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4 **TITLE PAGE**
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9 Accumulation of nitrogen and organic matter during primary succession of *Leymus*
10 *arenarius* dunes on the volcanic island Surtsey, Iceland
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1 **Accumulation of nitrogen and organic matter during
2 primary succession of *Leymus arenarius* dunes on the
3 volcanic island Surtsey, Iceland**

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7

8 **Abstract**

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

25 **1 Introduction**

26 Primary succession is the process of ecosystem development of barren surfaces with no
27 previous developed soil or plant cover, such as new lava flows or areas left in front of
28 retreating glaciers. Multiple environmental factors and ecosystem properties can act as
29 thresholds in primary succession of such areas, not least a lack of nutrients, water and

1 developed soil (del Moral and Grishin, 1999). Therefore the earliest colonists on volcanic
2 tephra fields are often confined to specific microsites that offer some physical protection and
3 enhanced nutrient resources from weathering, erosion or other nutrient inputs (Walker and del
4 Moral, 2003). As some vegetation cover establishes on the pristine surfaces, organic matter
5 (OM) and soil organic nitrogen (SON) start to accumulate, which again improves the growing
6 conditions for later successional species (Whittaker et al., 1989). Such ‘autogenic’ (internal)
7 factors are expected to determine the course of succession by traditional succession theory
8 (Walker and del Moral, 2003), but ‘allogenic’ (external) or stochastic factors (such as distance
9 to potential colonists) also play an important role in some cases (del Moral et al., 2009;
10 Marteinsdottir et al., 2010).

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

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

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

1 vegetation on the development of spatial variation in soil properties in the early stages of
2 primary succession.

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

9

10 **2 Material and methods**

11 **2.1 Site description**

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

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

1 **2.2 Selection of a *Leymus* chronosequence**

2 The close monitoring of the establishment of all vegetation on Surtsey enabled the location of
3 *Leymus* dunes of known age. Seven dunes of different age were selected on the southeast side
4 of the island (Fig. 1). The two oldest dunes included the first successful *Leymus* colonisation
5 and a dune from the first seeding episode in 1983 (Fridriksson, 1992), but younger dunes
6 were all close to permanent study plots (no 13, 14, 15 and 21; Magnusson and Magnusson,
7 2000) and their establishment could be dated from annual photographs of them. The age of
8 the dunes at the time of sampling was 3, 5, 9, 13, 17, 28 and 37 years.

9 [FIG. 1 HERE]

10 **2.3 Sampling protocol**

11 The dunes were mapped in July 2010 and 2011 by crossing two laterally levelled strings over
12 the highest midpoint of each dune and measuring distance to the soil surface and soil depth (to
13 75 cm) at 50 cm intervals along each string until the dune's edge was reached. Flowering
14 stems of *Leymus* were counted on the whole dune. Three 30x30 cm quadrats were randomly
15 placed on the top of each dune, except on the four youngest ones where only one quadrat
16 could be fitted because of their smaller size. Additionally quadrats were placed in the middle
17 slope and at the expanding edge of the three oldest dunes, as well as 5 m outside them for
18 comparison. In each quadrat, surface cover of all vascular plant species was recorded and the
19 number of *Leymus* shoots counted. Furthermore, all aboveground biomass was harvested by
20 cutting and subsequently, incremental soil samples of known volume taken within the
21 harvested quadrat. Continuous soil cores of known volume were taken to 5, 10, 20, 30, 45,
22 60, 75 cm depth, if bedrock was not reached earlier. All samples were sieved *in situ* through 1
23 cm sieve and visible roots were separated and stored.

