Final Author Response to the editor final comments on:

“*Accumulation of nitrogen and organic matter during primary succession of* Leymus arenarius *dunes on the volcanic island Surtsey, Iceland*” by G. Stefansdottir et al. Biogeosciences Discuss., 11, C3624–C3624, 2014

List of all changes made in the final-final version of the manuscript – Additional changes in the final-final version are indicated in red.

(all changes are indicated with red colour in the final manuscript and added “Comment” if text should only be deleted):

Pdf of the article in Open Discussion	Changes to be made
Page 6592 – lines 1-3 Page 6592 – lines 1-3	Delete the sentence ➔ The volcanic island of Surtsey has been a natural laboratory where the primary succession of flora and fauna has been monitored, since it emerged from the N-Atlantic Ocean in 1963. Add instead the sentence ➔ Initial soil development and enhanced nutrient retention are often important underlying environmental factors during primary succession.
Page 6592 – lines 4-6 Page 6592 – line 6	Add “on the pristine volcanic island Surtsey” ➔ Should read: Add We quantified the accumulation rates of nitrogen (N) and soil organic matter (SOM) in a 37 year long chronosequence of *Leymus arenarius* dunes on the pristine volcanic island Surtsey in order to illuminate… Delete the words “in primary succession” ➔ Should read: … illuminate the spatiotemporal patterns in their build-up.
Page 6596 – line 1	Delete the word “then”. ➔ Should read: …, incremental soil samples of known volume taken within the…
Page 6596 – line 27.	Change ($g\ cm^{-3}$) ➔ Should read ($g\ cm^{-2}$)
Page 6597 – line 1.	Change “per volume” ➔ should read: “per mass”.
Page 6597 – line 21.	Add the word “an” ➔ should read “To give an idea about…”
Page 6598 – lines 16-17	Delete the word “, however,”➔ Should read: Mean SOC and SON concentrations did increase exponentially with age …
Page 6598 – line 18.	Add the sentence after … the 3 year old dune, respectively (Table 1). ➔ Should read: … (Table 1). The actual concentrations were, however, always low, or on average 0.049% and 0.0037% for SOC and SON, respectively.
Page 6597 – line 22.	Add “an” before “idea”. ➔ Should read:
Page 6600 – line 19	Add a paragraph to the end of 4.1: ➔ As the dunes grew in size with age their total element stocks calculated to the same soil depth outside the dunes increased. It may be asked how much of this increase was just a function of increasing dune depth

Comment [BDS1]: Delete „in primary succession“

Comment [BDS2]: Delete „then“

Comment [BDS3]: Delete , however,

	and soil mass with age? The observed increase in average element concentrations (% DM) from the youngest to the oldest dune was 5.6 and 6.2 fold for SON and SOC, respectively, which clearly indicated that it was not simply an increasing size of the dunes which was causing the accumulation.
Page 6601 – lines 18-19.	Change the wording of: These roots are most likely mostly originating from the … ➔ These roots are most likely to originate from the.
Page 6612.	Please change the Figure legend for Figure 3. Add the words "to 75 cm depth" ➔ Should read: Figure 3. Mean shoot biomass (a), root biomass (b) and soil organic matter (c), all expressed in carbon units, in 75 cm deep cores taken in the centre, in the middle and at the expanding edge of three oldest *Leymus* dunes (No 5, 6 and 7). Additional cores were also taken to 75 cm depth ca. 5 m outside the dunes, for comparison. Vertical bars represent SE of n=3-5. Different letters above bars indicate significant differences (P<0.05) found with post-ANOVA LSD-tests.

Author responses to editor comments (in red):

The authors apologize that they missed addressing the comments made by the editor (dr. Jens-Arne Subke) when they prepared an earlier final submission to BG. This was due to an oversight of their part and because his comments were not listed within the open discussion forum of BGD, but were only found in an e-mail from the editor to the authors which they forgot/missed.

Please address the few points made, e.g. by discussing the likely role of arbuscular mycorrhizas in your system.
=> The few points made by the reviewers have been addressed (see above).

My main question concerns the calculation of N on the basis of density and dune area, as the main difference in dunes of different age is the size, so an increase in DON and DOC per area would result simply from an increase in sediment depth. You state that the tephra sands have a DON content of less than 0.01%. Looking at you results in table 1, it would follow that given a volume of 176 m3, and a bulk density of 1.16 (using dune #7 as an example), we would expect a dune mass of about 200 t, and hence a DON amount of around 20.4 kg. So for a dune area of 154 m2, a background DON concentration of around 132 g DON m-2 could be expected. I realise that the estimate of 0.01% is a coarse upper value, but my point is that the accumulation of N would result simply from substrate accretion and increased dune height, when expressing DOC and DON densities on an area basis, so the estimate of DOC and DON accumulation due to plant growth should take this into account. Can you propose how your analysis can adjust for this effect, and indicate whether you think your conclusions regarding N transfer from outside areas remains valid?

The statement in the Introduction "the sands have SON content of less than 0.01% is correct per se (this value was quoted from an older study, where the accuracy of the SON analysis was much less than in the present study). It was, however, what had been published before the present study took place…

In the present analysis it was found that in many cases (i.e. in soil layers in large parts of each dune) this concentration was even less than 0.0002% N and actually always < 0.005% N. This explains the "apparent overestimation when the editor used the earlier reported 0.01% N with the total measured volume and dune area to recalculate the N stocks per m-2.

=> The authors redid the calculations on SON stocks once more and found them to be correct as they are expressed in the manuscript.

=> The authors added a sentence into the Results giving the average SOC and SON concentrations in the present study to avoid this misunderstanding.

=> About the editor's request that the authors should propose how our analysis could adjust for the effect of the growing dunes that the

=> We also added sentences to the 4.1 in the Discussion which addressed the issue with the effect of larger dune size on increasing N and C stocks (as pointed out by the editor) and why we think our conclusions regarding N transfer from outside areas remains valid after taking this into account.

Some detailed comments:

Abstract: Rather than stating first that Surtsey is a good place to work, you should focus on the scientific background of your study. There is no indication of why it is worth knowing the spatial and temporal variation in organic matter, N accumulation etc. in dune systems. I appreciate that it is a good place to do science and address ecosystem development issues, but your motivation for the paper should be scientific, and this should be stated first. Please re-work the opening of the abstract to reflect this.

=> Done.

6596, l. 1: Delete "then".

=> Done.

6596, l. 27: You say you express results on an area basis, but give per-volume units; next line states per0-volume, but has units or per-mass…

=> This was a mistake. Corrected to (g cm^{-2}) and "per mass".

6597, l. 22: add "an" before "idea"

=> Done

6601, l.18/19: Better: "These roots are most likely to originate from…"

=> Done

Fig. 3: Please indicate whether soil depth in control areas outside dunes was also 75 cm.

➔ Done.

