Zealand landscapes, causing long-lasting impacts on the vegetation. Over the last 40 years we have been using a combination of the chronosequence and direct monitoring methodologies (Clarkson 1998; Walker et al. 2010) to research the pattern and process of vegetation change (succession) across young volcanic landscapes (currently active to <600 years), and long-inactive volcanoes (>6000 years).

Whakaari (White Island)

Whakaari is a 238 ha island volcano (highest point 321 m a.s.l.) located 50 km north of North Island mainland in the Bay of Plenty (Fig. 1). It has been in the state of continuous solfataric activity, with intermittent small steam and tephra eruptions

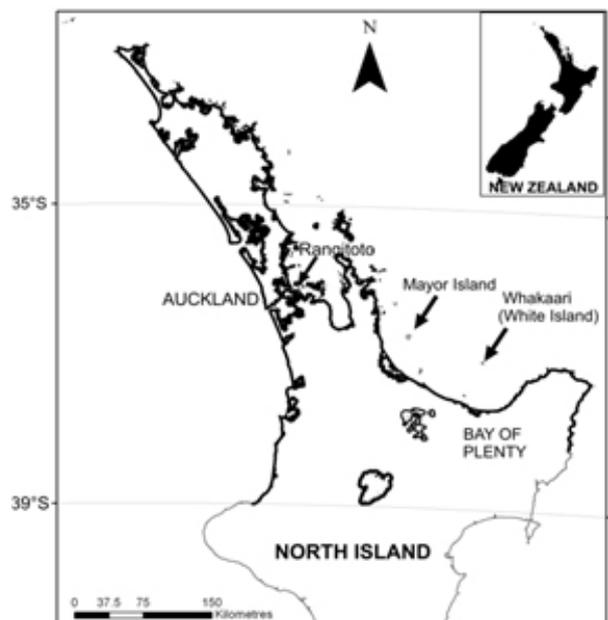


Figure 1: Map showing location of study sites, North Island, New Zealand. Dark line indicates general distribution of *Metrosideros excelsa*.

Table 1: Number of vascular taxa recorded on Whakaari (White Island) between 1912 and 2005 based on Oliver (1915), Hamilton (1959), Gillham (1965), Wilcox (1967), Clarkson & Clarkson 1994, Ecroyd & Clarkson unpubl. data (2005). * = exotic

Ferns	
1	<i>Asplenium northlandicum</i>
2	<i>Histiopteris incisa</i>
3	<i>Paesia scaberula</i>
4	<i>Pteridium esculentum</i>
5	<i>Pteris tremula</i>
Dicotyledonous herbs	
6	<i>Cakile maritima</i> subsp. <i>maritima</i> *
7	<i>Chenopodium trigonon</i> subsp. <i>trigonon</i>
8	<i>Cirsium vulgare</i> *
9	<i>Conyza sumatrensis</i> *
10	<i>Coronopus didymus</i> *
11	<i>Disphyma australe</i> subsp. <i>australe</i>
12	<i>Euchiton involucratus</i>
13	<i>Gamochaeta purpurea</i> *
14	<i>Hypochoeris radicata</i> *
15	<i>Jacobaea vulgaris</i> *
16	<i>Lobelia anceps</i>
17	<i>Paronychia brasiliiana</i> *
18	<i>Phytolacca octandra</i> *
19	<i>Pseudognaphalium luteoalbum</i> agg.
20	<i>Senecio bipinnatisectus</i> *
21	<i>Senecio sylvaticus</i> *
22	<i>Solanum nigrum</i> *
23	<i>Solanum nodiflorum</i> *
24	<i>Sonchus asper</i> *
25	<i>Stellaria media</i> subsp. <i>media</i> *
26	<i>Symphyotrichum subulatum</i> *
Dicotyledonous trees & shrubs	
27	<i>Coprosma repens</i>
28	<i>Metrosideros excelsa</i>
29	<i>Ozothamnus leptophyllus</i>
Monocotyledons	
30	<i>Cortaderia selloana</i> *
31	<i>Cyperus eragrostis</i> *
32	<i>Lachnagrostis filiformis</i>
33	<i>Phormium tenax</i>
34	<i>Poa anceps</i> subsp. <i>anceps</i>
35	<i>Poa annua</i> *
36	<i>Holcus lanatus</i> *

occurring since 1826. In recent times, major damage to the vegetation has resulted from significant and complex eruptive sequences between 1976–1981 and also 1984–1994. Further volcanic unrest began in July 2012 and has continued intermittently to the present day. Eruptive episodes have included explosive ejections of ash and gas emissions, with acid rain also

causing death and dieback of *M. excelsa* forest and *Disphyma–Chenopodium* herbfields. *Metrosideros excelsa* dominates a floristically depauperate forest community which, in places, comprises only two or three vascular species, namely *M. excelsa*, *Histiopteris incisa*, and *Phormium tenax*. The total vascular flora recorded on the island (36; Table 1) between 1912 and 2005 has ranged between seven and thirteen species before 1990, and approximately 33 species in 2005, which reflects the reduction in volcanic activity between these dates. The post-1990 arrivals, however, are mainly exotic dicotyledonous herbs, and *M. excelsa* remains the only tree species present on the island. *Metrosideros excelsa* is a mass seeder with wind dispersed seed and the ability to recover from canopy damage by epicormic resprouting. Direct succession of *M. excelsa* results from recovery and spread of an existing population or colonization of a newly emplaced surface by *M. excelsa* seed.

Rangitoto Island

Rangitoto Island, a basalt shield volcano covering 2311 ha and rising to 260 m a.s.l. is located in the Hauraki Gulf, 8 km north east of Auckland City (Fig. 1). It appears to have been active between 850 AD and 1800 AD, with a maximum lava activity around 1300 AD (Robertson 1986). The primary surface is mainly crusty aa basaltic lava but the summit consists of scoria cones. The last lava flows were followed by an emission of ash that filled most of the crevices and shallow hollows. *Metrosideros excelsa* is the prime lava colonizer and has coalesced to form continuous forest over large areas of the island. We have been monitoring *M. excelsa* patch establishment and development between 1980 and the present day in permanent plots established by one of us (JOJ). These plots were representative of the most extreme sites of largely un-vegetated aa lava. The number of vascular species is strongly positively correlated with the size of the *M. excelsa* patch ($r^2 = 0.742$; $n = 80$) with 1–4 species recorded in patches of $<0.1 \text{ m}^2$ and 16–19 species in patches of $>100 \text{ m}^2$. Using patch size in six size classes (midpoints = 1 m^2 , 3 m^2 , 6 m^2 , 12 m^2 , 24 m^2 , 48 m^2) and frequency of occurrence as a surrogate for age, it is possible to determine the orderly sequential establishment of species. Early establishers include *Coprosma robusta*, *Myrsine australis* and *Astelia banksii*. Middle and late establishers include *Pseudopanax*

arboreus, *Collospermum hastatum* and *Asplenium oblongifolium*. The fern, *Asplenium flaccidum*, which is mostly epiphytic on *M. excelsa*, is one of the last to arrive. Some species fluctuate in their frequency in relation to patch size, for example, *Brachyglottis kirkii*, *Ctenopteris heterophylla*, and *Asplenium flabellifolium*. These are usually patch edge dwellers and are sometimes lost as the *M. excelsa* canopy expands but may subsequently recolonise the edge of the patch. *Metrosideros excelsa* facilitates this deterministic establishment pattern by influencing the microclimate of the site. Surface temperature on open lava may exceed 50°C whereas in the interior of a large patch or extensive forest, it is less than 25°C. Relative humidity is less than 40% on open lava, exceeds 45% in large patches and is over 55% in the forest interior.

Comparison with *M. excelsa* forests elsewhere

Plant successions on volcanic landscape are extremely variable both in terms of rates of change and the sequence of species establishing. However, comparison of *M. excelsa* forest across young volcanic islands, long-dormant volcanic islands and the mainland illustrates some regularity in the patterns of succession that arise following disturbance. For example, Mayor Island (Tuhua), a dormant (c. 6000 years) volcano situated between Rangitoto and Whakaari c. 27 km east of the Coromandel Peninsula (Fig. 1), is dominated by *M. excelsa* forest. The current forest pattern there was likely initiated by Polynesian burning c. 450 BP. Vegetation change in permanent quadrats (1999–2009) shows proliferation of *Litsea calicaris* and the establishment of

Dysoxylum spectabile and *Corynocarpus laevigatus* in the forest understory. On the mainland, *L. calicaris*, *D. spectabile*, *C. laevigatus* commonly establish beneath closed canopy *M. excelsa* forest (usually >50 years old) and contribute to the replacement of *M. excelsa* in the canopy after a minimum period of c. 200 years. In contrast *Beilschmiedia tawa*, the most shade tolerant tree species to establish within *M. excelsa* forest, is late successional and requires c. 100 years before conditions are suitable for seedling establishment. On Rangitoto Island, *M. excelsa* facilitates the establishment of mid successional species; however their incursion is much slower than on less severe mainland sites and long-dormant volcanoes, where *M. excelsa* forest has largely been initiated by fire. On much older basaltic lava blocks flanking Mt Eden (c. 10 km SW of Rangitoto Island, on the mainland), *M. excelsa* shares dominance with *Vitex lucens*, *L. calicaris*, *D. spectabile*, *Alectryon excelsus* and *Myoporum laetum* and this might indicate future trends on Rangitoto.

Light is a key resource controlling plant species colonization of new sites and replacement in forest understories. The shade tolerance of key species in *M. excelsa* forest and scrub has been quantified using hemispherical photography (Bylsma et al. 2014). Light environment occupancy of key canopy species differs significantly ($P < 0.001$) according to the distribution of understory light environments available. Pioneer and early successional species (e.g., *M. excelsa*, *Myrsine australis*, *Kunzea ericoides*) occupy the higher spectrum of light environments, whereas mid and late successional tree species (e.g., *Litsea calicaris*, *Dysoxylum spectabile*,

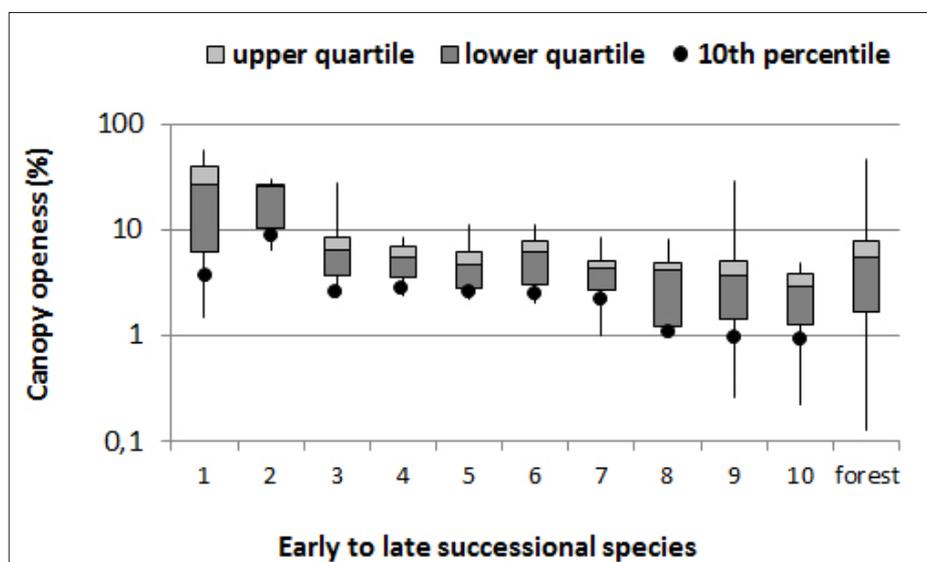


Figure 2: Species light environment distributions: (1) *Metrosideros excelsa*, (2) *Kunzea ericoides*, (3) *Piper excelsum*, (4) *Myrsine australis*, (5) *Geniostoma rupestre*, (6) *Hedycarya arborea*, (7) *Dysoxylum spectabile*, (8) *Corynocarpus laevigatus*, (9) *Litsea calicaris*, (10) *Beilschmiedia tawa*. Data collected from Ohope Scenic Reserve, Kohi Point Reserve and Matata Scenic Reserve, Bay of Plenty.