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

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

4 **2.4 Calculations and data analysis**

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

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

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

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

28

1 **3 Results**

2 **3.1 Dune size and volume**

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

10 [FIG 2 HERE]

11 **3.2 Soil and plant parameters per unit area**

12 Shoot density and surface cover of *Leymus* within each dune did not show a significant
13 increase with age (Table 1); on average each dune had 56 shoots/m² (SE ±5) and 20% (SE
14 ±1%) *Leymus* surface cover. The first flowering occurred in the 9 year old dune, but density
15 of flowering stems was not significantly related to dune age (Table 1). The *Honckenia* cover
16 increased exponentially with dune age and reached 14% on the oldest dune (Table 1), but no
17 other plant species were found on the dunes. Total aboveground biomass did not change
18 significantly with age, when expressed per unit area, but root biomass increased significantly
19 and linearly with age (Table 1). The root biomass per unit area increased on average by 9.1
20 g/m² annually. The belowground root biomass in the *Leymus* dunes far exceeded their
21 aboveground biomass (Fig. 2). The average R/S ratio was 19.1 (SE ±1.2), and did not change
22 significantly with dune age, even if root biomass increased slightly (Table 1; Fig. 2).

23 [TABLE 1 – BETWEEN PAGES]

24 The mean bulk density and C/N ratio in the top 75 cm of soil, or down to the bedrock, in each
25 dune were on average 1.16 g/cm³ (SE ±0.02) and 13.7 (±0.2) and did not change significantly
26 with age (Table 1). Mean SOC and SON concentrations did increase exponentially with age
27 and were 17.6 and 14.9 times larger in the 37 year old than in the 3 year old dune,
28 respectively (Table 1). The actual concentrations were, however, always low, or on average
29 0.049% and 0.0037% for SOC and SON, respectively.

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

5
$$fSOC = 8.4 + 0.9139 \times Age , \quad (1)$$

6 where age is in years. This function shows the first steps of soil development. It was also
7 noteworthy that both root biomass and SOC stocks were relatively stable with depth below
8 the ca. 10 cm surface layer, (Fig. 2) and where bedrock was not found at shallower depths.
9 The maximum sampling depth was 75 cm, but Fig. 2 indicates that the *Leymus* roots went
10 deeper if soil depth allowed. Above- and belowground C stock above 30 cm soil depth was
11 67% (SE $\pm 3.5\%$) of the total C stock down to 75 cm and this proportion did not change
12 significantly with age of the dunes ($P=0.11$).

13 **3.3 Spatial variability within the dunes**

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

20 [FIG 3 HERE]

21 **3.4 Variables expressed per total dune area or volume**

22 The exponential increase in shoot biomass and root and SOC stocks with age, associated with
23 larger surface area and total soil volume were even more apparent at a whole-dune scale (Fig.
24 4a). The annual SON accumulation rate was on average $6.6 \text{ kg N ha}^{-1} \text{ year}^{-1}$ (SE ± 0.9) and
25 did not show significant age-dependent trend (Fig. 4b). A very strong linear relationships (R^2
26 > 0.94 ; $P<0.001$) appeared between the amount of SON and the total shoot biomass (C_s), total
27 plant biomass (C_p) and SOC stocks, when expressed at a ln:ln scale (Fig 4c), showing that the
28 total ecosystem OM increased exponentially with time as more N became available. The
29 linear ln:ln SON:C functions were:

1 $\ln C_S = 0.6678 + 1.0705 \times \ln SON , \quad (2)$

2 $\ln C_P = 4.1541 + 0.8787 \times \ln SON , \quad (3)$

3 $\ln SOC = 2.4846 + 1.0190 \times \ln SON . \quad (4)$

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

8 $C_{tot} = -22,330 + 6039 \times N_{tot} , \quad (5)$

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

12 [FIG 4 HERE]

13 **4 Discussion**

14 **4.1 Dune size development**

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

23 As the dunes grew in size with age their total element stocks calculated to the same soil depth
24 outside the dunes increased. The observed increase in average element concentrations (%
25 DM) from the youngest to the oldest dune was 5.6 and 6.2 fold for SON and SOC,
26 respectively, which clearly indicated that it was not simply an increasing size of the dunes
27 which was causing the accumulation.