TITLE PAGE

Title:

Accumulation of nitrogen and organic matter during primary succession of *Leymus arenarius* dunes on the volcanic island Surtsey, Iceland

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Accumulation of nitrogen and organic matter during primary succession of *Leymus arenarius* dunes on the volcanic island Surtsey, Iceland

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Abstract

Initial soil development and enhanced nutrient retention are often important underlying environmental factors during primary succession. We quantified the accumulation rates of nitrogen (N) and soil organic matter (SOM) in a 37 year long chronosequence of *Leymus arenarius* dunes on the pristine volcanic island Surtsey in order to illuminate the spatiotemporal patterns in their build-up. The *Leymus* dune area, volume and height grew exponentially over time. Aboveground plant biomass, cover or number of shoots per unit area did not change significantly with time, but root biomass accumulated with time, giving a root-shoot ratio of 19. The dunes accumulated on average 6.6 kg N ha^{-1} year^{-1}, which was 3.5 times more than is received annually by atmospheric deposition. The extensive root system of *Leymus* seems to effectively retain and accumulate large part of the annual N deposition, not only deposition directly on the dunes but also from the adjacent unvegetated areas. SOM per unit area increased exponentially with dune age, but the accumulation of roots, aboveground biomass and SOM was more strongly linked to soil N than time: 1 g m^{-2} increase in soil N led on the average to 6 kg C m^{-2} increase in biomass and SOM. The *Leymus* dunes, where most of the N has been accumulated, will therefore probably act as hot-spots for further primary succession of flora and fauna on the tephra sands of Surtsey.

Comment [BDS1]: Delete „in primary succession“

1 Introduction

Primary succession is the process of ecosystem development of barren surfaces with no previous developed soil or plant cover, such as new lava flows or areas left in front of retreating glaciers. Multiple environmental factors and ecosystem properties can act as thresholds in primary succession of such areas, not least a lack of nutrients, water and developed soil (del Moral and Grishin, 1999). Therefore the earliest colonists on volcanic tephra fields are often confined to specific microsites that offer some physical protection and enhanced nutrient resources from weathering, erosion or other nutrient inputs (Walker and del Moral, 2003). As some vegetation cover establishes on the pristine surfaces, organic matter (OM) and soil organic nitrogen (SON) start to accumulate, which again improves the growing conditions for later successional species (Whittaker et al., 1989). Such ‘autogenic’ (internal) factors are expected to determine the course of succession by traditional succession theory (Walker and del Moral, 2003), but ‘allogenic’ (external) or stochastic factors (such as distance to potential colonists) also play an important role in some cases (del Moral et al., 2009; Marteinsdottir et al., 2010).

Pristine volcanic islands offer special conditions to study the processes of primary succession. New volcanic islands, or older islands totally disturbed by a volcanic activity in historic times, are few; hence only a limited number of such studies exists, including e.g., Krakatau in Indonesia which erupted in 1883 (cf. Whittaker et al., 1989) and most recently the Kasatochi Island in Alaska which erupted in 2009 (Talbot et al., 2010). More work has been done on primary succession of lava flows from continental volcanos or where parts of volcanic islands have been disturbed by a new eruption (reviewed by Walker and del Moral, 2003).

The island of Surtsey emerged in an eruption that lasted from November 1963 to June 1967. Its undeveloped soil (thephra sand) contained only minute amounts of soil organic matter (SOM) and SON in the beginning (Henriksson et al., 1987). Colonisation of vascular plants has been closely monitored on Surtsey since its emergence (Fridriksson, 1966; 1992; Magnusson and Magnusson, 2000; Magnusson et al., 2009; 2014). These studies show that the first plant community that successfully colonised the island consisted mainly of deep-rooted shore plants forming dense colonies of aboveground foliage (dunes or cushions) such as *Leymus arenarius* and *Honckenya peploides,* with large unvegetated areas in between.

The importance of spatial variation in early primary succession is receiving increasing attention (e.g., Cutler et al., 2008; del Moral et al., 2009; Cutler 2011; Garibotti et al., 2011). In patchy environments, positive feedback mechanisms can contribute to resource aggradation (cf. Rietkerk et al., 2002; Ehrenfeld et al. 2005), and we expect this to be the case for the *Leymus* dunes in Surtsey. Due to the careful monitoring of Surtsey’s vegetation, the exact age of each *Leymus* dune is known, which presents an opportunity to study the effects of vegetation on the development of spatial variation in soil properties in the early stages of primary succession.

The main objective of this study was to assess the accumulation rates of SON and OM in *Leymus arenarius* dunes during primary succession on Surtsey. We sampled a 37-year long chronosequence of seven different aged *Leymus* dunes, expecting to find a linear increase in the SON and SOC with dune age that would indicate a gradual improvement of growing conditions. Furthermore we expected the *Leymus* to grow more vigorously and form denser aboveground canopy as it got older and accumulated more resources.

2 Material and methods

2.1 Site description

Surtsey (Fig. 1; 63.3°N, 20.6°W) is the southernmost island of the Vestmannaeyjar archipelago, ca. 32 km off the south coast of Iceland. The local climate is cold temperate, oceanic, with an annual mean temperature of 5.0 °C and mean annual precipitation of 1576 mm during 1965–2005, as recorded at the weather station on the island of Heimaey, 15 km to the northeast of Surtsey (Icelandic Met Office).

The first *Leymus arenarius* seedling was found on the island in 1966, before the eruption ceased (Fridriksson, 1966), but it did not establish. The first successful establishment of *Leymus* was in 1974 and that colony produced seeds for the first time in 1979 (Fridriksson, 1992). In 1983, the first successful seedling emergence of *Leymus* from local seed sources was observed, and since then the species has spread over the whole island (Fridriksson, 1992; Magnusson et al., 2014). *Leymus* is currently, together with the *Honckenya*, the most widespread plant species on the island. They form sparse communities on sandy areas (Magnússon and Magnússon 2000), where the *Leymus* colonies accumulate characteristic sand dunes (cf. Greipsson and Davy, 1994). The vegetation cover of these tephra sands is generally below 20% (Magnússon and Magnússon 2000) and was only 2.3% on the average in 2012 at the site of the present study (Magnusson et al., 2014). The tephra sands are also extremely nutrient poor, with SON concentrations < 0.01% and SOC of < 0.05%, with relatively high pH of 7.6 (Sigurdsson and Magnusson, 2010).

2.2 Selection of a *Leymus* chronosequence

The close monitoring of the establishment of all vegetation on Surtsey enabled the location of *Leymus* dunes of known age. Seven dunes of different age were selected on the southeast side of the island (Fig. 1). The two oldest dunes included the first successful *Leymus* colonisation and a dune from the first seeding episode in 1983 (Fridriksson, 1992), but younger dunes were all close to permanent study plots (no 13, 14, 15 and 21; Magnusson and Magnusson, 2000) and their establishment could be dated from annual photographs of them. The age of the dunes at the time of sampling was 3, 5, 9, 13, 17, 28 and 37 years.