Beilschmiedia tawa) show bias towards the darker microsites (Fig. 2). Ranking species in order of their minimum light requirements (e.g., 10th percentile) approximates their order of arrival in *M. excelsa* forest development.

Comparison of vascular species richness, time since disturbance and island area reveals variable disharmonic floras. On Whakaari, continual volcanic disturbance, isolation and extreme soil conditions have resulted in a depauperate flora (36 spp.) and the simplest *M. excelsa* forest. On Rangitoto Island, the proximity to the mainland, less volcanic disturbance, larger size and relative stability since c. 1800 AD have contributed to a much higher number of species (582 spp.). In addition, the presence of beachside holiday homes since the 1930s has enabled the incursion of numerous exotic species.

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Mycorrhiza and primary succession

HÅKAN WALLANDER¹, ARI JUMPPONEN² AND JAMES TRAPPE³

¹Department of Biology, Lund University, 223 62 Lund, Sweden

²Division of Biology, Kansas State University, Manhattan, KS 66506, USA

³Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, USA, and U.S.Forest Service, Forestry Sciences Laboratory, Corvallis, OR 97331, USA

ABSTRACT

The importance of mycorrhizal fungi for soil formation and carbon sequestration has been highlighted in recent research. Here we discuss these findings in relation to primary successions by use of data from Surtsey and from lava fields around Mount Fuji in Japan.

Assembly of host associated fungal communities in remote islands such as Surtsey depend on numerous factors. Fungal propagules must come to the island, most likely by wind or birds, and the presence of compatible hosts determines what associations can form. However, to what extent these associations will be stable depends on environmental and biotic filters (Fig. 1). Associations between ectomycorrhizal (ECM) and arbuscular mycorrhizal (AM) fungi have been confirmed on Surtsey (Magnusson et al. 2009, Greipsson & El-Mayas 2000 and Eyjolfsdottir 2009), but little is known about the amount and composition of spores that arrive on the island. Based on the species of sporocarps found on Surtsey, ECM genera such as *Hebeloma*, *Laccaria* and *Inocybe* have established, but more species are likely present on root tips, but they have not been investigated. The root tip community is probably more diverse, because many ECM species do not form sporocarps or only do so occasionally or belowground.

It is generally recognized that the first plants establishing in primary succession are non-mycorrhizal, and it has been suggested that these are replaced by more competitive plants colonized by arbuscular mycorrhizal (AM) fungi, whereas

ericoid and ECM associations establish later when soil organic matter has accumulated (Reeves 1979). In Surtsey, three out of four Icelandic *Salix* species established during 1995-1999 (Magnusson et al., 2009). A possible reason for their relatively late and synchronous establishment may be that compatible host-fungal associations had not been encountered earlier. *Salix* spp. form associations with both ECM or AM fungi and it is possible that AM associations need to precede ECM associations which are well established today (Magnusson et al. 2009, Greipsson & El-Mayas 2000 and Eyjolfsdottir 2009). A better understanding of the prerequisite for *Salix* establishment in primary succession is needed.

Recent research has emphasized an important role of ECM associations for soil formation and carbon sequestration (Clemmensen et al. 2013), but this has not been investigated to any extent in primary successions. Production and turnover of external ectomycorrhizal mycelium (EMM) can be substantial, and residues of mycorrhizal necromass have been suggested to contribute significantly to soil organic matter (Ekblad et al. 2013). Studies using ingrowth mesh bags (Wallander et al. 2010) or ingrowth cores (Hendricks et al. 2006, Sims et al. 2007),

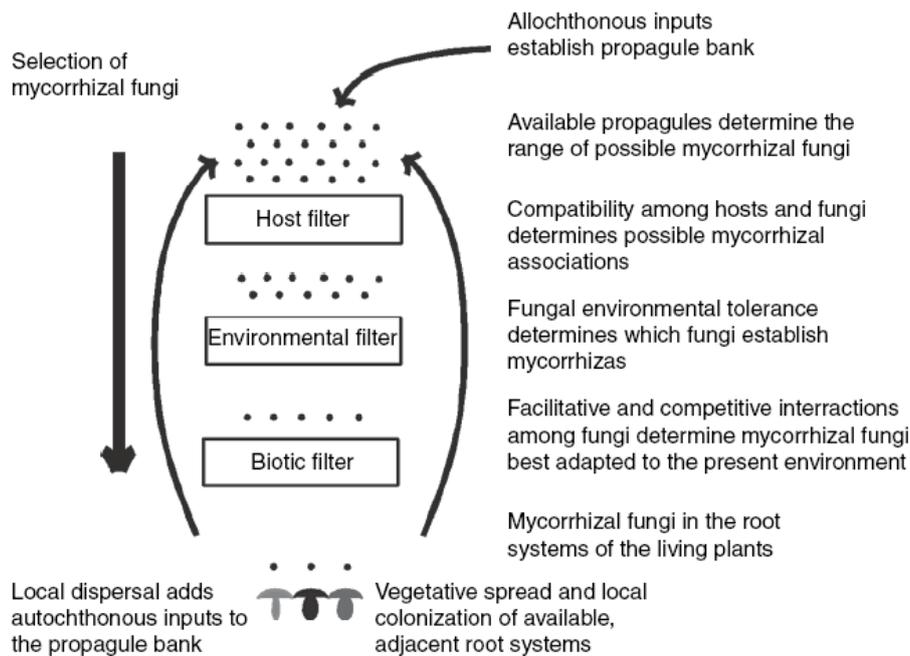


Figure 1. Conceptual community assembly model for mycorrhizal fungal communities during succession. Initially, out-of-site, allochthonous propagules establish available species pool (propagule bank). Successful component species are selected by filtering out those species that are incompatible with available hosts in their present physiological state (HOST filter), those species whose environmental tolerances do not include the prevailing conditions in the successional environment (ENVIRONMENTAL filter), and those species that are outcompeted by others in the prevailing environment (BIOTIC filter). Species with adequate fitness to reproduce contribute to the autochthonous propagule bank via production of vegetative mycelium or via production of sexual and asexual propagules (from Jumpponen and Egerton-Warburton 2005).

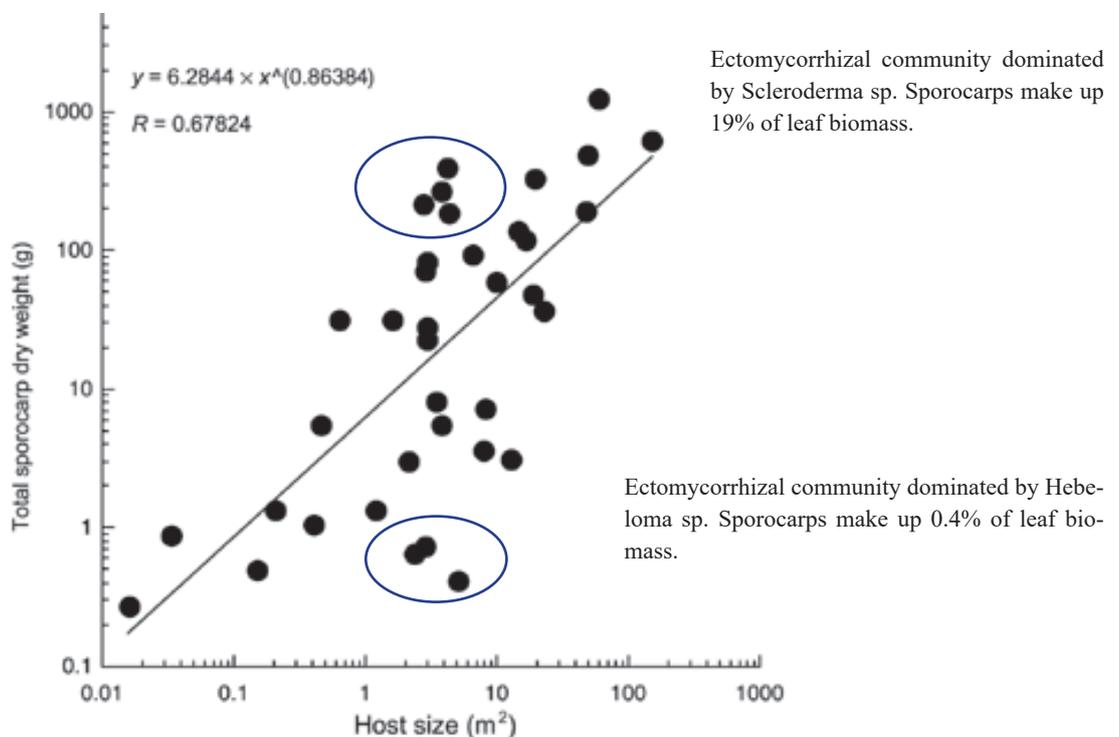


Figure 2. The biomass production of ectomycorrhizal sporocarps in relation to associated host size. The x-axis, shown logarithmically, indicates the area covered by *Salix renii* in each patch. The y-axis, shown logarithmically, represents the total ectomycorrhizal sporocarp biomass produced in each vegetation patch in 2000 and 2001. The correlation is statistically significant ($P < 0.01$). Modified from Nara (2006).

we demonstrated that EMM can constitute several hundred Kg of biomass per hectare in coniferous forests, whereas sporocarps usually produce only a few Kg of biomass per hectare per year. Still sporocarp formation constituted a major carbon sink (19% of leaf biomass) in *Salix renii* clones colonized by *Scleroderma* sp. on scoria substrate on the slopes of Mount Fuji, which had an eruption in 1707 (Nara 2006). In contrast, *S. renii* clones of similar age colonized by *Hebeloma* sp. produced only minute amounts of sporocarps (0.4% of leaf biomass), and the host plants performed much worse than those colonized by *Scleroderma* sp. (Nara 2006). However, it was not clear if this difference resulted from the ECM communities or if variable nutrient conditions in the volcanic substrate could explain the different growth rates of the hosts. However, the study firmly demonstrated that allocation of carbon to ECM fungi can be large in primary succession, and that this process can have large potential to enhance soil formation. Furthermore, the composition of the ECM community may have a major impact on soil formation: this is a subject that needs more research, especially in unique sites such as Surtsey, where plant succession has been followed in detail.

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GEOLOGY

The 2011-2012 El Hierro submarine eruption: a challenge of geochemical and thermal imaging for volcano monitoring

NEMESIO M. PÉREZ ^{1,2}

¹ Instituto Volcanológico de Canarias (INVOLCAN), 38400 Puerto de la Cruz, Tenerife, Canary Islands, SPAIN

² Instituto Tecnológico y de Energías Renovables (ITER), 38611 Granadilla de Abona, Tenerife, Canary Islands, SPAIN

e-mail: nperez@iter.es

ABSTRACT

A shallow submarine eruption occurred between October 12, 2011 and March 5, 2012 about 2 km off the southern coast of El Hierro, the youngest and smallest of the seven major islands of the Canarian archipelago. This submarine eruption rose from a depth of 363 meters and finally reached 89 meters bsl and provided us a unique chance to study a variety of precursory signals before the eruption as well as to evaluate for the very first time magma emission rates from a shallow submarine eruption using airborne thermal imaging.