28

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

1 colonising mosses in other more sheltered areas of the island, was found to be substantial
2 (Henriksson et al., 1987). No symbiotic N-fixing was found in *Honckenia* growing in the study
3 area in the 70s (Henriksson et al., 1974) and only low level of (free-living) N fixation was
4 detected in soils from *Leymus* dunes (Henriksson and Henriksson, 1978). Symbiotic N-
5 fixation has, however, been found in coastal dunes of the closely related *L. mollis* in Oregon,
6 USA (Dalton et al., 2004) and further investigation if symbiotic N-fixing occurs in the
7 *Leymus* in Surtsey is needed.

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

20 **4.3 *Leymus* growth**

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

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

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

6 The root-shoot ratio (R/S ratio) in the centre of the dunes did not show a significant trend with
7 time. The R/S ratio (average 19.1) was relatively high compared to vascular plants of tundra,
8 grasslands and cold deserts that have on the average R/S ratios of 4-5 (Mokany et al, 2006).
9 Our calculation of R/S ratio did not, however, take into consideration the *Leymus* roots that
10 extended outside the dunes or below 75 cm depth. Leblans et al. (2014) estimated R/S ratio of
11 45 for the general area in between dunes. The high R/S ratio of *Leymus* is probably the key
12 reason for its ability to colonise and survive in the nutrient poor and unstable tephra sands of
13 Surtsey. This is also in good accordance with the observation of Chapin (1993), who claimed
14 that adaptations for large nutrient acquisition and retention were generally key factors for the
15 success of early colonisers in primary succession.

16 **4.4 OM accumulation**

17 Carbon fixation (net photosynthesis) by the early colonisers, organic matter production, litter
18 fall and the microbial breakdown of litter and humus drive the accumulation of SOM, without
19 which soil will not develop during primary succession (del Moral and Grishin, 1999; Walker
20 and del Moral, 2003). After the first 5 years, aboveground biomass per unit dune area
21 remained more or less constant and the standing aboveground biomass was similar to that
22 reported in a 39 year chronosequence on previously eroded revegetation areas in Iceland
23 seeded by *Leymus arenarius* and initially fertilized with about 100 kg N ha⁻¹ (Aradóttir et al.,
24 2000). Root biomass and R/S ratio were, however, much higher in the present study than were
25 reported for the fertilized *Leymus* treatments. This was partly because in Aradóttir et al.
26 (2000) the sampling depth was limited to 30 cm, but could also be partly caused by difference
27 in fertility as N availability is known to strongly affect R/S ratios in plants (Marschner et al,
28 1996). SOC stocks of the dunes on Surtsey increased exponentially with age and the *fSOC*
29 ratio (ratio of SOC to total ecosystem C stock) increased linearly (Eq. 1). Still, after 37 years
30 the SOC stock in the top 30 cm was only ca. 15% of total living biomass (including roots
31 down to 30 cm), but ca. seven times higher than aboveground biomass per unit dune area. In
32 the Aradóttir et al. (2000) chronosequence on the mainland, the SOC ratio to aboveground

1 biomass was much higher after 39 years (ca. 22 times higher). The reasons for this could be
2 much faster root turnover in *Leymus* on the mainland, which is a known response to
3 fertilization of other ecosystems (Leppälämmi-Kujansuu et al., 2014). It can, however, not be
4 ruled out that some SOC remained since before the erosion took place in the mainland
5 chronosequences, which would also translate into similar differences.

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

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

21 **4.5 Conclusion**

22 The history of annually monitoring colonisation, growth and mortality of individual plants on
23 Surtsey since it emergence in 1963 offered a special opportunity to use a chronosequence
24 approach to study how autogenic (internal) factors develop after colonisation of a keystone
25 species in the primary succession. *Leymus arenarius*, with its high R/S ratios, is probably a
26 key player in N retention and soil development on the tephra sands of the island. The high
27 correlation between SON and OM stocks indicated that the rate of primary succession was
28 more strongly controlled by the amount of available N than time since colonisation per se.
29 The *Leymus* dunes, where N has been accumulated, will therefore probably act as hot-spots
30 for further primary succession of flora and fauna within this area of Surtsey; at least if new

1 sources of N will not appear, such as establishment of new seabird colonies or introduction of
2 new symbiotic N-fixing plant species.