[FIG. 1 HERE]

2.3 Sampling protocol

The dunes were mapped in July 2010 and 2011 by crossing two laterally levelled strings over the highest midpoint of each dune and measuring distance to the soil surface and soil depth (to 75 cm) at 50 cm intervals along each string until the dune’s edge was reached. Flowering stems of *Leymus* were counted on the whole dune. Three 30x30 cm quadrats were randomly placed on the top of each dune, except on the four youngest ones where only one quadrate could be fitted because of their smaller size. Additionally quadrats were placed in the middle slope and at the expanding edge of the three oldest dunes, as well as 5 m outside them for comparison. In each quadrat, surface cover of all vascular plant species was recorded and the number of *Leymus* shoots counted. Furthermore, all aboveground biomass was harvested by cutting and subsequently, incremental soil samples of known volume taken within the harvested quadrate. Continuous soil cores of known volume were taken to 5, 10, 20, 30, 45, 60, 75 cm depth, if bedrock was not reached earlier. All samples were sieved *in situ* through 1 cm sieve and visible roots were separated and stored.

Comment [BDS2]: Delete

Biomass samples (roots and shoots) were dried at 105 °C for 3-5 days and weighted for dry mass (DM). The roots were burned and their mass loss after ignition determined to correct for fine thephra sand that could not be cleaned from the roots. The soil samples were weighed after air drying until their DM was stable. They were then sieved through 2 mm, coarse fragments (>2 mm) weighed and their volume measured by water displacement method. All litter and fine roots found in the coarse fragments after sieving were weighed and added to the shoot and root samples, respectively. The fine soil fraction of all samples was ground for two minutes in a ball mill (MM200, Retsch, Haan, Germany) and their total soil organic carbon

(SOC) and nitrogen (SON) concentrations analysed by dry combustion on Macro Elementary Analyzer (Model Vario MAX CN, Hanau, Germany). Soil samples were then dried at 105 °C for 48 hours and weighed again.

2.4 Calculations and data analysis

Aboveground dune volume was calculated for different depths of the four measured topographical transects, assuming that the shape of each height layer was a trapezoid and the topmost layer conical. The soil volume under the whole dune was also calculated for each depth interval, down to 75 cm depth where bedrock was not shallower. The drip line area of each dune was used as the outer boundary, i.e. not including the soil volume containing extending roots away from the dune's edge.

Soil C and N concentrations of each sample were corrected for difference in between air dry DM and DM after drying at 105 °C. Sample bulk density (BD, g cm^{-3}) was calculated from fine-fraction DM and total sample volume after removal of the coarse-fraction volume. SOC and SON content per unit dune area (g m^{-2}) and per measured dune mass (kg $dune^{-1}$) was calculated from the element concentrations, volume and BD of each layer.

Biomass C (shoots and roots) was calculated from measured DM. Shoot DM was multiplied by 0.40, which is an unpublished factor based on measurements of *Leymus* shoot biomass and C by the Soil Conservation Service of Iceland (Johann Thorsson, pers. information). The relatively low observed C-fraction in *Leymus* plants is probably caused by the high dust content in the condition it grows in. Root C was calculated by multiplying the measured DM by 0.50 (Schiborra et al., 2009), after using the loss by ignition to adjust the DM to normal mineral content of 2.6% for grasses (Agricultural University of Iceland, unpublished data).

Differences in mean C stocks at different locations within the three oldest dunes was tested by post-ANOVA Fisher's LSD tests in the SAS statistical program (SAS system 9.1, SAS Institute Inc., Cary, NC, USA). Age-dependent changes in C and SON stocks were tested by linear or exponential regression analysis in the SigmaPlot program (Version 11.0, Systat Software, Inc., San Jose, CA, USA).

3 Results

3.1 Dune size and volume

The surface area, height, aboveground volume and total volume to 30 and 75 cm soil depth of the *Leymus* dunes grew exponentially with age (Table 1), for the age-span included in the present study (3-37 years). The soil depth outside the dunes was not significantly different, indicating that the starting conditions were comparable for all the dunes. To give an idea about relative size differences, the 10, 20 and 30 year old dunes had ca. 45, 210, 550% larger surface area, were 70, 400, 1,350% taller and had 70, 405, 1,390%, greater volume than the 5 year old dunes, respectively.

[FIG 2 HERE]

3.2 Soil and plant parameters per unit area

Shoot density and surface cover of *Leymus* within each dune did not show a significant increase with age (Table 1); on average each dune had 56 shoots/m^2 (SE ±5) and 20% (SE ±1%) *Leymus* surface cover. The first flowering occurred in the 9 year old dune, but density of flowering stems was not significantly related to dune age (Table 1). The *Honckenia* cover increased exponentially with dune age and reached 14% on the oldest dune (Table 1), but no other plant species were found on the dunes. Total aboveground biomass did not change significantly with age, when expressed per unit area, but root biomass increased significantly and linearly with age (Table 1). The root biomass per unit area increased on average by 9.1 g/m^2 annually. The belowground root biomass in the *Leymus* dunes far exceeded their aboveground biomass (Fig. 2). The average R/S ratio was 19.1 (SE ±1.2), and did not change significantly with dune age, even if root biomass increased slightly (Table 1; Fig. 2).

[TABLE 1 – BETWEEN PAGES]

The mean bulk density and C/N ratio in the top 75 cm of soil, or down to the bedrock, in each dune were on average 1.16 g/cm^3 (SE ±0.02) and 13.7 (±0.2) and did not change significantly with age (Table 1). Mean SOC and SON concentrations did increase exponentially with age and were 17.6 and 14.9 times larger in the 37 year old than in the 3 year old dune, respectively (Table 1). The actual concentrations were, however, always low, or on average 0.049% and 0.0037% for SOC and SON, respectively.

Comment [BDS3]: Delete , however,

The fraction of SOC of total ecosystem C stock (*fSOC*) remained low, or between 15-20%, until the dunes exceeded ca. 15 years; then the ratio increased and was 42% in the oldest dune (Fig. 2). The age-dependent increase in this fraction was significant ($P<0.002$; $R^2 = 0.88$) and could be described by a positive linear function:

$$fSOC = 8.4 + 0.9139 \times Age\ , \qquad (1)$$

where age is in years. This function shows the first steps of soil development. It was also noteworthy that both root biomass and SOC stocks were relatively stable with depth below the ca. 10 cm surface layer, (Fig. 2) and where bedrock was not found at shallower depths. The maximum sampling depth was 75 cm, but Fig. 2 indicates that the *Leymus* roots went deeper if soil depth allowed. Above- and belowground C stock above 30 cm soil depth was 67% (SE ±3.5%) of the total C stock down to 75 cm and this proportion did not change significantly with age of the dunes ($P=0.11$).