INTRODUCTION

El Hierro is the smallest and most south-western Island of the Canarian archipelago with an area of 278 km² (Figure 1a). It represents the summit of a volcanic shield elevating from the surrounding seafloor at depth of 4,000m to up to 1,501m above sea level. El Hierro Island is the youngest in the Canarian archipelago, with the oldest subaerial rocks dated at 1.12 Ma (Guillou et al., 1996). Recent volcanic activity occurred mainly along the three volcanic ridges bearing NE, S and SW with respect to the center of the island. Before the 2011-2012 submarine eruption and for the last 500 years, Hernández Pacheco (1982) reported a single volcanic eruption during 1793 at Lomo Negro, although its occurrence is questionable (carbon-14 indirect dating) and most probably consisted of an offshore eruption (Romero and Guillén, 2012). In the last 37 ka, El Hierro has been covered with lavas erupted in the last stage of its volcanic evolution, and deep embayment has been

produced by giant landslides between the three rift zones. The most recent one was the El Golfo failure on the northwest flank of El Hierro, which took place approximately 15 ka ago (Masson, 1996). Stroncik et al. (2009) carried out a thermobarometric and petrologic study on basanites erupted from young volcanic cones along the submarine portions of the three El Hierro rift zones to reconstruct magma plumbing and storage beneath the island. They concluded that small, intermittent magma chambers might be a common feature of oceanic islands fed by plumes with relatively low magma fluxes, which results in limited and discontinuous magma supply.

After hundreds of years of repose, on October 12, 2011, an eruption of El Hierro occurring under water was detected by visual observations off the coast of El Hierro, about 2 km south of the small village of La Restinga. This submarine volcanic eruption was preceded by (i) an unusual increase of seismicity

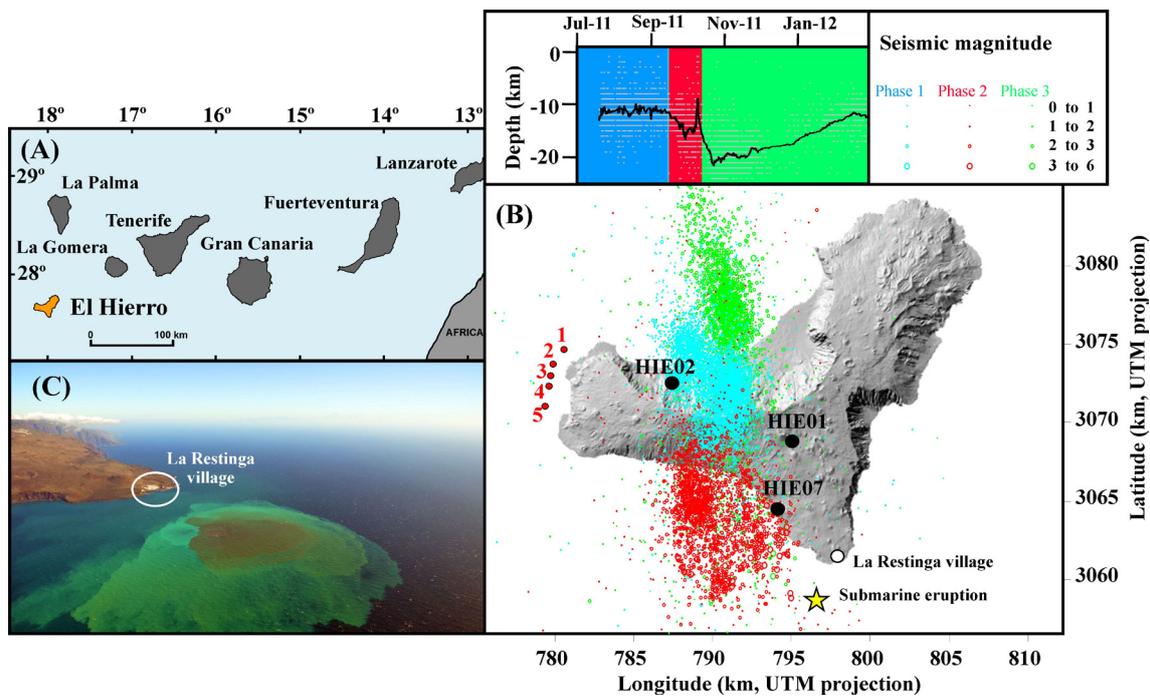


Figure 1. A: Geographic location of El Hierro Island (Canary Islands, Spain). B: Epicenter locations of 12,178 seismic events recorded until 9 February 2012. Different phases of seismicity described by Ibáñez et al. (2012) are displayed in blue, red, and green. Temporal evolution of hypocentral depth of earthquakes is depicted by 100 event moving average (black line). Star indicates location of submarine eruption (UTM—Universal Transverse Mercator). Black dots indicate location of geochemical stations and red dots location of submarine plumes. C: Water discoloration south of La Restinga produced by submarine eruption.

(more than 9000 seismic events) recorded by the National Geographical Institute of Spain (IGN) since July 19, 2011 (Figure 1b), (ii) a significant ground deformation detected by the seven-GPS network (Nagoya University-ITERGRAFCAN) deployed at El Hierro (Sagiya et al. 2012), and (iii) by significant changes in the volcanic gas emissions, detected both by the continuous geochemical monitoring network (Pérez et al. 2012; Padilla et al. 2013) and by discrete geochemical surveys of diffusive helium emission and $^3\text{He}/^4\text{He}$ ratio data of dissolved gases in groundwater (Padrón et al. 2013) and diffuse CO_2 emissions (Melián et al. 2014). From the starts of the submarine eruption, a large area of discolored water in the sea was observed most of the time (Figure 1c), from light green to dark brown color, caused by chemical interaction of seawater with the intensely discharging of high-temperature volcanic hydrothermal fluids plus magmatic gases. Throughout December 2011 and January 2012, the seismicity gradually declined and the eruption subsided, with earthquake rates returning to low levels, close to background, and tremor considerably reduced in amplitude (Ibáñez et al. 2012). On March 5, 2012, the Scientific Committee stated that the submarine eruption was over, but the volcanic process that started on mid July 2011 had

not finished (Smithsonian report, 29 February to 6 March 2012).

In fact, since June 2012, a new episode of volcano-seismic unrest started, with a high rate of seismicity occurring from June 25 to July 13. During this period, more than a thousand volcano-tectonic earthquakes occurred west of El Hierro Island (Figure 1b). This increase of seismic activity was sudden and seemed to be triggered by a first earthquake of magnitude 3.2, located by the IGN seismic network at 21:26:01 (local time) with coordinates N27.7897 and W18.0642 at a depth of 20 km. Seismicity was characterized by a larger number of seismic events with magnitude >2.5 (715 events in 21 days) compared to the period July 2011 to March 2012 (748 events in 230 days), the largest with magnitude 4.4 occurred on July 2, 2011. García-Yeguas et al., 2014, reported 3D images of the structure beneath El Hierro Island from a seismic tomography study, which showed a strong low-velocity anomaly beneath the west offshore area of the island.

Submarine volcanoes are widespread on the sea floor but are mainly concentrated along the convergent and divergent margins of tectonic plates and at hot spots (Smith and Jordan 1987; Smith and Cann 1992). Due to the water depths where

this volcanic activity occurs, monitoring submarine volcanic eruptions is a very difficult task. However, when a submarine eruption occurs at shallow depths (tens to few hundred meters), there is an excellent opportunity to monitor and study it. Nowadays, knowledge about submarine eruptions is increasing rapidly, and new techniques allow detection and observation of signals of submarine volcanic unrest.

GEOCHEMICAL MONITORING

Continuous soil CO₂ and H₂S monitoring

Observing changes in the composition and discharge rates of volcanic gases is an important part of volcanic monitoring programs, because some gases released by progressive depressurization of magma during ascent are highly mobile and reach the surface well before their parental magma (Hernández et al., 2001; Granieri et al., 2006). Among volcanic gas studies at volcanoes, diffuse CO₂ degassing phenomena, has played an important role owing to the special characteristics of CO₂: it is the major gas species after water vapor in both volcanic fluids and magmas and it is an effective tracer of sub-surface magma degassing (Gerlach and Graeber, 1985). In contrast to these studies on CO₂, very few studies have focused on diffuse H₂S measurements in volcanic areas, as the gas is much harder to detect.

On September 25, 2003, a geochemical station (HIE01) was installed at Llanos de Guillén, in the interception center of the three volcanic rifts of El Hierro Island (Lat.: N 27°42'58.2"; Long.: W 18°01'8.8"), where previous CO₂ efflux surveys indicated one of the highest CO₂ efflux values measured in El Hierro Island during inter-eruptive periods. The second automatic geochemical station (HIE07) was installed near Tacorón cove, south El Hierro Island (Latitude: N 27°40'56.9"; Longitude: W 8°1'44.5") on October 7, 2011, almost one week before the starts of the submarine eruption. Both stations measured hourly CO₂ and H₂S efflux, and CO₂ and H₂S air concentrations. To filter the possible influence of external parameters in the endogenous CO₂ and H₂S emissions, soil water content and temperature at a 40-cm depth and atmospheric parameters (wind speed and direction, air temperature and humidity, rainfall, and barometric pressure 1 m above the ground), were recorded simultaneously.

During the period of study, the observed CO₂ efflux values recorded at HIE01 ranged from non-

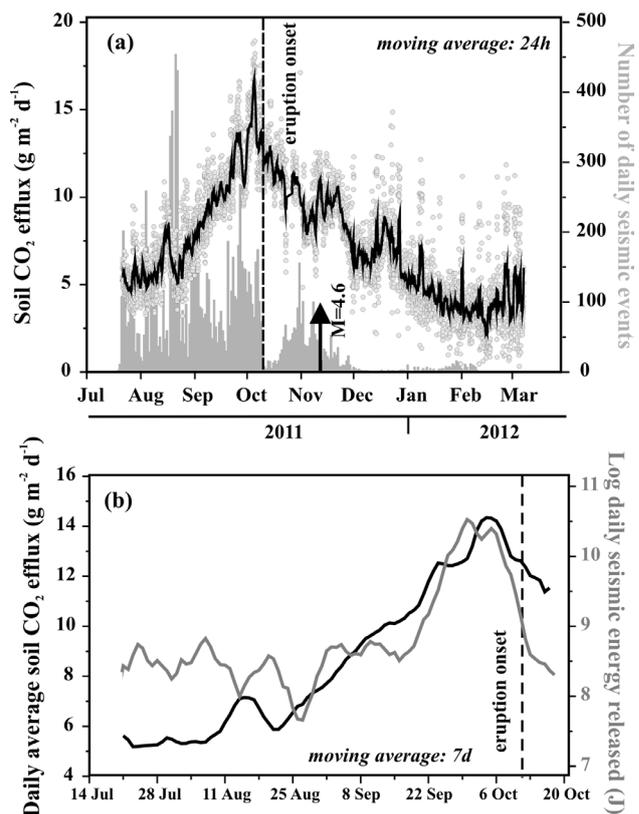


Figure 2. (a) Time series of the measured CO₂ efflux during the 2011–2012 period of volcanic unrest at HIE01; moving average is shown as well as the recorded seismicity during the same time period by the seismic network of IGN. (b) Daily average CO₂ efflux measured at HIE01 and daily seismic energy released during the geochemical precursory time window.

detectable values to 18.9 gm⁻²d⁻¹ with an average of 8.0 gm⁻²d⁻¹ (Figure 2a). From the beginning of the observation time to August 10, 2011, soil CO₂ efflux time series was characterized by a low variance with CO₂ efflux values showing a median value of 5.6 gm⁻²d⁻¹. From August 10 to 17, a sharp increase on CO₂ efflux rate occurred, reaching a value of 11 gm⁻²d⁻¹. This peak in CO₂ efflux was observed one day before the most intense seismic activity in terms of number of seismic events during the period of study, with 1,863 earthquakes occurring between August 18 and August 23. Later, from August 23 to October 5, a continuous increase in the CO₂ efflux time series was observed, culminating in the maximum CO₂ efflux measured during this study, 18.9 gm⁻²d⁻¹. The greatest rate of increase occurred one week before the initiation of the submarine eruption south of El Hierro Island. Figure 2b shows the daily average CO₂ efflux and the daily released seismic energy between the mid-July and October 20, the time of the observed precursory CO₂ efflux signal at HIE01.

