Ecosystem carbon fluxes of *Leymus arenarius* and *Honckenya peploides* on Surtsey in relation to water availability: a pilot study

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ABSTRACT

Large parts of Surtsey are covered by sparse plant communities, with *Honckenya peploides* and *Leymus arenarius* as the key species. The objective of the present pilot study was to investigate ecosystem fluxes of moist and dry areas covered by those two species. Light saturated gross photosynthesis (GPP), expressed on soil surface area basis, was 45% higher in *L. arenarius* at dry sites, but similar for both species at moist sites. This may indicate that *L. arenarius* is better adapted to habitats with low water availability. When carbon fluxes were compared at moist and dry conditions across both species, it was clear that both ecosystem respiration and GPP were much higher at the moist site. This may indicate that periodic water stress due to low water holding capacity of the young volcanic ash may be an important limiting factor for biological activity on Surtsey, in addition to the low nutrient availability.

INTRODUCTION

Surtsey is a volcanic island that emerged from the North Atlantic Ocean in 1963. Vascular plants have dominated the primary succession on the island, and their colonisation and succession has been intensively studied (*e.g.* Fridriksson 1966, Magnússon 1992, Magnússon & Magnússon 2000, Magnússon, Magnússon & Fridriksson 2009).

The first twenty years after Surtsey appeared were characterised by colonisation and succession of costal plants, with *Honckenya peploides* and *Leymus arenarius* as key species, forming sparse vegetation cover on sandy areas of the island (Fridriksson 1992). During the past 15 years swards of grasses and forbs have formed on the southern part of the island, after colonisation by seagulls (*Larus* sp.). The gulls have carried seeds of new plant species and fertilized the sterile soil with their droppings and food brought to the nest sites from the sea. Vegetation development on other parts of the island have on the other hand remained slow by comparison. There the *H. peploides* and *L. arenarius*

are the key plant species in most cases, along with e.g. *Mertensia maritime* and *Cardaminopsis petraea* (Magnússon & Magnússon 2000, Magnússon, Magnússon & Fridriksson 2009).

Biological activity of terrestrial ecosystems can be indirectly measured as CO₂ being taken up and emitted from the soil surface (Larcher 2003). As soil organic matter is decomposed CO₉ is released. Hence, CO₉ efflux from the soil surface may partly indicate the decomposition rate and activity of soil organisms (bacteria, fungi and soil fauna). The second major contributor of CO₂ to the atmosphere from the soil surface is the metabolism of living plant roots. Together these two fluxes are termed soil respiration (R_s) . When above ground parts of living plants are included in respiration measurements, the process is often termed ecosystem respiration (R_{a}) . The rate of R_{a} depends therefore on plant growth and maintenance respiration and soil decomposition activity. Gross photosynthesis (GPP) is only a measure of plant activity and represents the first step in their growth process (Larcher 2003).

Ecosystem function has not been studied as much on Surtsey as the ecosystem structure. In the early years Henriksson & Rodgers (1978) and Henriksson & Henriksson (1982) studied terrestrial nitrogen cycle. Frederiksen et al. (2000) studied soil development on Surtsey. Klamer et al. (2000) also studied the amount of microbial activity in unvegetated and vegetated soil. Magnússon (1992) studied how soil respiration changed with increasing cover of L. arenarius and H. peploides on the island. He found that respiration rates were related to differences in vegetation cover and root biomass. Since these early measurements, no gas exchange measurements have been made in situ on Surtsey until the present study. The objective of the study was to compare patches of H. peploides and L. arenarius found at dry and moist conditions to test if soil humidity was important for ecosystem fluxes on Surtsey.

MATERIAL AND METHODS

Surtsey is the southernmost of the Vestmannaeyjar islands. The climate is mild and oceanic, with annual mean temperature of 5.0 °C and mean annual precipitation of 1576 mm during 1965 – 2005, as recorded on the Heimaey weather station 15 km to the northeast of Surtsey (Icelandic Meterological Office).