3.3 Spatial variability within the dunes

The average C stocks in aboveground biomass, root biomass or SOC did not vary significantly among locations within dunes (Fig. 3). The top and middle areas of the dunes had significantly higher C stocks in all three compartments than the sparsely vegetated areas around them, which only contained a few small *Honckenia* plants, no *Leymus* shoots and very low aboveground biomass. The areas around the dunes had, however, 41% and 29% respectively of the roots and SOC found in the dunes.

[FIG 3 HERE]

3.4 Variables expressed per total dune area or volume

The exponential increase in shoot biomass and root and SOC stocks with age, associated with larger surface area and total soil volume were even more apparent at a whole-dune scale (Fig. 4a). The annual SON accumulation rate was on average 6.6 kg N ha^{-1} $year^{-1}$ (SE ±0.9) and did not show significant age-dependent trend (Fig. 4b). A very strong linear relationships ($R^2 > 0.94$; $P<0.001$) appeared between the amount of SON and the total shoot biomass (C_S), total plant biomass (C_P) and SOC stocks, when expressed at a ln:ln scale (Fig 4c), showing that the total ecosystem OM increased exponentially with time as more N became available. The linear ln:ln SON:C functions were:

$$\ln C_S = 0.6678 + 1.0705 \times \ln SON\ , \qquad (2)$$

$$\ln C_P = 4.1541 + 0.8787 \times \ln SON\ , \qquad (3)$$

$$\ln SOC = 2.4846 + 1.0190 \times \ln SON\ . \qquad (4)$$

When the total ecosystem C stock (C_{tot}, g m^{-2}) to 75 cm depth at the dune's edge (or down to bedrock if shallower than 75 cm) in different dunes was compared to the total dune SON stock (SON_{tot}, g m^{-2}), a significant linear relationship appeared ($P = 0.03$, $R^2 = 0.57$; data not shown):

$$C_{tot} = -22{,}330 + 6039 \times N_{tot}\ , \qquad (5)$$

In other words, there was 6.0 kg C m^{-2} accumulation in the dunes for every one g m^{-2} increase in the SON stock during the ca. 40 years after first establishment on the pristine volcanic island, giving an estimation of the average annual “nitrogen use efficiency” of the *Leymus*.

[FIG 4 HERE]

4 Discussion

4.1 Dune size development

The *Leymus* dunes are formed as eroding volcanic tephra sand is trapped by the vegetated patches. Their growth rate therefore depends both on the intercepting capacity of the *Leymus* plants and the intensity of the aeolian transport. All the dunes in our study, except the youngest one, were located within relatively small and homogeneous area (Figure 1), where the aeolian transport can be assumed to be similar. The dune height, surface area and volume increased exponentially with age. This is in contrast with previous studies on *Leymus* that assumed more-or-less constant growth rates and hence expressed their height increment with a single annual average (Greipsson and Davy, 1996).

As the dunes grew in size with age their total element stocks calculated to the same soil depth outside the dunes increased. It may be asked how much of this increase was just a function of increasing dune depth and soil mass with age? The observed increase in average element concentrations (% DM) from the youngest to the oldest dune was 5.6 and 6.2 fold for SON and SOC, respectively, which clearly indicated that it was not simply an increasing size of the dunes which was causing the accumulation.

4.2 Accumulation of SON

The accumulation of SON has been slow on Surtsey, except in an area where seabirds formed a dense breeding colony after 1985 (Magnusson and Magnusson, 2000; Magnusson et al., 2009; 2014) and increased the ecosystem N accumulation with their droppings by ca. 50 kg N ha^{-1} year^{-1} (Leblans et al., 2014). Elsewhere on the island, where the sparse *Leymus* and *Honckenya* community is dominant, the average SON accumulation rate is ca. 1 kg N ha^{-1} year^{-1} (Leblans et al., 2014), which is about half of the expected atmospheric N deposition of areas in Iceland with annual precipitation of 1500 mm (1.8-2.0 kg N ha^{-1} year^{-1}; Gíslason et al., 1996; Sigurðsson et al., 2005).

The mean annual accumulation rate of SON within the dunes in our study was 6.6 kg N ha^{-1} year^{-1}, or ca. six times higher than on average in the soil of same area on Surtsey (Leblans et al., 2014). There are several possible explanations for this difference: i) translocation of N into the dunes from the unvegetated areas around with root transport, ii) accumulation of N with wind-blown organic material that is trapped by the dunes, iii) if birds transport more N to dunes than to other areas, v) free-living N-fixation of soil bacteria within the dunes or vi) symbiotic N-fixing with *Leymus* or *Honckenya*. The present experimental setup does not allow us to determine which individual pathways are responsible, but we argue that process i) is the main contributor. The average *Leymus* surface cover of the permanent study plots in the same area (plots 13-16) in 2012 was only 0.9% and total plant cover was only 2.3% (Magnusson et al., 2014); i.e. 97.7% of the surface was unvegetated. Relatively large amounts of plant roots were, however, present in all soil samples taken between *Leymus* dunes in this area (Fig. 3 b; Leblans et al., 2014). These roots are most likely to originate from the scattered *Leymus* dunes and can translocate nutrients and water into the dunes.

Of the other pathways, the aboveground translocation of N with wind-blown material and entrapment by dunes is probably also important. Such a pathway has been used to explain how *Leymus* and other dune-building species accumulate nutrients in barren and N-poor environments (Greipsson and Davy, 1994; Walker and del Moral, 2003). Some allochthonous nutrient inputs from birds cannot be ruled out either, but since breeding density on this part of the island is low (Petersen, 2009), it is probably mostly limited to overflying birds and therefore unlikely to be preferential towards the *Leymus* dunes. Free-living N-fixing has been found to be absent or extremely low in the tephra sand in the present study area (Henriksson and Henriksson, 1974), while N-fixing by the cyanobacterium *Nostoc*, associated with colonising mosses in other more sheltered areas of the island, was found to be substantial (Henriksson et al., 1987). No symbotic N-fixing was found in *Honckenia* growing in the study area in the 70s (Henriksson et al., 1974) and only low level of (free-living) N fixation was detected in soils from *Leymus* dunes (Henriksson and Henriksson, 1978). Symbiotic N-fixation has, however, been found in coastal dunes of the closely related *L. mollis* in Oregon, USA (Dalton et al., 2004) and further investigation if symbiotic N-fixing occurs in the *Leymus* in Surtsey is needed.