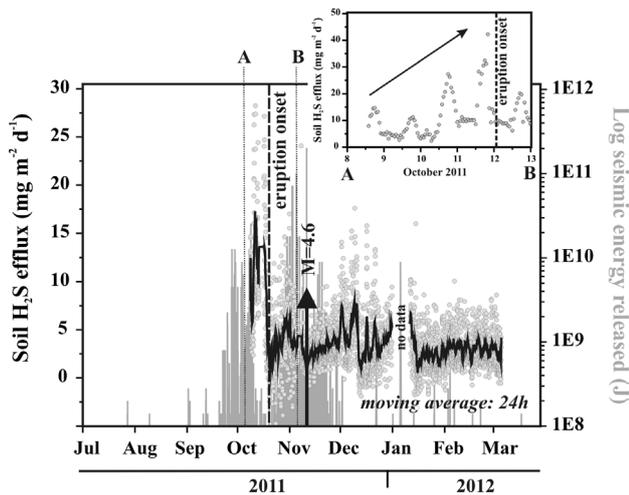


Figure 3. Time series of the measured H_2S efflux recorded during the period October 8, 2011–March 5, 2012, at HIE07; moving average is shown as well as the recorded seismicity during the same time period by the seismic network of IGN.

Both time series show a good temporal correlation, which supports the hypothesis that there was a precursory diffuse CO_2 efflux signal before the onset of the submarine eruption. At HIE07, a sharp increase in the H_2S diffuse emissions was observed between the installation on October 7, 2011, and the eruption onset, increasing from <2 to $42 \text{ mgm}^{-2}\text{d}^{-1}$ (Figure 3).

The observed increasing rate of diffuse emission at HIE01 likely suggested that ascent of magma occurred in a regular rate, but this observation contradicts the hypocenters of the seismicity time series observed along the crisis, which did not show such a regular behavior, as it should have been expected. The increasing on pressure of the magmatic gases might have driven the magma movement to the surface, being reflected as an increase of CO_2 diffuse emission at HIE01. The observed temporal change on the CO_2 diffuse emission at HIE01 before the eruption onset has proven as a good indicator of changes of energy of the magmatic plumbing system at depth, which triggered the ascent of magma towards surface.

Continuous soil radon monitoring

With the aim of providing a multiparametric geochemical approach, in August of 2005, two geochemical stations (HIE02 and HIE03) were installed at HIE02 (San Simon well; Figure 1b, $\text{N}27^\circ45.28'$; $\text{W}18^\circ6.41'$; 26ma.s.l.), and at HIE03 (La Restinga Village; Figure 1b, $\text{N}27^\circ38.54'$; $\text{W}17^\circ58.97'$; 30ma.s.l.), to measure ^{222}Rn and ^{220}Rn activities by means of a SARAD RTM-2010-2 radon monitors during a period of volcanic quiescence. Time series

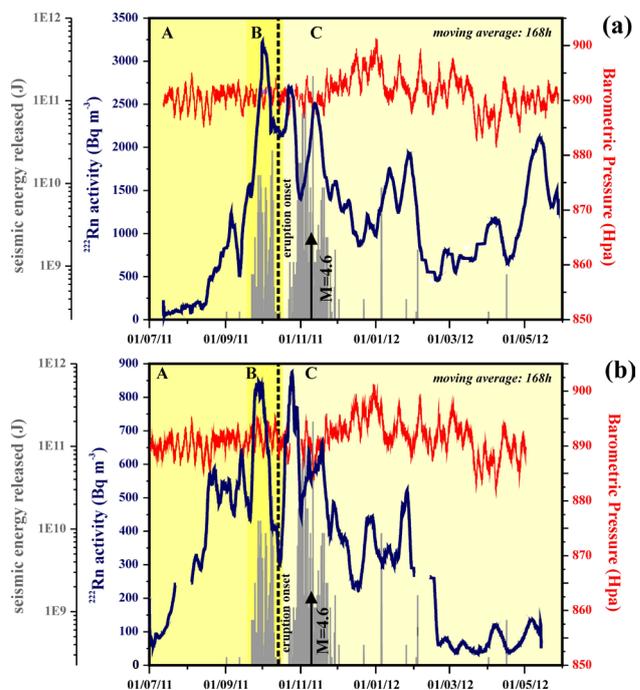


Figure 4. Temporal plot of the moving average of ^{222}Rn time series measured at HIE02 (a) and HIE03 (b) geochemical stations (Blue line), respectively. At each graph, red line indicates barometric pressure measured at HIE01 station. Light grey bars show the seismic energy release during the study period. The radon time series was divided into three segments (A, B and C) according to distinct regimes of earthquake occurrence (Ibañez et al., 2012).

of soil ^{222}Rn showed variations ranging between 0 to $16,459 \text{ Bqm}^{-3}$, and 0 to $1,646 \text{ Bqm}^{-3}$ for HIE02 and HIE03 geochemical stations, respectively. Figure 4a and 4b show the 168 h moving average of soil ^{222}Rn measured at HIE02 and HIE03 stations, respectively, together with hourly barometric pressure and daily released seismic energy. Phases A, B and C (Ibañez et al., 2012) are also shown. During most of phase A, radon degassing is mainly characterized by a deep magma contribution reflecting the initial intrusion of magma from the upper mantle into the crust, with the highest deep contribution occurring at the end of phase A, just before the start of the first significant seismic energy release (phase B) which ended in the submarine eruption. From September 21 to October 10, 2011 (phase B), just before the eruption onset on October 12, highest ^{222}Rn and ^{220}Rn activities were recorded during all observation periods, indicating strong deep and shallow contributions due to the magma movement to the surface. Finally, from October 11, 2011, (phase C), when the largest magnitude earthquakes were recorded reflecting crustal relaxation around the magma reservoir that

had fed the submarine eruption, the shallow degassing component for radon was predominant.

As soil gas radon activities and soil CO₂ increased prior to the occurrence of major seismic volcanic events and prior to the eruption onset, these gases can be efficiently used as an initial warning sign of the pressurization of magma beneath El Hierro Island, together with other geochemical and geophysical data.

Diffusive helium emission surveys

In summer 2003, the first diffusive helium emission survey of El Hierro Island was performed by analyzing the helium content of soil gas at 473 sampling points located homogeneously across the entire surface of the island. Since the beginning of the recent 2011–2012 seismic-volcanic unrest period at El Hierro, another 14 helium emission surveys have been carried out, with 601 sampling sites. Simultaneously, the ³He/⁴He ratio in groundwater has been measured regularly at HIE02 (Figure 1b). Sampling of dissolved gas from HIE02 for ³He/⁴He ratio was performed regularly from July, 2011, and analyzed at the lab facilities of the Geochemical Research Center of The University of Tokyo. The determination of helium isotopic ratios as well as ⁴He and ²⁰Ne concentrations is done following the method described by Sumino et al. (2001).

Diffusive helium emissions in the 2003 survey amounted for 9 ± 1 kgd⁻¹ for the entire area of El Hierro Island. This value is interpreted as the background helium emission of El Hierro Island in a period of volcanic quiescence, and it is depicted in Figure

5a, which shows both diffusive helium emissions for the entire island and the corrected ³He/⁴He ratio for the dissolved gases in the San Simon waters together with the seismic energy released 9 February 2012. By mid-September, a drastic increase in the 2 geochemical parameters had been observed, several days before the beginning of a significant increase in the seismic activity on the island. The increase in diffusive helium emissions continued over 2 more surveys, reaching a relative maximum of 30 ± 2 kgd⁻¹ in October 6, several days before the occurrence of the submarine eruption. A significant decrease to 13 kgd⁻¹ was estimated almost 10 days after the beginning of the eruption, followed by a sudden increase to 38 kgd⁻¹ several days before the largest seismic event of the volcanic crisis (M = 4.6) occurred on November 11. On 5 March, the submarine eruption was over, but the volcanic process that started in mid-July 2011 had not finished. By the end of June 2012, a new seismic unrest episode occurred, accompanied by the highest deformation rate measured in the island during the unrest period. Within this phase, a new increase on the diffusive helium emission (up to 20 kgd⁻¹) was observed.

Figure 5b depicts the evolution of the magmatic and crustal emission rate over the volcanic unrest period. The magmatic helium time series began with <1 kgd⁻¹ and increased to ~20 kgd⁻¹ several days before the eruption onset. However, the crustal helium emission remained at ~1 kgd⁻¹ throughout the volcanic unrest period, except on the survey performed between 2 November and 8 November 2011, when it reached 12 kg/d immediately before

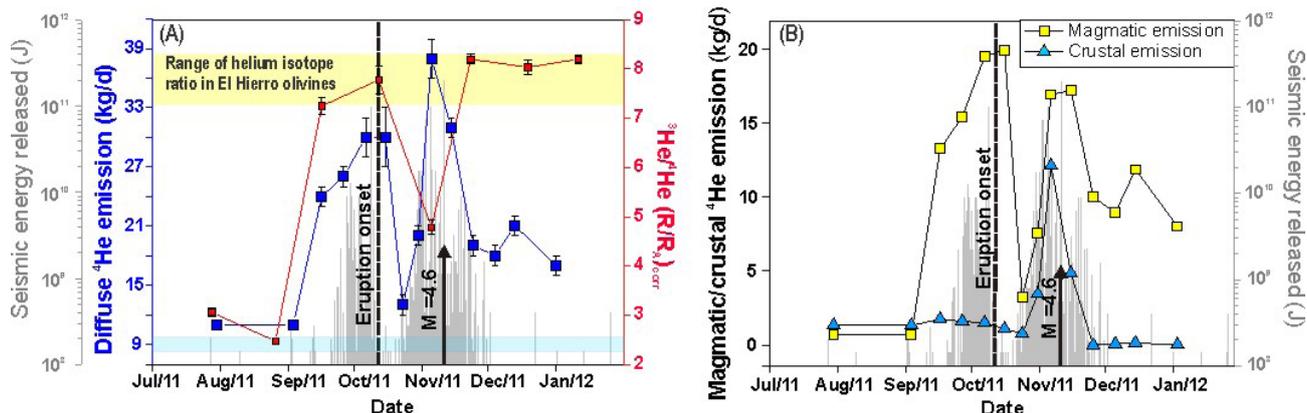


Figure 5. (a) Temporal evolution of seismic energy released (gray), diffusive helium emission at entire island (blue squares), and air-corrected ³He/⁴He ratio in San Simon groundwater (red squares). R_A = atmospheric ³He/⁴He ratio. Errors on diffusive helium emission values are 1σ of 50 equiprobable realizations by sequential Gaussian simulation. Yellow band represents range of ³He/⁴He ratios measured on olivine phenocrysts at El Hierro lavas, 7.2–8.2 R_A (Day and Hilton, 2011). (b) Temporal evolution of estimated magmatic (yellow squares) and crustal (blue triangles) helium emission during volcano-seismic unrest and seismic energy released (gray bars).