3

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11

12 **References**

- 13 Aradóttir, Á. L., Svavarsdóttir, K., Jónsson, Þ. H., and Guðbergsson, G.: Carbon
14 accumulation in vegetation and soils by reclamation of degraded areas, Icelandic Agric. Sci.,
15 13, 99-113, 2000.
- 16 Chapin III, F. S.: Physiological controls over plant establishment in primary succession, in:
17 Primary Succession on Land, edited by: Miles, J., and Walton, D. W. H., Special publications
18 of the British Ecological Society, 12, Blackwell Scientific Publications, London, UK, 1993.
- 19 Cutler, N.: Vegetation-environment interactions in a sub-arctic primary succession, Polar
20 Biol., 34, 693-706, 10.1007/s00300-010-0925-6, 2011.
- 21 Cutler, N. A., Belyea, L. R., and Dugmore, A. J.: The spatiotemporal dynamics of a primary
22 succession, J. Ecol., 96, 231-246, 10.1111/j.1365-2745.2007.01344.x, 2008.
- 23 Dalton, D. A., Kramer, S., Azios, N., Fusaro, S., Cahill, E., and Kennedy, C.: Endophytic
24 nitrogen fixation in dune grasses (*Ammophila arenaria* and *Elymus mollis*) from Oregon,
25 FEMS Microbiol. Ecol., 49, 469-479, doi:10.1016/j.femsec.2004.04.010, 2004.
- 26 del Moral, R., and Grishin, S. Y.: Volcanic disturbances and ecosystem recovery, in:
27 Ecosystems of Disturbed Ground, edited by: Walker, L. R., Elsevier Science B.V.,
28 Amsterdam, The Netherlands, 1999.

- 1 del Moral, R. and Magnússon, B.: Surtsey and Mount St. Helens: a comparison of early
2 succession rates. *Biogeosciences*, 11, 2099-2111, 2014, doi:10.5194/bg-11-2099-2014.
- 3 del Moral, R., and Wood, D. M.: Early primary succession on the volcano Mount St. Helens,
4 *J. Veg. Sci.*, 4, 223-234, 10.2307/3236108, 1993.
- 5 del Moral, R., Sandler, J. E., and Muerdter, C. P.: Spatial factors affecting primary succession
6 on the Muddy River Lahar, Mount St. Helens, Washington, *Plant Ecol.*, 202, 177-190,
7 10.1007/s11258-008-9506-y, 2009.
- 8 Ehrenfeld, J. G., Ravit, B., and Elgersma, K.: Feedback in the plant-soil system, in: Annual
9 Review of Environment and Resources, *Ann. Rev. Env. Resour.*, 75-115, 2005.
- 10 Fridriksson, S.: The pioneer species of vascular plants in Surtsey, *Cakile edentula*, Surtsey
11 Res. Prog. Rep., 2, 63-65, 1966.
- 12 Fridriksson, S.: Vascular plants on Surtsey 1981-1990, Surtsey Res. Prog. Rep., 10, 17-30,
13 1992.
- 14 Garibotti, I. A., Pissolito, C. I., and Villalba, R.: Spatiotemporal pattern of primary
15 Succession in relation to meso-topographic gradients on recently deglaciated terrains in the
16 Patagonian Andes, *Arct. Antarct. Alp. Res.*, 43, 555-567, 10.1657/1938-4246-43.4.555, 2011.
- 17 Gíslason, S. R., Arnórsson, S., and Ármannsson, H.: Chemical weathering of basalt in
18 southwest Iceland: effects of runoff, age of rocks and vegetative/glacial cover, *Am. J. Sci.*,
19 296, 837-907, 1996.
- 20 Greipsson, S., and Davy, A.J.: *Leymus arenarius*. Characteristics and uses of a dune-bulding
21 grass, *Icelandic Agric. Sci.*, 8, 41-50, 1994.
- 22 Greipsson, S., and Davy, A. J.: Sand accretion and salinity as constraints on the establishment
23 of *Leymus arenarius* for land reclamation in Iceland, *Ann. Bot.*, 78, 611-618,
24 doi:10.1006/anbo.1996.0168, 1996.
- 25 Henriksson, L. E., and Henriksson, E.: Studies in the nitrogen cycle of Surtsey in 1972,
26 Surtsey Res. Prog. Rep., 7, 36-44, 1974.
- 27 Henriksson, L. E., and Rodgers, G. A.: Further studies in the nitrogen cycle of Surtsey, 1974-
28 1976, Surtsey Res. Prog. Rep., 8, 30-40, 1978.