Whatever the source, the *Leymus* dunes have accumulated SON much faster than anticipated and that would have been estimated from the average atmospheric N-deposition. If mainly derived with translocation from the unvegetated area around the dunes, then the *Leymus* is playing a very important role in N-retention and build-up on the tephra sands of Surtsey. The *Leymus* in Surtsey is a classic example of a primary coloniser that acts as an environmental engineer that modifies its habitat with time and contributes to patchiness in resource availability (cf. Walker and del Moral, 2003; Ehrenfeld, 2005; del Moral et al., 2009). This is a typical example of reversed ‘Robin Hood’ effect, where poor areas of the landscape are robbed of their scarce resources for the benefit of the richer patches in areas that are highly resource limited (cf. Ludwig and Tongway, 2000). On a new volcanic substrate like in Surtsey, the formation of such ‘hot spots’ of resource availability may be essential for the subsequent formation of plant communities.

4.3 *Leymus* growth

It was noteworthy that neither the *Leymus* surface cover, shoot density nor aboveground biomass per unit area changed significantly during the 37 years chronosequence, even if dune area grew exponentially with both age and SON stock. The *Leymus* apparently used the additional resources mainly to add new shoots at the dune’s edge. The cover (density) of *Leymus* is, however, also dependent on the site’s N availability, when compared across a wider N-availability range than was done in the present study. On the permanent study plots on tephra sand within the seagull colony on Surtsey, where annual N accumulation was much higher (Leblans et al., 2014), the surface cover of *Leymus* was almost double, or 34% (Magnusson et al., 2014).

Leymus arenarius is a long-lived grass species (Greipsson and Davy, 1994) and there were no indications for any dieback within the oldest dunes, neither aboveground nor belowground.

Such dieback may, however, occur when the dunes have reached a certain size (Greipsson and Davy, 1994). The earliest flowering of *Leymus* was seen in a nine year old dune, but a five year old dune did not have any flowering stems. This fits well with the development of *Leymus* after the first successful colonisation on Surtsey, but it produced the first seeds six years after establishment (Fridriksson, 1992).

The root-shoot ratio (R/S ratio) in the centre of the dunes did not show a significant trend with time. The R/S ratio (average 19.1) was relatively high compared to vascular plants of tundra, grasslands and cold deserts that have on the average R/S ratios of 4-5 (Mokany et al, 2006). Our calculation of R/S ratio did not, however, take into consideration the *Leymus* roots that extended outside the dunes or below 75 cm depth. Leblans et al. (2014) estimated R/S ratio of 45 for the general area in between dunes. The high R/S ratio of *Leymus* is probably the key reason for its ability to colonise and survive in the nutrient poor and unstable tephra sands of Surstey. This is also in good accordance with the observation of Chapin (1993), who claimed that adaptations for large nutrient acquisition and retention were generally key factors for the success of early colonisers in primary succession.

4.4 OM accumulation

Carbon fixation (net photosynthesis) by the early colonisers, organic matter production, litter fall and the microbial breakdown of litter and humus drive the accumulation of SOM, without which soil will not develop during primary succession (del Moral and Grishin, 1999; Walker and del Moral, 2003). After the first 5 years, aboveground biomass per unit dune area remained more or less constant and the standing aboveground biomass was similar to that reported in a 39 year chronosequence on previously eroded revegetation areas in Iceland seeded by *Leymus arenarius* and initially fertilized with about 100 kg N ha^{-1} (Aradóttir et al., 2000). Root biomass and R/S ratio were, however, much higher in the present study than were reported for the fertilized *Leymus* treatments. This was partly because in Aradóttir et al. (2000) the sampling depth was limited to 30 cm, but could also be partly caused by difference in fertility as N availability is known to strongly affect R/S ratios in plants (Marschner et al, 1996). SOC stocks of the dunes on Surtsey increased exponentially with age and the *fSOC* ratio (ratio of SOC to total ecosystem C stock) increased linearly (Eq. 1). Still, after 37 years the SOC stock in the top 30 cm was only ca. 15% of total living biomass (including roots down to 30 cm), but ca. seven times higher than aboveground biomass per unit dune area. In the Aradóttir et al. (2000) chronosequence on the mainland, the SOC ratio to aboveground biomass was much higher after 39 years (ca. 22 times higher). The reasons for this could be much faster root turnover in *Leymus* on the mainland, which is a known response to fertilization of other ecosystems (Leppälammi-Kujansuu et al., 2014). It can, however, not be ruled out that some SOC remained since before the erosion took place in the mainland chronosequences, which would also translate into similar differences.

It should be noted when C stocks were scaled to whole dune level and down to 75 cm depth below the dunes (where depth to bedrock allowed) as in Table 1 and Figure 4, the fraction of SOC to living biomass changed, since the surface area scaled less than volume.

The strong relationships between SON and both biomass and SOC stocks found in the present study, and that those relationships were stronger predictor of OM accumulation than time (age) since colonisation, suggest strongly that N availability plays a major role in the primary succession on the tephra sands on Surtsey. This further supports such indications found for vascular plant cover and species composition in different habitats on the island (Magnusson and Magnusson, 2000; Magnusson et al., 2009; 2014; del Moral and Magnusson, 2014) and for process rates, such as ecosystem respiration (Sigurdsson and Magnusson, 2010). Therefore the “nitrogen use efficiency” for ecosystem C-stocks estimated by Eq. 5 and the SON relationships for individual C-components reported in Eq. 2-4 might be used for modelling the primary succession of *Leymus arenarius* in similar habitats. An interesting extension of the present work could also be to further study the importance of symbiotic mycorrhizal fungi in the N scavenging of the *Leymus* roots.

4.5 Conclusion

The history of annually monitoring colonisation, growth and mortality of individual plants on Surtsey since it emergence in 1963 offered a special opportunity to use a chronosequence approach to study how autogenic (internal) factors develop after colonisation of a keystone species in the primary succession. *Leymus arenarius*, with its high R/S ratios, is probably a key player in N retention and soil development on the tephra sands of the island. The high correlation between SON and OM stocks indicated that the rate of primary succession was more strongly controlled by the amount of available N than time since colonisation per se. The *Leymus* dunes, where N has been accumulated, will therefore probably act as hot-spots for further primary succession of flora and fauna within this area of Surtsey; at least if new sources of N will not appear, such as establishment of new seabird colonies or introduction of new symbiotic N-fixing plant species.

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References

Aradóttir, Á. L., Svavarsdóttir, K., Jónsson, Þ. H., and Guðbergsson, G.: Carbon accumulation in vegetation and soils by reclamation of degraded areas, Icelandic Agric. Sci., 13, 99-113, 2000.

Chapin III, F. S.: Physiological controls over plant establishment in primary succession, in: Primary Succession on Land, edited by: Miles, J., and Walton, D. W. H., Special publications of the British Ecological Society, 12, Blackwell Scientific Publications, London, UK, 1993.

Cutler, N.: Vegetation-environment interactions in a sub-arctic primary succession, Polar Biol., 34, 693-706, 10.1007/s00300-010-0925-6, 2011.