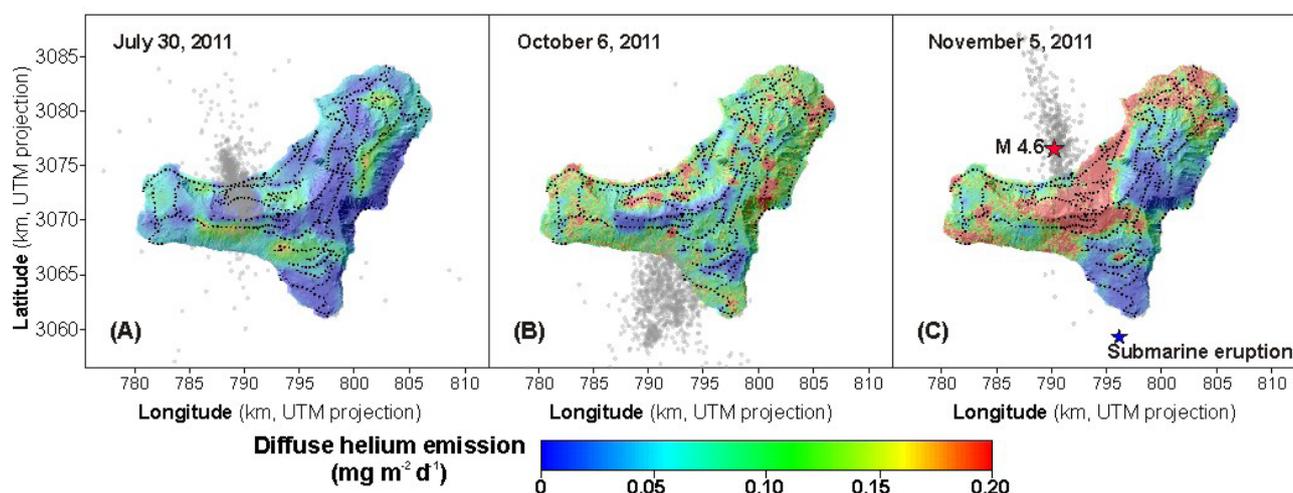


Figure 6. Spatial distribution of diffusive helium emission values (UTM-Universal Transverse Mercator.) Gray dots indicate seismicity in sampling period; black dots indicate sampling sites. A: Measured in first 2011 survey, 25 July through 4 August 2011. (b) Measured immediately before occurrence of submarine eruption, 2–10 October 2011. (c) Measured immediately before occurrence of largest earthquake of seismic-volcanic unrest period (M 4.6, red star), 2–8 November 2011. Blue star indicates location of submarine eruption.

the occurrence of the biggest earthquake of the unrest period. Figures 6a and 6b reveal that the density of warm colors is higher prior to the eruption than at the beginning of the unrest period, indicating an increase in helium emissions from $11 \pm 1 \text{ kgd}^{-1}$ to $30 \pm 2 \text{ kgd}^{-1}$.

At the beginning of the seismic-volcanic unrest period, magma movement beneath El Hierro Island generated new fracture and microfracture systems, allowing volcanic gases to travel to the surface. Helium could easily ascend from deep areas through structures of high vertical permeability, thereby enhancing the helium content of soil gases. This fact was confirmed by an increase in the amount of mantle-derived gases dissolved in the San Simon waters exhibited by the $^3\text{He}/^4\text{He}$ ratio. The increases in the diffusive helium emission values over the entire island preceded episodes of seismic energy release. Similar results were observed by continuous monitoring of diffuse CO_2 and H_2S emissions by using two different geochemical stations (Pérez et al., 2012). The onset of the submarine eruption produced a sudden release of volcanic gases, and consequently, a decrease in the volcanic gas pressure of the magma bodies moving beneath the island, reflected by a drastic decrease in the diffusive helium emissions measured between 20 and 26 October 2011.

These results clearly show the critical role that helium can play in the prediction of major volcanic events and the importance of continuous monitoring of this gas in active volcanic regions, mainly when magma migrates aseismically, i.e., silently, toward

the surface.

Diffuse CO_2 emission surveys

Since 1998, diffuse CO_2 emission has been investigated at El Hierro volcanic system in a yearly basis during the summer periods (10 surveys). Since July 2011, and due to the start of the seismic-volcanic crisis at El Hierro, 19 diffuse CO_2 emission surveys were undertaken until 25 March 2012 (Melián et al., 2014). The same sampling grid of 601 soil CO_2 efflux measurements sites was repeated 29 times during the study period. The sampling grid was initially designed covering all the surface of El Hierro with site spacing about 400m (Figure 7a). To warrant a correct location of the sampling sites, their coordinates were stored in a hand-sized GPS. The closed accumulation chamber method (Parkinson, 1981) was used to measure the CO_2 efflux in all the 29 surveys. Measurements were carried out by means of a portable non-dispersive infrared CO_2 analyzer LICOR-820 system, with a measurement range of 0–2000 ppmV (optical bench 14 cm). The LICOR analyzer is interfaced to a hand size computer running the data acquisition software.

Soil CO_2 efflux data were used to construct spatial distribution maps using sequential Gaussian simulation (sGs) provided by the sgsim program (Deutsch and Journel, 1998), which has been applied during recent years to soil CO_2 diffuse degassing at many volcanic and geothermal sites. The final maps were always constructed as an average of 100 equiprobable realizations performed over a grid of

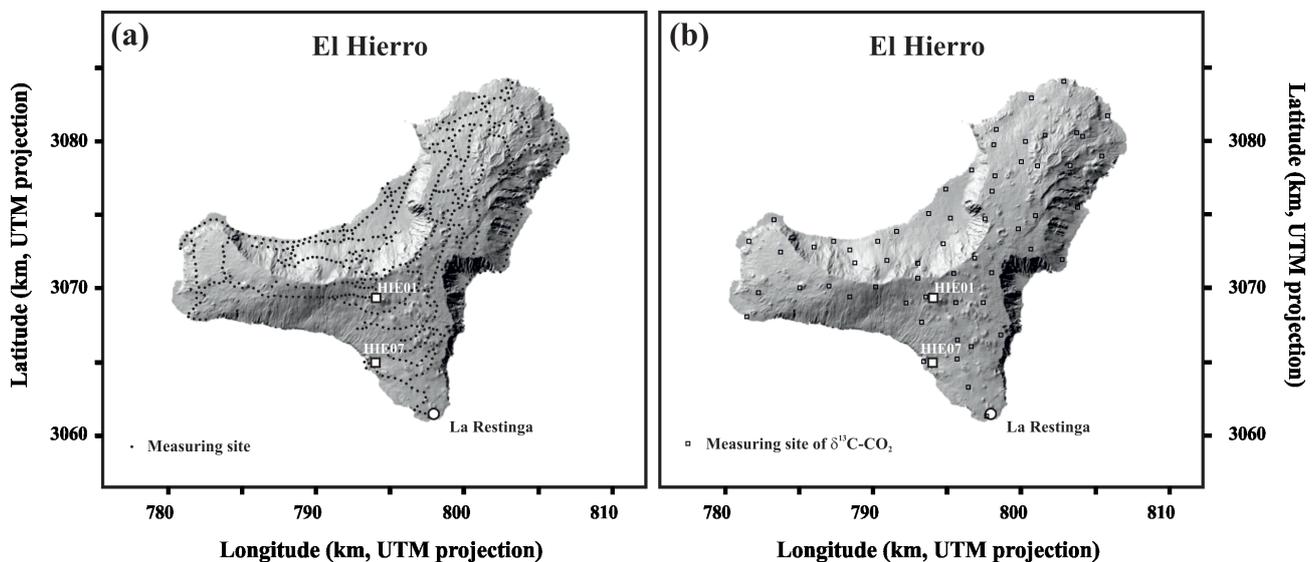


Figure 7. Location of (a) measurement sites (black dots) of diffuse CO₂ efflux and (b) sampling sites for δ¹³C-CO₂ and CO₂ content analysis in the soil gases (open squares). The white square indicates the location of the geochemical stations HIE01 and HIE07.

27,999 squared cells (100m×100m) following the variogram model and the experimental variograms for the 29 surveys were fitted with spherical theoretical model (Melián et al., 2014). Since quantification of the uncertainty of the total CO₂ is an important task for a correct interpretation of the temporal variations, the mean, and the standard deviation of the 100 simulated values of total CO₂ output were assumed to be the characteristics values of the CO₂ released and of its uncertainty (Cardellini et al., 2003).

To investigate the carbon isotopic composition of the soil CO₂, 60 sampling sites were selected homogeneously along the study area in 9 of the 29 surveys. The sampled sites selected to measure the carbon isotopic composition of the CO₂ were the same in the 9 surveys, in order to minimize the effect caused by differences in the sampling grid (Figure 7b). Soil gas samples were collected at 40 cm depth using a metallic probe, stored in glass vials, and analyzed by means of a Thermo Finnigan MAT 253 isotope ratio mass spectrometer by continuous flow injection from a Finnigan GasBench II (δ¹³C standard error ± 0.1‰).

Soil CO₂ efflux values range from nondetectable (~0.5 gm⁻²d⁻¹) up to 457 gm⁻²d⁻¹, with an average value of 3.5 gm⁻²d⁻¹ during the entire study. The range of measured CO₂ efflux values is similar to that observed at other volcanic systems of the Canaries (Hernández et al., 2012a; Padrón et al., 2008), and even though these values are lower than those measured in other active volcanic areas, the highest

values can be explained as a mixture of biogenic and an endogenous source. Figure 8 shows 6 selected maps of the 29 based on the mean simulated total CO₂ output value obtained for El Hierro between July 2011 and March 2012. During this study, soil CO₂ efflux showed a large variability. The maps show that most of higher soil CO₂ efflux values occur along the volcanic rifts of the island. These volcanic structures are characterized by a higher vertical permeability favoring endogenous gases rising to the surface. Vegetation at these areas (pine forest) might also contribute to the observed CO₂ efflux values. In the other hand, lower values of CO₂ effluxes are mainly observed along the edges of the investigated area (near the coast), where scarce vegetation exists. A visual inspection of these two maps reveals that the density of warm colors is higher during November 2011, just after the eruption onset and during the occurrence of the biggest earthquake of the unrest period, indicating the increase in CO₂ emissions.

