Ecosystem CO_2 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, ast the two other species did not successfully colonise until 1973 (Fridriksson 1978).

The plant species in this community are all commonly found in costal 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 kg ha^{-1} $year^{-1}$ (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.

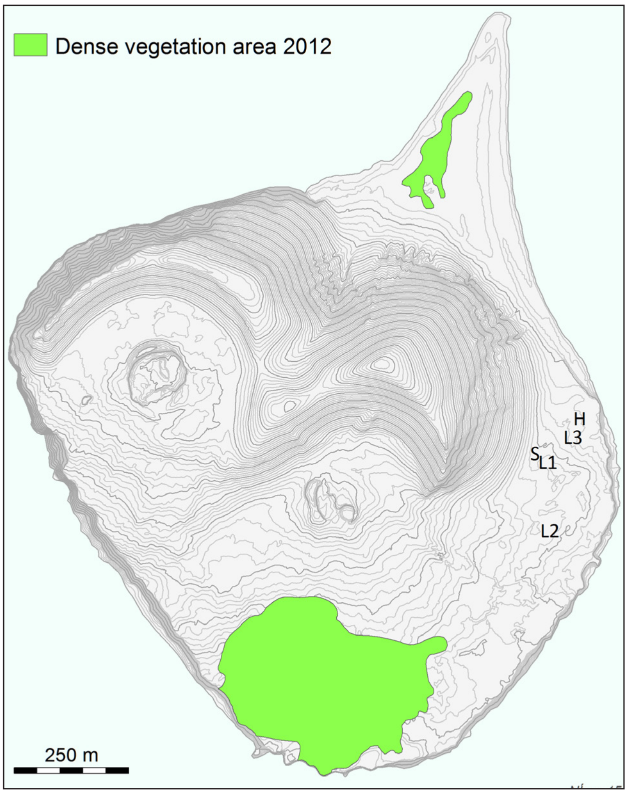

Figure 1. Location of the study plots on Surtsey. Plots L1, L2 and L3 were established in 2009-2010 on top of 17, 28 and 37 year old *Leymus arenarius* dunes, respectively. Plots S and H were established in 1987 on unvegetated sandy surface (S) and on a surface that contained relatively high *Honckenya 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.

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 (Stefansdottir 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 x 1 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 x 1 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 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 Stefansdottir 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).

CO_2 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 CO_2 flux chamber (PP Systems, UK) were used to measure changes in atmospheric CO_2 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 CO_2 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

CO_2 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).

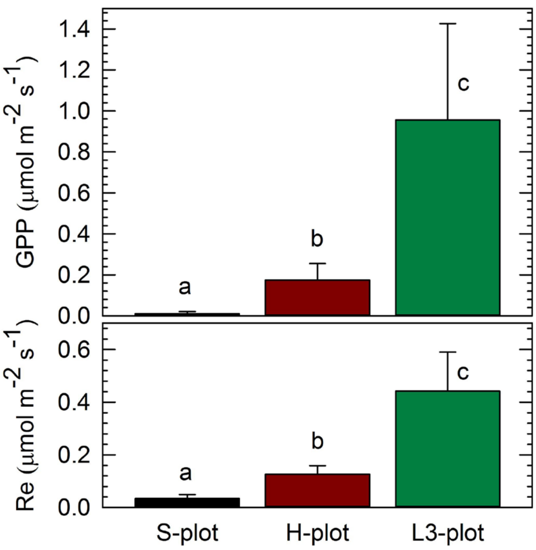

Figure 3. Mean gross photosynthetic rate ±SE in (GPP; top panel) and ecosystem respiration (Re; bottom panel) in the three main surface types found outside the seagull colony on Surtsey: Sparsely vegetated plot with <2 % vegetation surface cover (S-plot), *Honckenya peploides* dominated plot (H-plot) with 14%±6% cover and *Leymus arenarius* dune (L3-plot) with 27%±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 µmol photons m^{-2} s^{-1} and mean soil temperature was 17.3 °C at 10 cm depth.

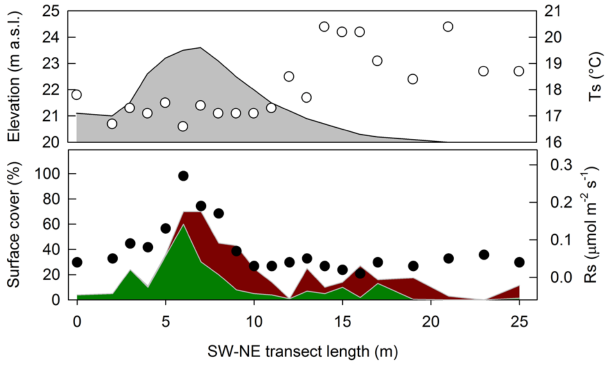

Figure 4. Soil temperature at 10 cm depth (open symbols) at 1-2 m intervals along a 25 m transect across the L3 dune (top panel) in July 2009. Surface cover of *Leymus arenerius* (green area) and *Honckenya peploides* (brown area) and soil respiration (Rs; black circles; bottom panel).