Cutler, N. A., Belyea, L. R., and Dugmore, A. J.: The spatiotemporal dynamics of a primary succession, J. Ecol., 96, 231-246, 10.1111/j.1365-2745.2007.01344.x, 2008.

Dalton, D. A., Kramer, S., Azios, N., Fusaro, S., Cahill, E., and Kennedy, C.: Endophytic nitrogen fixation in dune grasses (*Ammophila arenaria* and *Elymus mollis*) from Oregon, FEMS Microbiol. Ecol., 49, 469-479, doi:10.1016/j.femsec.2004.04.010, 2004.

del Moral, R., and Grishin, S. Y.: Volcanic disturbances and ecosystem recovery, in: Ecosystems of Disturbed Ground, edited by: Walker, L. R., Elsevier Science B.V., Amsterdam, The Netherlands, 1999.

del Moral, R. and Magnússon, B.: Surtsey and Mount St. Helens: a comparison of early succession rates. Biogeosciences, 11, 2099-2111, 2014, doi:10.5194/bg-11-2099-2014.

del Moral, R., and Wood, D. M.: Early primary succession on the volcano Mount St. Helens, J. Veg. Sci., 4, 223-234, 10.2307/3236108, 1993.

del Moral, R., Sandler, J. E., and Muerdter, C. P.: Spatial factors affecting primary succession on the Muddy River Lahar, Mount St. Helens, Washington, Plant Ecol., 202, 177-190, 10.1007/s11258-008-9506-y, 2009.

Ehrenfeld, J. G., Ravit, B., and Elgersma, K.: Feedback in the plant-soil system, in: Annual Review of Environment and Resources, Ann. Rev. Env. Resour., 75-115, 2005.

Fridriksson, S.: The pioneer species of vascular plants in Surtsey, *Cakile edentula*, Surtsey Res. Prog. Rep., 2, 63-65, 1966.

Fridriksson, S.: Vascular plants on Surtsey 1981-1990, Surtsey Res. Prog. Rep., 10, 17-30, 1992.

Garibotti, I. A., Pissolito, C. I., and Villalba, R.: Spatiotemporal pattern of primary Succession in relation to meso-topographic gradients on recently deglaciated terrains in the Patagonian Andes, Arct. Antarct. Alp. Res., 43, 555-567, 10.1657/1938-4246-43.4.555, 2011.

Gíslason, S. R., Arnórsson, S., and Ármannsson, H.: Chemical weathering of basalt in southwest Iceland: effects of runoff, age of rocks and vegetative/glacial cover, Am. J. Sci., 296, 837-907, 1996.

Greipsson, S., and Davy, A.J.: *Leymus arenarius*. Characteristics and uses of a dune-bulding grass, Icelandic Agric. Sci., 8, 41-50, 1994.

Greipsson, S., and Davy, A. J.: Sand accretion and salinity as constraints on the establishment of *Leymus arenarius* for land reclamation in Iceland, Ann. Bot., 78, 611-618, doi:10.1006/anbo.1996.0168, 1996.

Henriksson, L. E., and Henriksson, E.: Studies in the nitrogen cycle of Surtsey in 1972, Surtsey Res. Prog. Rep., 7, 36-44, 1974.

Henriksson, L. E., and Rodgers, G. A.: Further studies in the nitrogen cycle of Surtsey, 1974-1976, Surtsey Res. Prog. Rep., 8, 30-40, 1978.

Henriksson, E., Henriksson, L. E., Norrman, J. O., and Nyman, P. O.: Biological dinitrogen fixation (acetylene reduction) exhibited by blue-green algae (cyanobacteria) in association with mosses gathered on Surtsey, Iceland, Arct. Alp. Res., 19, 432-436, 1987.

Leblans, N., Roefs, P., Thuys, R., Sigurdsson, B. D., Magnusson, B. and Janssens, I. A.: Effects of seabird nitrogen input on biomass and carbon accumulation during 50 years of primary succession on a young volcanic island, Surtsey, Biogeosciences Discuss., 11, 6269-6302, 2014

Leppälammi-Kujansuu, J., Salemaa, M., Kleja, D., Linder, S., and Helmisaari, H.-S.: Fine root turnover and litter production of Norway spruce in a long-term temperature and nutrient manipulation experiment, Plant Soil, 374, 73-88, 10.1007/s11104-013-1853-3, 2014.

Ludwig, J. A., and Tongway, D. J.: Viewing rangelands as landscape systems, in: Rangeland Desertification, edited by: Arnalds, O., and Archer, S., Kluwer Academic Publishers, Dordrecht, The Netherlands, 39-52, 2000.

Magnússon, B., and Magnússon, S. H.: Vegetation succession on Surtsey during 1990-1998 under the influence of breeding gulls, Surtsey Res. Prog. Rep., 11, 9-20, 2000.

Magnússon, B., Magnússon, S. H., and Fridriksson, S.: Development in plant colonization and succession on Surtsey during 1999-2008, Surtsey Res., 12, 57-76, 2009.

Magnússon, B., Magnússon, S. H., Ólafsson, E. and Sigurdsson, B. D..: Plant colonization, succession and ecosystem development on Surtsey with reference to neighbour islands. Biogeosciences Discuss., 11, 9379-9420, 2014

Marteinsdottir, B., Svavarsdottir, K., and Thorhallsdottir, T. E.: Development of vegetation patterns in early primary succession, J. Veg. Sci., 21, 531-540, doi:10.1111/j.1654-1103.2009.01161.x, 2010.

Marschner, H., Kirkby, E. A., and Cakmak, I.: Effect of mineral nutritional status on shoot-root partitioning of photoassimilates and cycling of mineral nutrients, J. Exp. Bot., 47, 1255-1263, doi:10.1093/jxb/47.Special_Issue.1255, 1996.

Mokany, K., Raison, R. J., and Prokushkin, A. S.: Critical analysis of root : shoot ratios in terrestrial biomes, Glob. Change Biol., 12, 84-96, doi:10.1111/j.1365-2486.2005.001043.x, 2006.

Petersen, A.: Formation of a bird community on a new island, Surtsey, Iceland, Surtsey Res., 12, 133-148, 2009.

Rietkerk, M., Boerlijst, M. C., van Langevelde, F., HilleRisLambers, R., van de Koppel, J., Kumar, L., Prins, H. H. T., and de Roos, A. M.: Self-organization of vegetation in arid ecosystems, Am. Nat., 160, 524-530, 10.1086/342078, 2002.

Schiborra, A., Gierus, M., Wan, H. W., Bai, Y. F., and Taube, F.: Short-term responses of a *Stipa grandis*/*Leymus chinensis* community to frequent defoliation in the semi-arid grasslands of Inner Mongolia, China, Agric. Ecosyst. Environ., 132, 82-90, 2009.