- 1 Henriksson, E., Henriksson, L. E., Norrman, J. O., and Nyman, P. O.: Biological dinitrogen
2 fixation (acetylene reduction) exhibited by blue-green algae (cyanobacteria) in association
3 with mosses gathered on Surtsey, Iceland, *Arct. Alp. Res.*, 19, 432-436, 1987.
- 4 Leblans, N., Roefs, P., Thuys, R., Sigurdsson, B. D., Magnusson, B. and Janssens, I. A.:
5 Effects of seabird nitrogen input on biomass and carbon accumulation during 50 years of
6 primary succession on a young volcanic island, Surtsey, *Biogeosciences Discuss.*, 11, 6269-
7 6302, 2014
- 8 Leppälammi-Kujansuu, J., Salemaa, M., Kleja, D., Linder, S., and Helmisaari, H.-S.: Fine
9 root turnover and litter production of Norway spruce in a long-term temperature and nutrient
10 manipulation experiment, *Plant Soil*, 374, 73-88, 10.1007/s11104-013-1853-3, 2014.
- 11 Ludwig, J. A., and Tongway, D. J.: Viewing rangelands as landscape systems, in: *Rangeland*
12 *Desertification*, edited by: Arnalds, O., and Archer, S., Kluwer Academic Publishers,
13 Dordrecht, The Netherlands, 39-52, 2000.
- 14 Magnússon, B., and Magnússon, S. H.: Vegetation succession on Surtsey during 1990-1998
15 under the influence of breeding gulls, *Surtsey Res. Prog. Rep.*, 11, 9-20, 2000.
- 16 Magnússon, B., Magnússon, S. H., and Fridriksson, S.: Development in plant colonization
17 and succession on Surtsey during 1999-2008, *Surtsey Res.*, 12, 57-76, 2009.
- 18 Magnússon, B., Magnússon, S. H., Ólafsson, E. and Sigurdsson, B. D.: Plant colonization,
19 succession and ecosystem development on Surtsey with reference to neighbour islands.
20 *Biogeosciences Discuss.*, 11, 9379-9420, 2014
- 21 Marteinsdottir, B., Svavarsdottir, K., and Thorhallsdottir, T. E.: Development of vegetation
22 patterns in early primary succession, *J. Veg. Sci.*, 21, 531-540, doi:10.1111/j.1654-
23 1103.2009.01161.x, 2010.
- 24 Marschner, H., Kirkby, E. A., and Cakmak, I.: Effect of mineral nutritional status on shoot-
25 root partitioning of photoassimilates and cycling of mineral nutrients, *J. Exp. Bot.*, 47, 1255-
26 1263, doi:10.1093/jxb/47.Special_Issue.1255, 1996.
- 27 Mokany, K., Raison, R. J., and Prokushkin, A. S.: Critical analysis of root : shoot ratios in
28 terrestrial biomes, *Glob. Change Biol.*, 12, 84-96, doi:10.1111/j.1365-2486.2005.001043.x,
29 2006.