To test if soil humidity was important for ecosystem fluxes on Surtsey, measurements were made on 19 July 2006 on patches with 100% surface cover of *L. arenarius* and *H. peploides* on two permanent plots, where the volcanic ash profile was freely drained and discharge was not likely to be substantial (Fig. 1 – plots 3 and 17; Magnússon & Magnússon 2000). For comparison, patches with

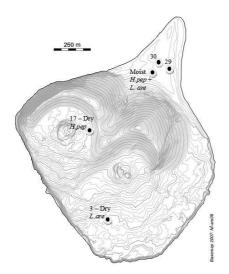


Figure 1. Location of the dryer permanent vegetation plots no. 3 and 17 covered by *Leymus arenarius* and *Honckenya peploides*, respectively, and the place at the low ness where the two species grew at more moist conditions. Also shown are the permanent plots no. 29 and 30.

Table 1. Soil acidity (pH, in water), total carbon (SOC,%), total nitrogen (N, %) and the soil C/N ratio of permanent survey plots on Surtsey used in the present study. Data from Magnússon, Magnússon & Fridriksson (2009).

Plots No	Soil depth	рН	Ν	SOC	C/N ratio
3	> 35	7.3	0.051	0.56	10.8
17	> 35	8.5	0.005	0.03	5.5
29	> 35	8.9	0.001	0.01	8.3
30	> 35	9.4	0.003	0.03	8.7

100% surface cover of the same two species were measured at the edge of the lowland ness, just below a relatively large discharge area formed by the two craters of Surtsey (ca. 80-130 m SW of plots 30 and 29; Fig. 1). There the volcanic ash profile was humid and ground water was found at ca. 30 cm depth. Both species showed clear signs of more favorable growing conditions at the more humid site, as they were darker green in color and had denser foliage. The area at the ness had, however, less soil nitrogen than the two dryer sites (Table 1). The dryer *L. arenarius* plot (no 3) was found within a seagull colony that had greatly increased the soil fertility, while the dry H. peploides plot (no 17) was not much affected by the seagulls (Magnússon et al. 2009).

EMG-4 infrared gas analyser and a CPY-2 transparent cuvette (PP Systems) were used to measure the carbon fluxes. First, the transparent chamber was fitted to the surface of the dense patches and net ecosystem exchange (NEE) was measured. Then, the chamber was covered with black cloth and the measured was repeated at the same spot in total darkness, yielding ecosystem respiration (R_e). Gross photosynthesis (GPP) was then estimated as:

$$GPP = NEE + R_{e} \tag{1}$$

All carbon flux measurements took place during daytime hours in high solar radiation and 3–5 measurements were made for each vegetation type. The average solar radiation during the measurements was ca. 1400 μ mol m⁻² s⁻¹ PAR and the average soil temperature at 10 cm depth was 16.5 °C.

RESULTS

When carbon fluxes were compared at moist and dry conditions across both species, it was clear that light saturated carbon uptake (GPP) was substantially higher under the more moist conditions (+115%; Fig. 2). The relative change in R_e , which indicates respiration and decomposition activity, was even stronger at the moist site (+665%). The

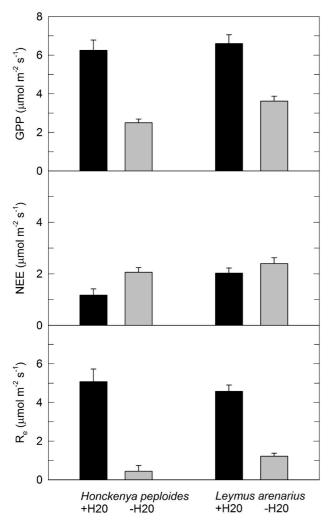


Figure 2. Gross photosynthesis (GPP), net ecosystem exchange (NEE) and ecosystem respiration (R_e) in a moist area (+H20) and dry area (-H20) on Surtsey in July 2006. Means and SE of 3–5 measurements per site.

large increase in R_e led to 28% lower NEE under the moist conditions. The net effect was therefore that 18% more carbon was accumulating in the dry patches when the measurements took place than in the moist ones, even though their uptake rate was much lower.