Sigurðsson, A.S., Magnússon, S.H., Thorlacius, J.M., Hjartarson, H., Jónsson, P., Sigurðsson, B.D., Magnússon, B., and Óskarsson, H.: Integrated monitoring at Litla-Skard, Iceland. Project overview 1996-2004, Umhverfisstofnun, Reykjavik, Iceland, 65, 2005.

Sigurdsson, B. D., and Magnusson, B.: Ecosystem respiration, vegetation development and soil nitrogen in relation to breeding density of seagulls on a pristine volcanic island, Surtsey, Iceland, Biogeosciences, 7, 883-891, doi:10.5194/bg-7-883-2010, 2010.

Talbot, S., Talbot, S., and Walker, L.: Post-eruption legacy effects and their implications for long-term recovery of the vegetation on Kasatochi Island, Alaska. Arct. Antarct. Alp. Res., 42, 285-296, doi:10.1657/1938-4246-42.3.285, 2010.

Walker, L. R., and del Moral, R.: Primary succession and ecosystem rehabilitation, Cambridge University Press, UK, 2003.

Whittaker, R. J., Bush, M. B., and Richards, K.: Plant recolonization and vegetation succession on the Krakatau Islands, Indonesia, Ecol. Monogr., 59, 59-123, doi:10.2307/2937282, 1989.

Figure 1. Location of the different-aged *Leymus arenarius* dunes selected on the south east side of Surtsey, Iceland. See Table 1 for further information about different colonies.

Figure 2. Distribution of aboveground (green; in carbon units; above the dotted line) and belowground plant biomass (green; below the dotted line) and soil organic carbon (brown) in a chronosequence of seven *Leymus arenarius* dunes on Surtsey ranging in age between 3 and 37 years. The profiles are all from the top of each dune. Above the diagram are the fractions of total ecosystem C stock found above 30 cm depth and the fraction of ecosystem C stock in soil organic matter (*fSOC*).

Figure 3. Mean shoot biomass (a), root biomass (b) and soil organic matter (c), all expressed in carbon units, in 75 cm deep cores taken in the centre, in the middle and at the expanding edge of three oldest *Leymus* dunes (No 5, 6 and 7). Additional cores were also taken to 75 cm depth ca. 5 m outside the dunes, for comparison. Vertical bars represent SE of n=3-5. Different letters above bars indicate significant differences ($P<0.05$) found with post-ANOVA LSD-tests.

Figure 4. a) Age-related changes in total *Leymus* dune C stocks (kg C dune^{-1}) down to 75 cm soil depth at the dune's edge in shoots, roots and soil organic carbon (SOC). Note the logarithmic scale on the y-axis. b) Mean annual accumulation of soil organic nitrogen (SON) in different aged *Leymus* dunes. c) The ln:ln relationship between total SON stocks in the different aged dunes and total SOC stocks (circles), shoot biomass (triangles) and whole-plant biomass (squares), all expressed in kg C dune^{-1}. The lines indicate significant linear regressions.

Table 1. Age (years) of the *Leymus arenarius* colonies/dunes, dune area (m^2), dune aboveground height (H; cm), mean depth to bedrock under the colony (D, cm), aboveground dune volume (V_A; m^3), dune volume to 30 cm depth (V_{30}; m^3), dune volume to 75 cm depth or less if it had shallower depth limit (V_{75}; m^3), *Leymus* cover (C_L; %), *Honckenia* cover (C_H; %), shoot density (S; no m^{-2}), flowering stems (F; no m^{-2}), aboveground biomass carbon (B_a; g C m^{-2}), root biomass carbon (B_r; g C m^{-2}), root/shoot ratio (R/S), mean soil bulk density (BD, g cm^{-3}), soil organic carbon (SOC; g C m^{-2}) and soil organic nitrogen (SON; g C m^{-2}) and the C/N ratio (C/N) of the dunes that were studied in Surtsey. The outcome of a linear or exponential regression analysis between age (x=years) and each variable; P = ANOVA significance of the regression (ns = >0.05; * = ≤0.05; ** = <0.01; *** =<0.001), R^2 = coefficient of determination, a = intercept of linear or exponential function, b or e = slope or exponent of linear or exponential function, respectively, depending on which function had higher R^2.

	Dunes							Plants							Soil			
No	Age	Area	H	D	V_A	V_{30}	V_{75}	C_L	C_H	S	F	B_a	B_r	R/S	BD	SOC	SON	C/N
1	3	0.12	1	25	0.00	0.03	0.03	7	1	28	0	3.9	118.5	30.4	0.82	26.8	2.8	12.2
2	5	0.07	1	54	0.01	0.02	0.05	8	2	28	0	2.1	264.5	24.2	1.29	48.9	3.8	13.8
3	9	2.0	2	75*	0.01	0.6	1.5	30	5	119	0.50	36.4	462.4	12.7	1.24	98.7	6.6	16.2
4	13	2.8	12	32	0.12	0.9	1.0	30	2	83	0.36	37.5	234.7	6.3	1.32	55.5	4.3	13.3
5	17	11.6	27	75*	1.69	5.2	10.4	24	1	55	0.43	36.3	401.7	16.2	1.20	133.7	10.5	14.2
6	28	211	45	70	39.0	102.4	184.2	18	5	31	0.13	33.1	531.7	23.6	1.09	333.6	20.4	12.0
7	37	153.9	124	71	64.6	110.6	176.1	22	14	46	0.11	43.9	483.1	20.5	1.16	470.5	41.6	13.9
P		*	***	ns	***	**	*	ns	**	ns	ns	ns	*	ns	ns	***	***	ns
R^2		0.67	0.99	0.29	0.92	0.79	0.74	0.10	0.65	0.00	0.00	0.11	0.56	0.00	0.01	0.96	0.99	0.00
a		11.89	2.34	-	1.26	4.72	9.13	-	0.69	-	-	-	210.4	-	-	44.1	2.48	-
b		-	-	-	-	-	-	-	-	-	-	-	9.14	-	-	-	-	-
e		0.075	0.107	-	0.108	0.088	0.084	-	0.080	-	-	-	-	-	-	0.065	0.076	-

* No bedrock reached at maximum depth of 75 cm

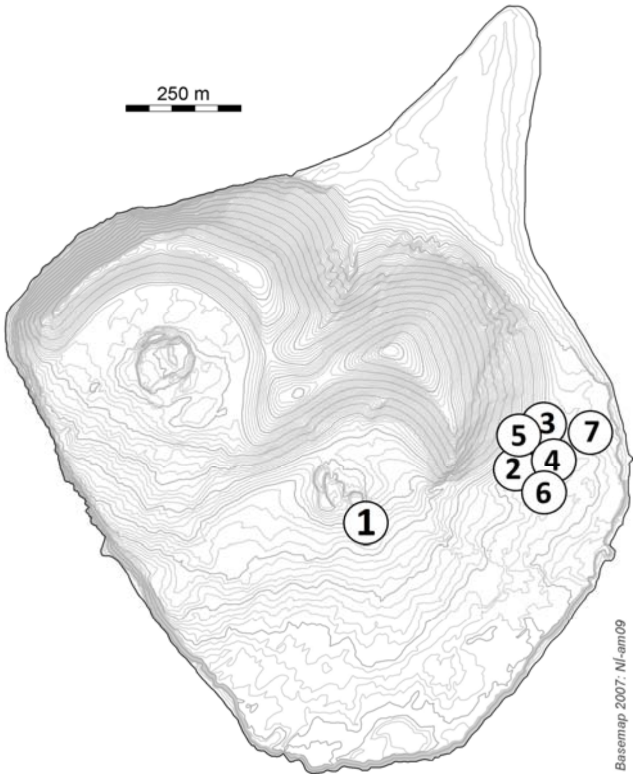

Figure 1.