- 1 Petersen, A.: Formation of a bird community on a new island, Surtsey, Iceland, *Surtsey Res.*,
2 12, 133-148, 2009.
- 3 Rietkerk, M., Boerlijst, M. C., van Langevelde, F., HilleRisLambers, R., van de Koppel, J.,
4 Kumar, L., Prins, H. H. T., and de Roos, A. M.: Self-organization of vegetation in arid
5 ecosystems, *Am. Nat.*, 160, 524-530, 10.1086/342078, 2002.
- 6 Schiborra, A., Gierus, M., Wan, H. W., Bai, Y. F., and Taube, F.: Short-term responses of a
7 *Stipa grandis/Leymus chinensis* community to frequent defoliation in the semi-arid grasslands
8 of Inner Mongolia, China, *Agric. Ecosyst. Environ.*, 132, 82-90, 2009.
- 9 Sigurðsson, A.S., Magnússon, S.H., Thorlacius, J.M., Hjartarson, H., Jónsson, P., Sigurðsson,
10 B.D., Magnússon, B., and Óskarsson, H.: Integrated monitoring at Litla-Skard, Iceland.
11 Project overview 1996-2004, *Umhverfisstofnun, Reykjavik, Iceland*, 65, 2005.
- 12 Sigurdsson, B. D., and Magnusson, B.: Ecosystem respiration, vegetation development and
13 soil nitrogen in relation to breeding density of seagulls on a pristine volcanic island, Surtsey,
14 Iceland, *Biogeosciences*, 7, 883-891, doi:10.5194/bg-7-883-2010, 2010.
- 15 Talbot, S., Talbot, S., and Walker, L.: Post-eruption legacy effects and their implications for
16 long-term recovery of the vegetation on Kasatochi Island, Alaska. *Arct. Antarct. Alp. Res.*,
17 42, 285-296, doi:10.1657/1938-4246-42.3.285, 2010.
- 18 Walker, L. R., and del Moral, R.: Primary succession and ecosystem rehabilitation,
19 Cambridge University Press, UK, 2003.
- 20 Whittaker, R. J., Bush, M. B., and Richards, K.: Plant recolonization and vegetation
21 succession on the Krakatau Islands, Indonesia, *Ecol. Monogr.*, 59, 59-123,
22 doi:10.2307/2937282, 1989.
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1 Figure 1. Location of the different-aged *Leymus arenarius* dunes selected on the south east
2 side of Surtsey, Iceland. See Table 1 for further information about different colonies.

3 Figure 2. Distribution of aboveground (green; in carbon units; above the dotted line) and
4 belowground plant biomass (green; below the dotted line) and soil organic carbon (brown) in
5 a chronosequence of seven *Leymus arenarius* dunes on Surtsey ranging in age between 3 and
6 37 years. The profiles are all from the top of each dune. Above the diagram are the fractions
7 of total ecosystem C stock found above 30 cm depth and the fraction of ecosystem C stock in
8 soil organic matter (*fSOC*).