With the aim of evaluating the temporal evolution of the total diffuse soil CO₂ emission from El Hierro volcanic system and its relationship with the seismic-volcanic activity, we have consider first the temporal evolution of the total diffuse CO₂ emission in a quiescence period. Figure 9 shows the temporal evolution of the mean simulated values of yearly total CO₂ outputs between 1998 and 2010, a year before the onset of anomalous seismic activity with the limits representing the one standard deviation of the cutoff mean value. In the period 1998–2010, diffuse CO₂

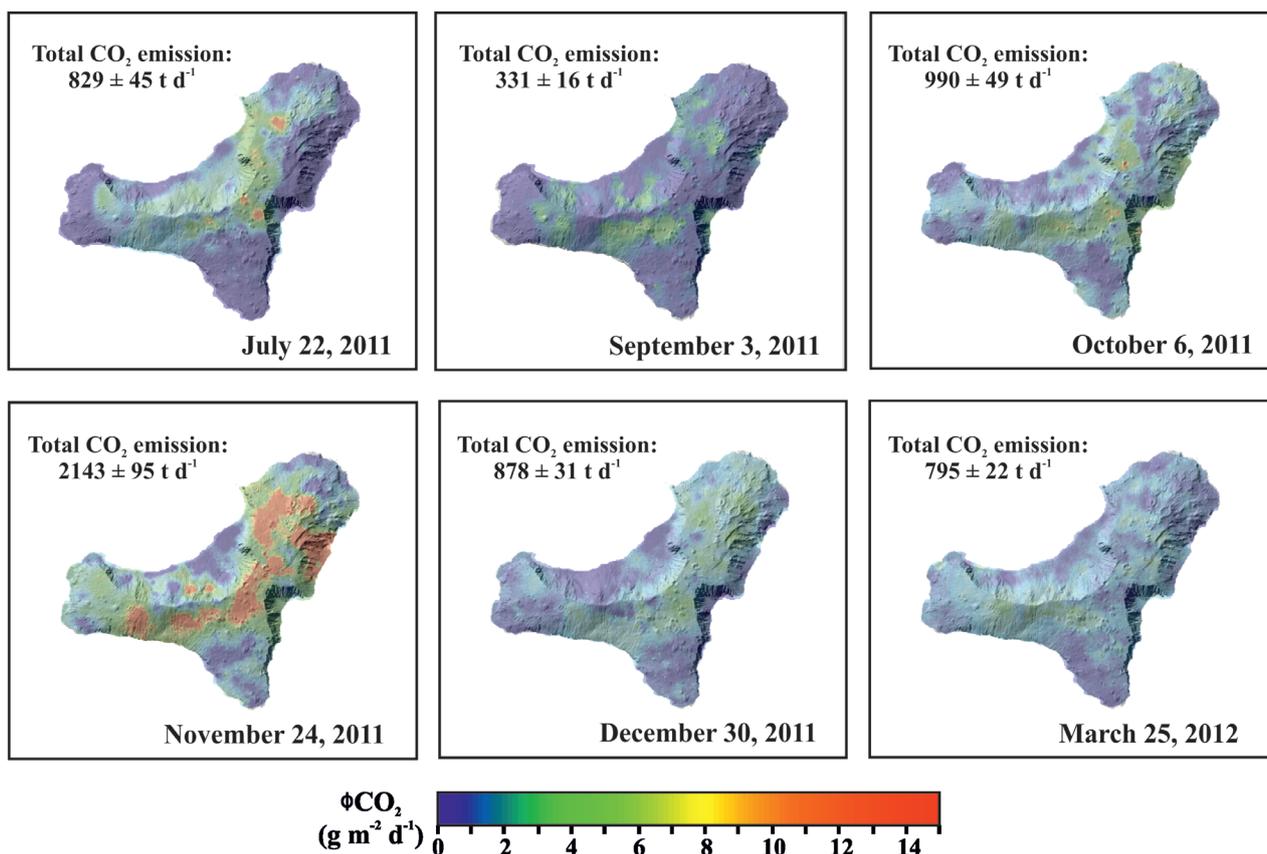


Figure 8. Selected soil CO₂ efflux maps at El Hierro constructed from an average of 100 realizations using the sGs method.

emission showed a high variability (minimum value: 358 td⁻¹ in 2003 and maximum value: 1,434 td⁻¹ in 2004). The most remarkable characteristics of the temporal evolution in this period are the following: (i) The maximum emission value was observed in 2004 (higher than the cutoff background emission +1σ), concurrently with the relative maximum of the seismicity in the period 1998–2010; (ii) The descending degassing pattern of the diffuse CO₂

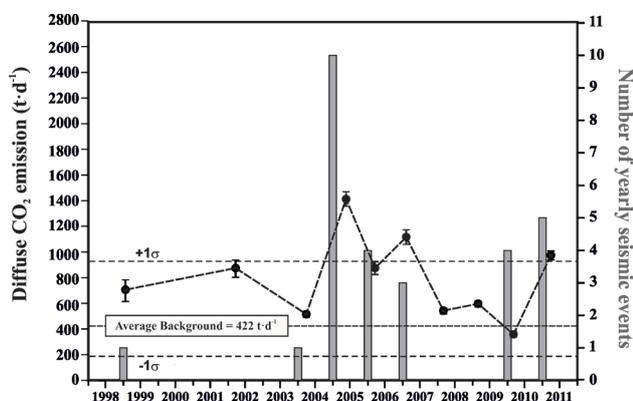


Figure 9. Temporal evolution of total diffuse CO₂ emission rate for the 1998–2010 surveys at El Hierro and yearly number of seismic event in and around EL Hierro (source IGN).

emission in the period 2004–2009, with an exception in 2006, changed significantly after the 2010 survey.

Figure 10 depicts a daily estimation between end of July 2011 and end of March 2012. Based on changes in emission trend and the geological process observed in the time series, we divided the time series in seven stages for the period July 2011 (beginning of the seismic-volcanic unrest) and March 2012 (end of the submarine eruption). The different phases observed prior to the submarine eruption are described as:

Phase A (21 July to 8 September 2011). It represents a decreasing trend on the diffuse CO₂ emission from the start of the seismicity to 9 September (Figure 10), which was characterized by high earthquake rates and relatively low magnitudes, reflecting the initial intrusion of magma from the upper mantle into the crust (Phase 1 at Ibáñez et al. 2012). Estimated CO₂ output values for this phase ranged from 378 to 938 td⁻¹ (average = 627 td⁻¹) and were mostly always higher than the average background emission (422 td⁻¹). Pérez et al., 2012, reported for the period 19 July to 10 August, soil CO₂ efflux values characterized by a low variance and showing a median value of 5.6

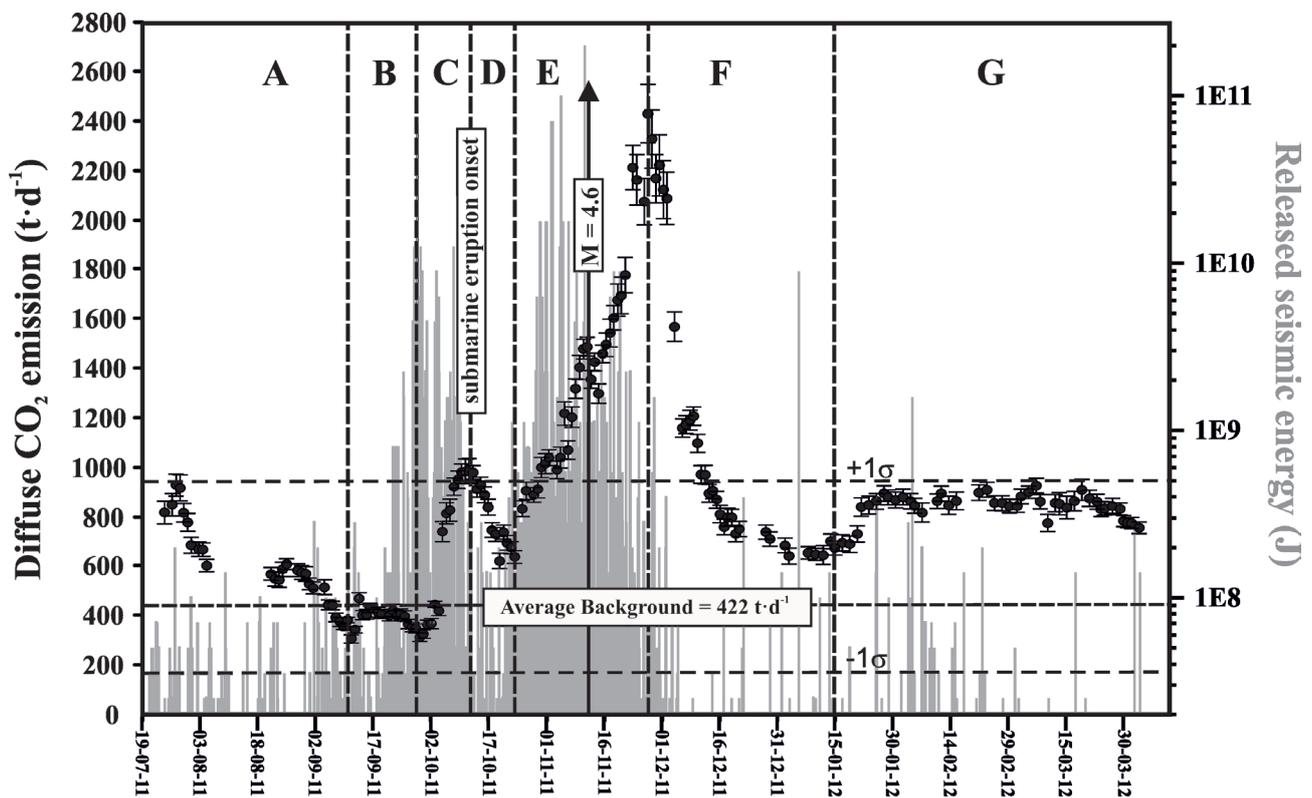


Figure 10. Temporal evolution of total diffuse CO₂ emission rates for the period July 2011 to March 2012 and seismic energy released (light gray vertical bars, source IGN). Capital letters correspond to the adopted phases. Average background emission with $\pm\sigma$ is also shown.

gm²d⁻¹ at the station HIE01, whereas Padrón et al., 2013, for the same period, reported diffusive helium emission values of 11 ± 1 kd⁻¹, slightly higher than the background emission measured in 2003 (9 ± 1 kd⁻¹) as well as ³He/⁴He isotopic ratios of 2.48 ± 0.07 R_A in groundwater. According to Sagiya et al., 2012, from the middle of July to middle of September, steady magmatic inflation occurred at the center of the island. The inflated volume of the first stage was estimated to be about 1.3×10^7 m³ at the depth of about 5 km. The absence of an ascending trend in the diffuse CO₂ degassing is consistent with the above observations.

Phase B (between 9 and 28 September 2011). It represents a period of stability in the rate of CO₂ emissions, with CO₂ output values ranging from 331 to 490 td⁻¹ (average = 410 td⁻¹) and was characterized by the occurrence of relatively low magnitude seismic events (Figure 10). The last 8 days of this period, coincide with the Phase 2 in Ibáñez et al. 2012 (21 September to 15 October 2011), when seismicity migrated to the south with an apparent ordinary tectonic activity. Since early September, a magmatic degassing process was observed by a

continuous increase in the degassing rate measured in an automatic geochemical station at the center of the island (Pérez et al., 2012). By mid-September, the magmatic degassing process was reaffirmed by a drastic increase in the diffusive helium emission in the whole island and its magmatic fraction in groundwater (Padrón et al., 2013). These geochemical observations preceded the significant increment in the seismic activity (number and magnitude of the seismic events increased) registered after 20 September (Phase 2 in Ibáñez et al. 2012).