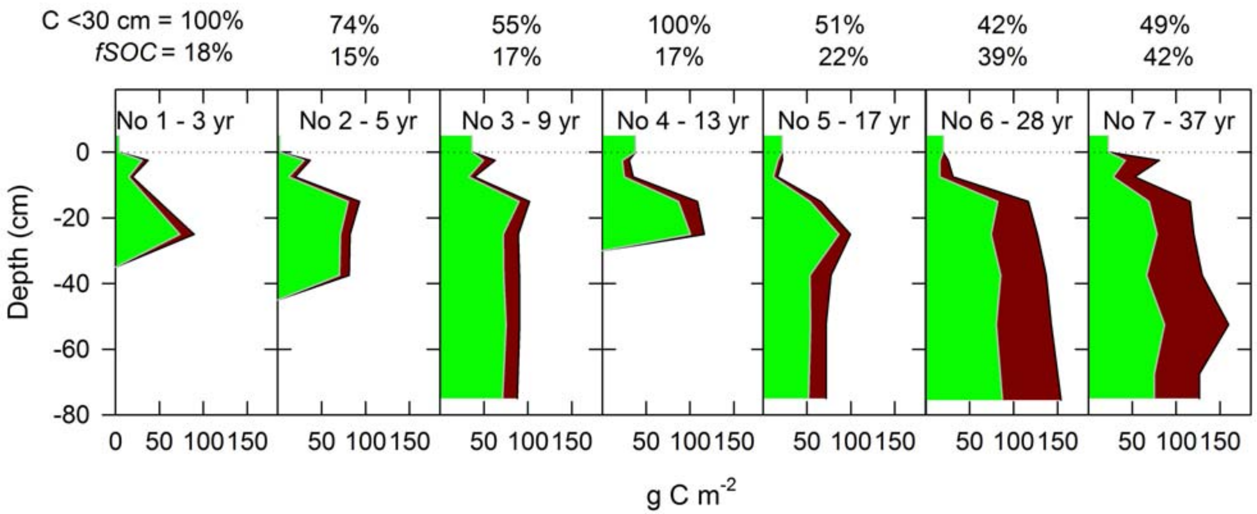
C <30 cm = 100%
fSOC = 18%
74%
15%
55%
17%
100%
17%
51%
22%
42%
39%
49%
42%
No 1 - 3 yr
No 2 - 5 yr
No 3 - 9 yr
No 4 - 13 yr
No 5 - 17 yr
No 6 - 28 yr
No 7 - 37 yr
Depth (cm)
0
-20
-40
-60
-80
0 50 100 150
g C m-2

Figure 2.

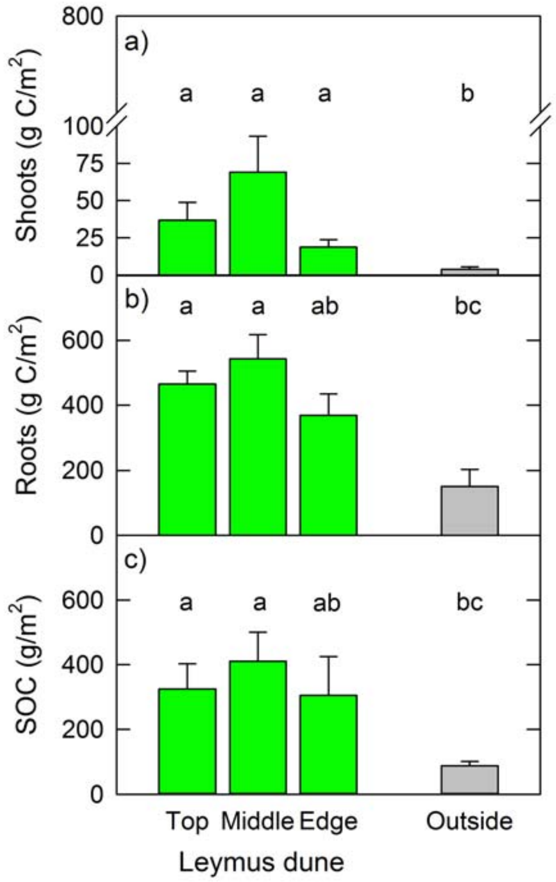
a)
b)
c)
Shoots (g C/m^2)
Roots (g C/m^2)
SOC (g/m^2)
800
100
75
50
25
0
600
400
200
0
600
400
200
0
a
a
a
b
a
a
ab
bc
a
a
ab
bc
Top
Middle
Edge
Outside
Leymus dune

Figure 3

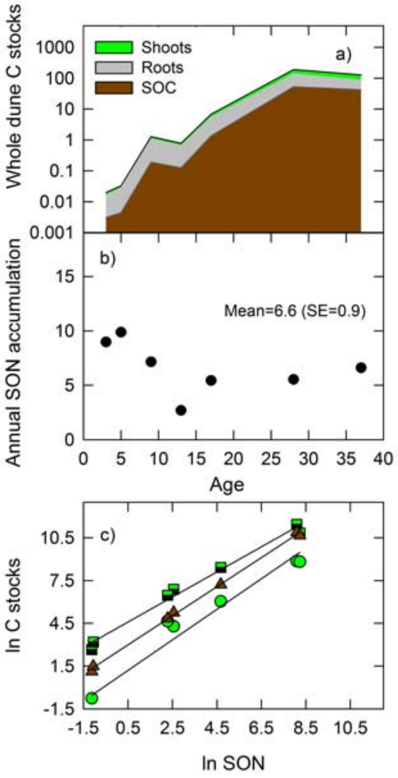
Whole dune C stocks
1000
100
10
1
0.1
0.01
0.001
Shoots
Roots
SOC
a)
b)
Annual SON accumulation
15
10
5
0
Mean=6.6 (SE=0.9)
0
5
10
15
20
25
30
35
40
Age
c)
ln C stocks
10.5
7.5
4.5
1.5
-1.5
-1.5
0.5
2.5
4.5
6.5
8.5
10.5
ln SON

Figure 4