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

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

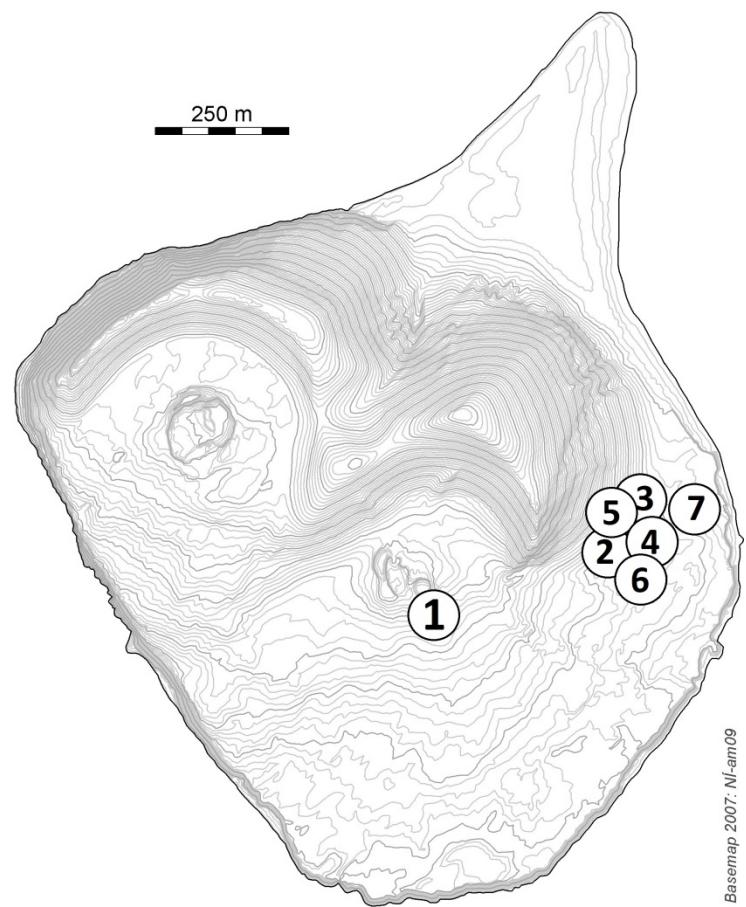
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6 Table 1. Age (years) of the *Leymus arenarius* colonies/dunes, dune area (m^2), dune aboveground height (H; cm), mean depth to bedrock under
7 the colony (D, cm), aboveground dune volume (V_A ; m^3), dune volume to 30 cm depth (V_{30} ; m^3), dune volume to 75 cm depth or less if it had
8 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}),
9 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
10 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.
11 The outcome of a linear or exponential regression analysis between age (x=years) and each variable; P = ANOVA significance of the
12 regression (ns = >0.05 ; * = ≤ 0.05 ; ** = <0.01 ; *** = <0.001), R^2 = coefficient of determination, a = intercept of linear or exponential function,
13 b or e = slope or exponent of linear or exponential function, respectively, depending on which function had higher R^2 .
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No	Dunes							Plants							Soil			
	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	-

1 * No bedrock reached at maximum depth of 75 cm

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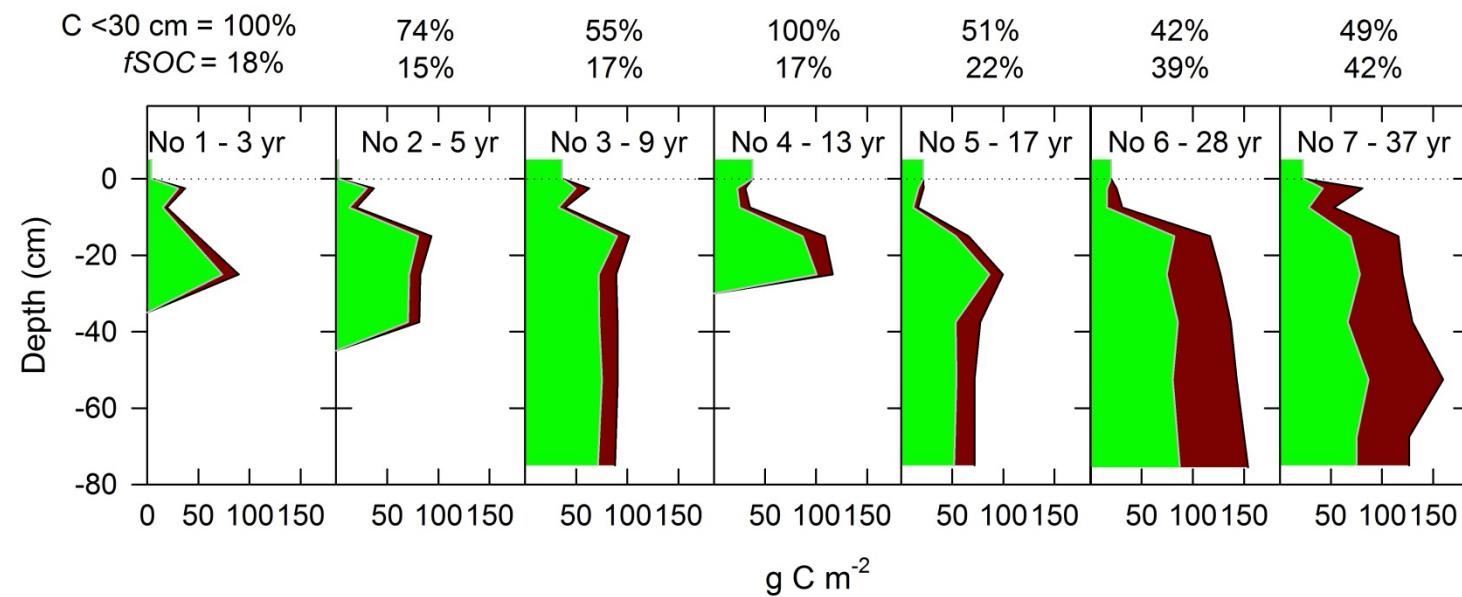