Phase C (29 September to 12 October 2011). It's characterized by a sharp increase in the rate of CO₂ emissions (Figure 10), with CO₂ output values ranging from 350 to 991 td⁻¹ (average = 735 td⁻¹). During this phase, the submarine eruption occurred (12 October) with a substantial lack of shallow seismicity between 8 km depth and the surface, probably because the magma found a preexisting fragile area, which would permit an aseismic migration toward the surface (Ibáñez et al., 2012). The observed increase on the CO₂ emission started almost 2 weeks before the onset of the submarine eruption, reflecting a clear geochemical anomaly in

CO₂ emission, most likely due to increasing release of deep-seated magmatic gases to the surface, and coincides with a sharp increase in the soil CO₂ efflux measured at HIE01 station (Pérez et al., 2012). During this phase, the increase in diffusive helium emission continued, reaching a relative maximum of $30 \pm 2 \text{ kd}^{-1}$, which also preceded the onset of the submarine eruption (Padrón et al., 2013). The ³He/⁴He ratio measured in groundwater also showed a relative maximum (Padrón et al., 2013). This period was also characterized by the accelerated deformation due to the upward as well as southward migration of magma (Sagiya et al., 2012). Additional inflation of about $2.1 \times 10^7 \text{ m}^3$ occurred in the depth range of 1–2 km. During this Phase, a ML 4.3 earthquake occurred on 8 October (4 days before the submarine volcanic eruption). Domínguez Cerdeña et al., 2014, pointed out that this earthquake did not trigger the magma ascent because magma velocity should have been too high. Our data support that magma was already ascending before the occurrence of the ML 4.3 earthquake as was suggested by Domínguez Cerdeña et al., 2014.

Phase D (13 October to 24 October 2011). It corresponds to a new decreasing trend on the diffuse CO₂ emission after the onset of the submarine volcanic eruption (Figure 10). From 15 October, earthquake epicenters migrated north of the El Golfo area (Ibáñez et al., 2012) and location depths were deeper than during the period 19 July to 14 October, between 15 and 25 km. Estimated CO₂ output values for this period ranged from 638 to 937 td⁻¹ (average of 777 td⁻¹). This decrease on the CO₂ emission occurred together with the decrease of soil CO₂ efflux at HIE01 station (Pérez et al., 2012), and a decreasing in diffusive helium emission and ³He/⁴He ratio (Padrón et al., 2013), indicating a decrease in the volcanic gas pressure of the magma moving beneath the island, about 3 weeks after the first submarine eruption. During this stage, submarine eruption continued while no significant surface deformation was observed (Sagiya et al., 2012), indicating that magma supply from a deeper magma reservoir continued during this period.

Phase E. This phase, between 24 October and 27 November 2011, is characterized by a new sharp increase in the rate of CO₂ emissions (Figure 10), reaching in 27 November the maximum CO₂ output estimated value of all time series, 2,398 t d⁻¹ (average = 735 td⁻¹). The observed CO₂ emissions

increase during this phase preceded an increment in the amplitude of the tremor signal and episodes of maximum degassing observed as vigorous bubbling at the sea surface in 3–7 November. The CO₂ emissions increase continued reaching a relative maximum 1 day before the highest magnitude earthquake occurred in the studied period (ML 4.6). In late November 2011, a new input of fresh magma caused the start of a second eruptive episode. This observation might support the maximum CO₂ degassing rate observed in El Hierro during the study period (27 November 2011). This increase on the diffuse CO₂ emission was preceded by an increase of diffusive helium emission, reaching the absolute maximum of the series ($38 \pm 2 \text{ kgd}^{-1}$) on the survey performed between 2 and 8 November (Padrón et al., 2013).

Phase F (28 November 2011 to 3 January 2012). It corresponds to a new decreasing trend on the diffuse CO₂ emission after the maximum CO₂ output observed (Figure 10). Estimated CO₂ output values for this period ranged from 657 to 2,299 td⁻¹, with an average of 1,169 td⁻¹.

Phase G (15 January to 5 March 2012). It represents a new increase and stability in the rate of CO₂ emissions, with CO₂ output values ranging from 661 to 934 td⁻¹, with an average value of 834 td⁻¹ (Figure 10). The end of this phase corresponds to the time when Scientific Committee stated that the submarine eruption was over (Smithsonian report, 29 February to 6 March 2012). Volume change in the magmatic reservoir observed by González et al., 2013, suggests the ascent of one or two more primitive magma pulses from an upper mantle source during January–February 2012, which is consistent with the slight new increase in the rate of CO₂ emissions depicted in Figure 10.

Figure 11 combine the results obtained through continuous monitoring of the diffuse CO₂ emission at HIE01 station reported by Pérez et al., 2012, with the discrete surveys described in this work. Both time series show a positive correlation ($r^2 = 0.89$) with a delay of 28 days in the discrete emission data. This correlation seems to be only apparent, because the higher peak in the HIE01 station should be related to the first increase in the survey emission (Phase C) and not to the Phase E. The bulk of the seismicity in Phase E was located off the northern coast of El Hierro (Phase 3 in Figure 2), which indicates that magma movements were occurring at the farthest site from HIE01 station of the study period. This

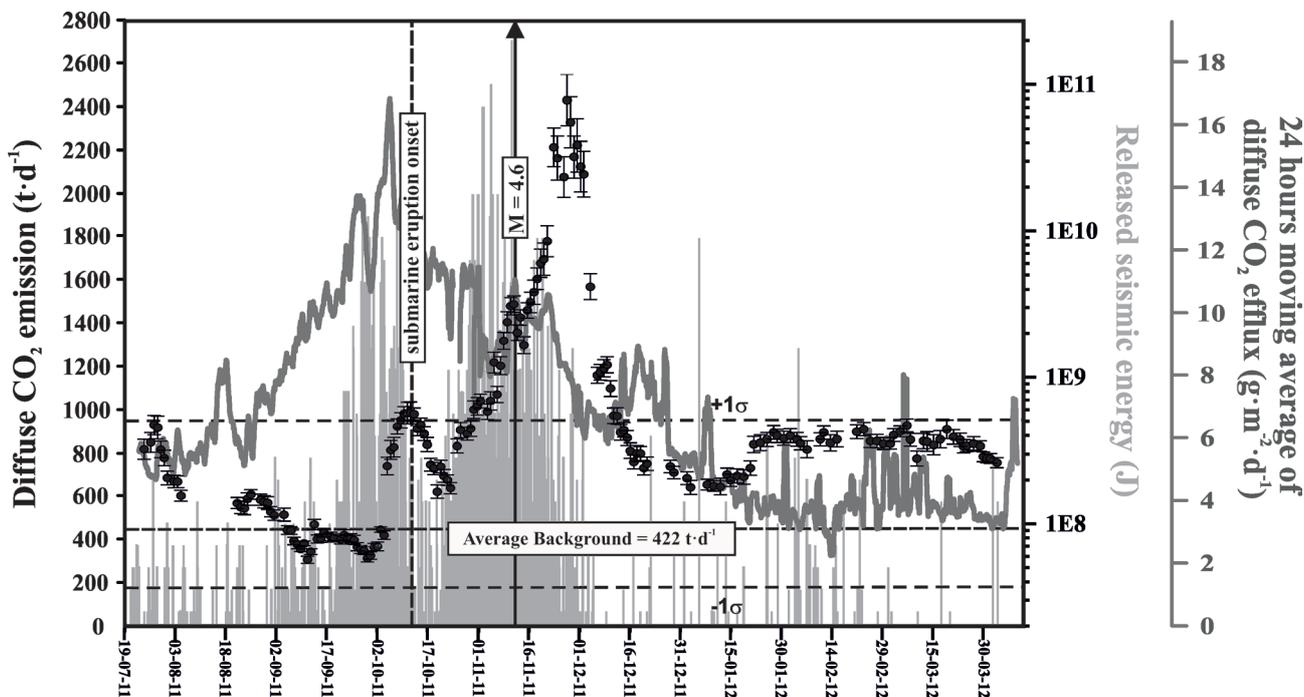


Figure 11. Time series of the 24 h moving average of diffuse CO₂ efflux at HIE01 station reported by Pérez et al., 2012, and temporal evolution of total diffuse CO₂ emission rate during 2011–2012. The seismic energy released recorded by the seismic network of IGN during the same time period is also shown.

disadvantage inherent to the study in a continuous mode is minimized in the discrete surveys carried out at El Hierro.

Soil gas samples collected in 2011 and 2012 showed a wide range of $\delta^{13}\text{C-CO}_2$ values (Melián et

al., 2014). Figure 12 shows the correlation diagrams between the $1/\text{CO}_2$ content and $\delta^{13}\text{C-CO}_2$ (‰) values in soil gas samples for 9 of the 29 survey Air, biogenic gas, and deep CO₂ reservoirs were considered in the diagram. Most of the data plot in

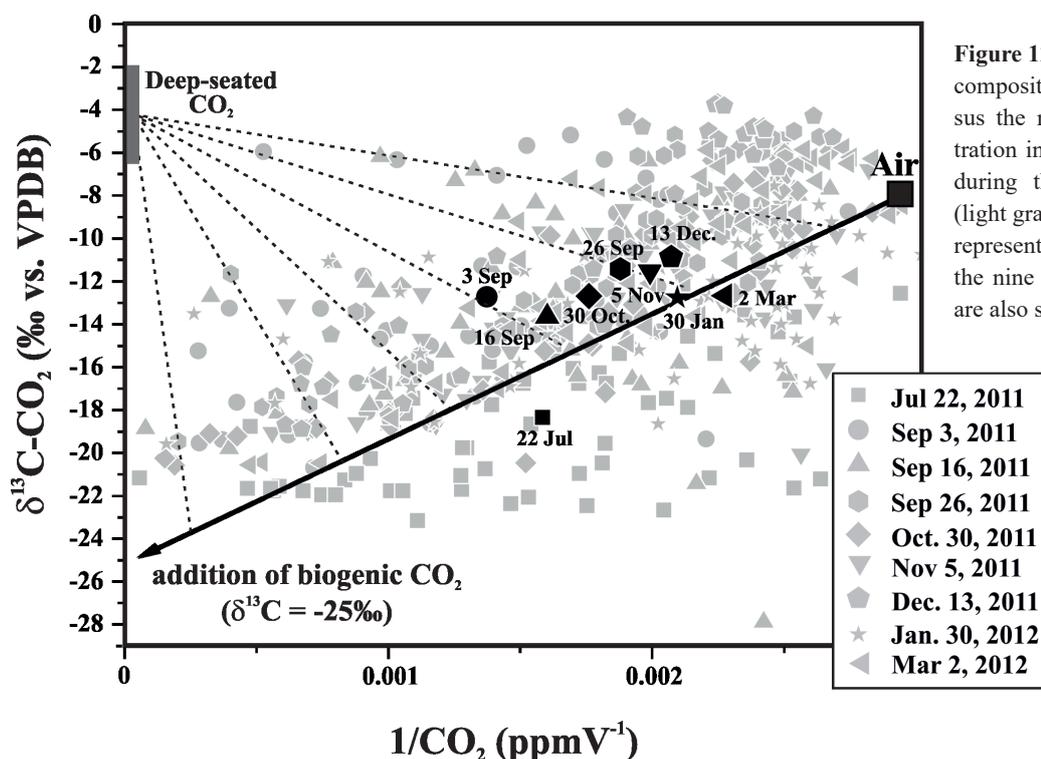


Figure 12. Graph of carbon isotopic composition ($\delta^{13}\text{C}$) of soil CO₂ versus the reciprocal of CO₂ concentration in the gas samples collected during the nine selected surveys (light gray symbols). Black symbols represent average values for each of the nine surveys. CO₂ mixing lines are also shown.

and around the line of addition of biogenic CO₂, with points plotting along the mixing line of biogenic CO₂ with atmospheric air. The isotopic data plotted out of the triangle made by the atmospheric, biogenic gas, and deep-seated CO₂ end-members can be explained by an almost pure biogenic CO₂ with concentrations slightly higher or similar to that of air. Although not significant, several points present an increase on the magmatic contribution. The CO₂ increase observed in the fall-winter season of 2011–2012 does not seem to be driven mainly by an enhanced biogenic CO₂ production in the soils of El Hierro, because the isotopic composition of the CO₂ in the 5 November and 13 December samples did not follow the expected trend for a biogenic CO₂ addition in Figure 12, suggesting other different origin (deep seated) for the gas. The dispersion of the CO₂ efflux isotope compositions can be ascribed to the simultaneous occurrence of different processes such as the natural isotopic variability of the biogenic CO₂ produced in the soils, the mixing of the biogenic CO₂ with variable amounts of endogenous gas and the uncertainties of

the method which are higher at low CO₂ efflux values (Chiodini et al., 2008).