In July 2010, the CO_2 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 µmol CO_2 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 CO_2 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 CO_2 surface efflux (respiration) increases exponentially with soil temperature (Ts; Chapin et al. 2002), a phenomenon also reported from Surtsey

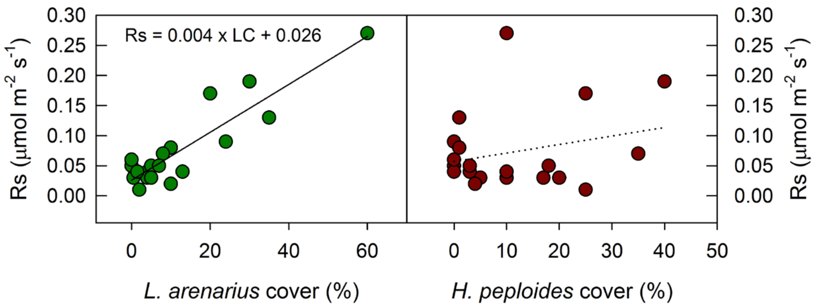

Figure 5. The relationship between a) *Leymus arenarius* surface cover (LC; right) and *Honckenya peploides* surface cover (left) and soil respiration (Rs; µmol CO_2 m^{-2} s^{-1}), shown in Fig. 3. The solid line indicates a significant regression relationship between LC and Rs (P<0.001; normality and 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 Ts was actually ca. 2 °C lower where the vegetation cover and Rs were highest, the variation in Ts should actually have buffered the CO_2 fluxes there, not enhanced them. Therefore the spatial variation in the Rs should have mirrored spatial variability in respiration activity rather than soil temperature.

When the measured Rs 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 Rs 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 Rs

The strong relationship between Rs 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 (Rs or Re) could be used as a proxy to survey differences in these belowground stocks. However, when the Rs measurements were repeated at the four subplots along the transect in July 2010, the measured Rs rates showed a very different pattern within the L3 dune; i.e. many of the measurements higher up in the dune showed very low Rs 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 Rs and soil volumetric water content (SWC) in 2010 within the L3 dune:

$$Rs = 0.04 \times SWC - 0.10 \qquad (1)$$

This explained the reversed spatial pattern in Rs 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 Rs measurements over longer times at different soil moisture conditions (or Ts) 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 Rs measurements could be used within a shorter time period when soil moisture and Ts conditions did not differ so much, as a proxy for SOM contents and/or root biomass in different aged *L. arenarius* dunes. When Rs 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 Rs between all groups (Figure 6).

When compared across all groups shown in Figure 6, a linear regression relationship between Rs (µmol CO_2 m^{-2} s^{-1}) and root biomass (R; g C m^{-2}) was highly significant (P<0.001; R^2 = 0.86):

$$Rs = 2009.1 \times R + 92.3 \qquad (2)$$

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

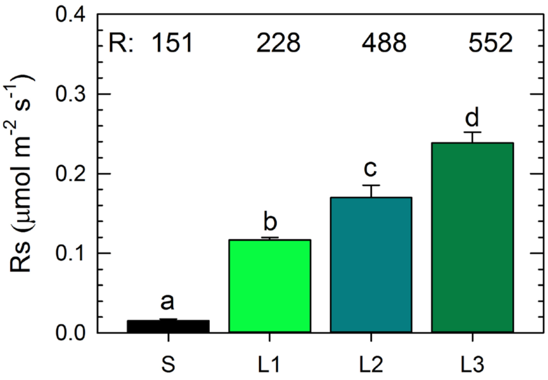

Figure 6. The average soil respiration flux ±SE (Rs; µmol CO_2 m^{-2} s^{-1}) at measurement spots with soil volumetric water content >5% in the top 5 cm layer, outside (S-plot) and inside a 17 (L1), a 28 (L2) and a 37 year old *L. arenarius* dune (L3-plot). The numbers shown at the top are the amount 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 ($R^2 = 0.76$):

$$Rs = 1163.2 \times SOC + 59.6 \qquad (3)$$

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 CO_2 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.

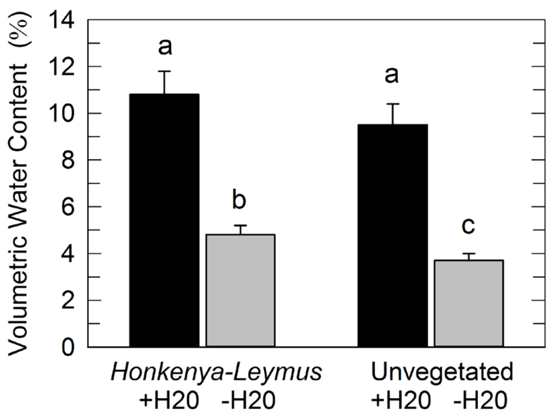

Fig. A1. Soil volumetric water content (%) in the top 5 cm of soil in *vegetated Leymus arenarius* and *Honckenya peploides* cushions and in the unvegetated soil surface in a moist area (+H20) and a dry area (-H20) on Surtsey in July 2010. These are the same plots as used for comparison of CO_2 fluxes 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.