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3 Figure 1.

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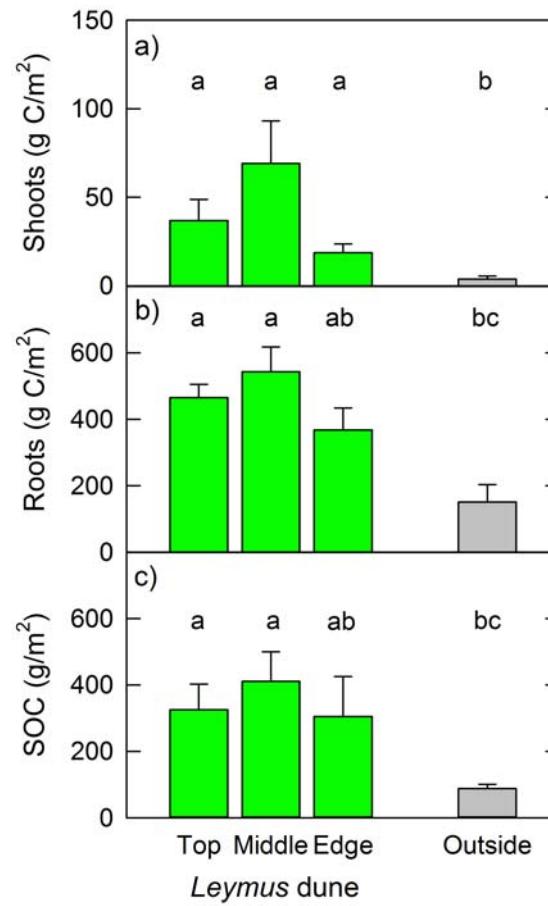
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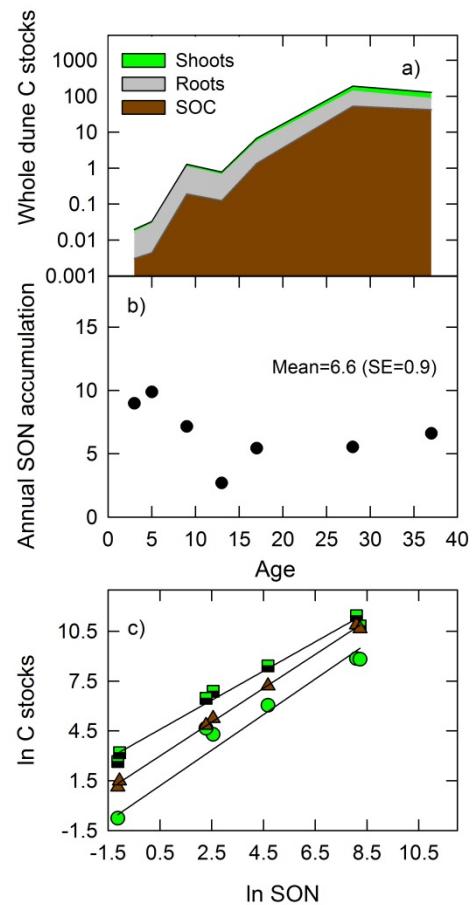
3 Figure 2.

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2 Figure 3



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2 Figure 4