THERMAL MONITORING

Thermal images were collected by means of a hand-held FLIR Thermal Camera P65 during the eruptive period. The accuracy of the instrument (% of reading) is ± 2 °C or ± 2%. Erupted magma volumes were calculated from 19 October 2011 to 28 February 2012 by means of thermal imaging of a brown patch of warm seawater observed in front of La Restinga (Figure 13). During this period, we carried out thermal surveys every time we had the availability of a helicopter, allowing a total of 21 thermal surveys. Images were recorded taking care to avoid solar reflection (with cloudy weather) or at times of the day without direct sunlight (Pinkerton, James, & Jones, 2002). Air temperature and humidity were measured in situ during every flight with a hand-held digital thermometer–hygrometer before thermal image collection, and distance from the target was measured via the altimeter of the helicopter. Since

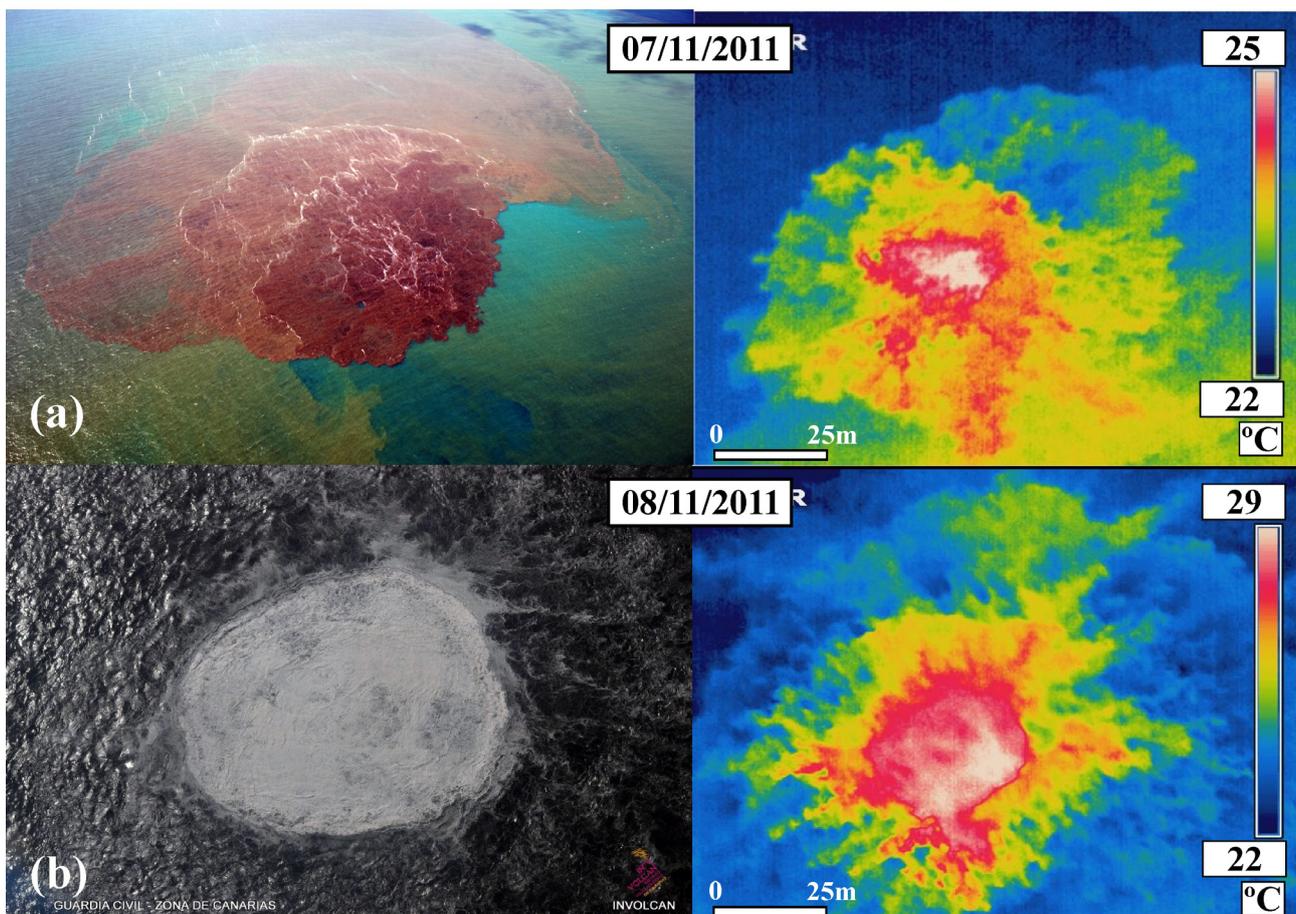


Figure 13. (a) Thermal infrared image of the discolored seawater area over the eruption site taken on November 7, 2011; (b) Thermal infrared image of the discolored seawater area over the eruption site taken on November 8, 2011.

apparent temperatures are sensitive to viewing distance, thermal surveys from the helicopter were always carried out at three fixed altitudes over the eruption spot, ~305, ~460 and ~610 m. Thermal images of the sea surface were collected as perpendicular as possible to the sea surface in order to avoid atmospheric attenuation of source radiation (Spampinato et al., 2011).

The erupted volume of lava and pyroclastic was calculated on the basis of the temperature difference (heat flux exponential reduction) between the seawater contained within the dark patch visible at the sea surface (T_{surface}), and the boiling temperature of seawater next to the eruptive vent. After correction, maximum sea water temperatures within the discolored area ranged from 18.6 °C to 30.9 °C, compared with sea surface temperature of 18–20 °C outside the eruption site. Maximum apparent temperatures obtained from thermal images of the sea surface showed interesting changes during the period of observation (Figure 14). The first and most important peak in Figure 14 was probably caused by strong emission of lava and release of hot hydrothermal fluids from the widening vent during the initial phase of the eruption. Eruptive activity between 5 and 10 November 2011 (Figure 13a and b) coincided with the occurrence of (i) large explosive “bubbles” at the sea surface, some potentially as high as 25 m on November 5, and (ii) the largest earthquake ($M=4.6$) on November 11 (Ibáñez et al., 2012).

To estimate the erupted volume of lava flow and pyroclastic, we measured the surface area of heated seawater, depth of the submarine volcanic cone (lava effusion spot) and temperature of seawater not affected

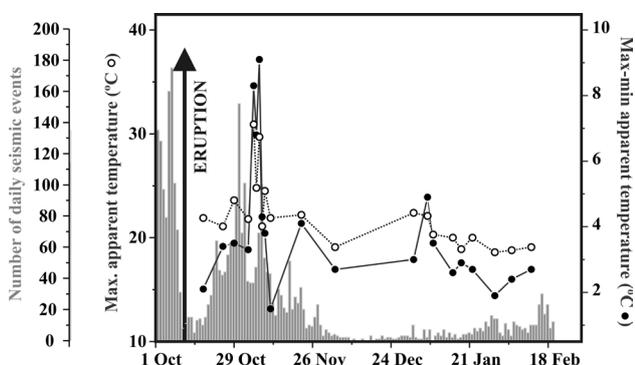


Figure 14. Temporal evolution of maximum apparent temperatures (open circles) and difference between maximum and minimum apparent temperatures (black circles) measured at the sea-water surface. Daily seismic events are indicated with light gray bars (source IGN).

by the eruption. For the 21 thermal infrared surveys, pixels containing temperatures that exceeded normal seawater temperatures were selected, allowing us to calculate the area of anomalous heating. Figure 13a shows a thermal infrared image of the seawater surface at the eruption site, taken on November 11 2011, a few days after the onset of the submarine volcanic activity. After computing total seawater volumes and depths of the submarine volcanic cone, Eq. (2) in Hernández et al., 2014, was used to estimate the daily erupted volumes.

Figure 15 shows the estimated erupted volumes for the 21 thermal surveys. In order to reconstruct the submarine eruptive thermal behavior and estimate the total erupted volume, a graphical interpolation was done between each survey, to obtain the cumulative erupted magma volume (black line in Figure 15). On this basis we obtained a total erupted volume of lava flows and pyroclastic of $300 \times 10^6 \text{ m}^3$ during the period of study (October 18, 2011–February 12, 2012), resulting in a TADR of $\sim 25 \text{ m}^3 \text{ s}^{-1}$. This volume, although roughly estimated, is very close to the total accumulated volume of 329×10^6 non-dense rock equivalent m^3 estimated by the IEO using bathymetric surveys (Rivera et al., 2013). These similar volume estimations suggest that the lava flows that erupted during the submarine eruption at El Hierro were very fluid due to their composition and most of the heat released was used to heat the surrounding seawater (Applegarth et al., 2010). Figure 15 displays two mean peaks in the curve of the erupted volume. The first peak was recorded at the start of the survey on

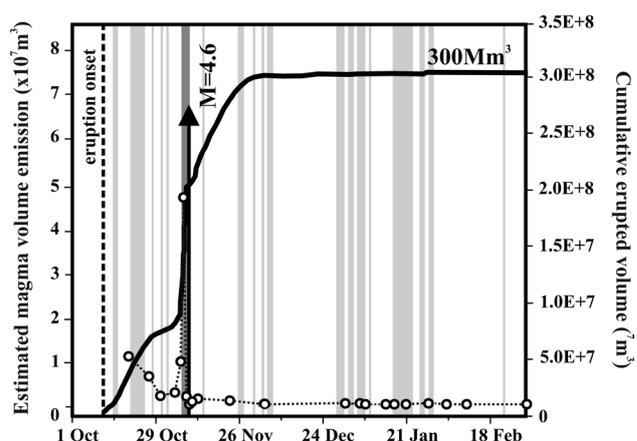


Figure 15. Temporal evolution of estimated magma volume emission (white circles) and cumulative erupted volume (solid black line) during the period of study. Light gray bars indicate formation of a patch with brown color and floating rocks. The dark gray bar indicates the days with stronger eruptive activity (bubbling columns at the sea surface).

October 18, six days after eruption onset and due to the intense explosive activity during the early stages of the eruption; with a maximum of $\sim 152 \times 10^6$ m³ erupted magma averaged over 24 h on October 19, 2011. The thermal measurement reached a climax between 5 and 7 November 2011, corresponding to a maximum of $\sim 656 \times 10^6$ m³ erupted magma averaged over 24 h on November 7, 2011. The maximum erupted magma volume is very close to the peak volcanic tremor, suggesting that it was produced by both strong explosive activity, building up a submarine cinder cone, and vigorous lava output, typically recorded during the initial phases of fissure eruptions (Calvari et al., 2005, 2010; Harris et al., 2011).

The 2011–2012 submarine eruption at El Hierro has been a unique opportunity to monitor for the first time the volume of lava spreading over the sea bottom on the basis of thermal data collected from a helicopter. Our thermal data, together with seismicity and visual observations, have allowed us to reconstruct the temporal evolution of the eruption and to estimate the total magma volume emitted during the submarine eruption.

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