The GPP was similar for the two species when they were growing under more moist conditions, or 6.2 and 6.6 µmol $CO_2 m^2 s^{-1}$ for *H. peploides* and *L. arenarius*, respectively (Fig. 2). However, when the two species were compared at drier conditions, the *L. arenarius* had 45% higher uptake rate than *H. peploides*. Ecosystem respiration was slightly higher in the *H. peploides* than the *L. arenarius* at moist conditions (+11%), but much lower at dry conditions (-36%; Fig. 2). This led to the instantaneous carbon accumulation (NEE) in the two species was higher for *L. arenarius* both under moist and dry conditions (+73% and +17%, respectively).

DISCUSSON

Comparison to earlier measurements on Surtsey

Magnússon (1992) used an alkali absorption method to measure R_s in areas with three different surface types, bare sand, 13% H. peploides cover and 21% L. arenarius cover. This method does not give absolute values but rather a relative measure of respiration intensity between sites (Reiners 1968; Magnússon 1992). The difference of the alkali method from true respiration is dependent on the flux rate, but typically it overestimates respiration at low rates (Óskarsson 1998). When converted to molar units, Magnússon (1992) found on average 0.55, 0.70 and 1.78 μ mol CO₂ m⁻² s⁻¹ R_s from the bare, H. peploides and L. arenarius surfaces. These R_{a} rates are similar as the measured R_{a} at the dry sites in the present study $(0.4-1.2 \,\mu\text{mol CO}_{2} \,\text{m}^{-2} \,\text{s}^{-1})$ where the plant cover was 100%.

Differences between Leymus and Honckenya

The two plant species chosen for the present study (*Leymus arenarius* and *Honckenya peploides*) were the most successful colonizers during the first 20 years of primary succession on Surtsey (Fridriksson 1992). Both have seeds that tolerate submergence in sea water and are common in costal plant communities in Iceland (Kristinsson 1987), both tolerate sand blaster and allocate much of their resources to root growth and are therefore well adapted to survive the infertile conditions (Fridriksson 1992; Magnússon & Magnússon 2000).

The present study showed that L. arenarius maintained higher GPP than H. peploides under dry conditions on the island, even if their GPP was not much different under moist conditions. This is in line with a difference in their growth habitats in Iceland, but H. peploides rarely grows above the coastline while L. arenarius can also grow on dry inland sandy sites (Greipsson 1994). A controlled drought experiment on *H. peploides* and another Leymus species, Leymus mollis, at Hudson Bay, Canada, showed that L. mollis maintained higher survival under drought stress (Gagné & Houle 2002). The observed difference in GPP may therefore possibly indicate that the L. arenarius is better adapted to survive where water availability is scarce, e.g. due to deeper root system.

The comparison between the two dryer sites in the present study is, however, complicated by their difference in soil fertility (Table 1). The relatively higher GPP in *L. arenarius* than *H. peploides* at the dry site could therefore also be a result of higher photosynthetic capacity per surface area, a well known response of plants to fertilization (Larcher 2003).

Differences between moist and dry sites

When carbon fluxes were compared under moist and dry conditions across both species, it was clear that light saturated carbon uptake (GPP) and ecosystem respiration (R_e) were much higher at the moist sites, indicating that water stress may be important factor limiting plant growth on Surtsey. Further, the higher R_e indicated more biologic activity in the moist soil. Earlier studies that have studied biological activity of soils from Surtsey with various methods have not reported on the importance of soil moisture (Frederiksen et al. 2000; Klamer et al. 2000).

It has to be stated that other environmental factors than water availability alone may have differed between the moist and dry sites in the present study. The moist sites were found closer to the sea and it could be expected that they had benefitted from sea-derived organic matter washed onshore. In the earlier mentioned experiment on H. peploides and L. mollis, both species were shown to respond strongly to nutrient availability, but they did not significantly differ in their response (Gagné & Houle 2002). When the soil nutrient status in different permanent plots on Surtsey was investigated in 2006 (Magnússon et al. 2009; also see Table 1), soil nitrogen was found to be lower in nearby permanent plots at the ness than in the two plots at the dryer sites. Apparently it was therefore not higher soil nutrient status that explained the higher carbon uptake, soil activity and more vigorous growth in the moist area.

More research should be conducted on which environmental factors limit biological activity on Surtsey, where direct measurements of soil water content and nutrient status should be part of the experimental setup.

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