Substrate induced respiration and microbial growth in soil during the primary succession on Surtsey, Iceland

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ABSTRACT

The accumulation of organic matter and nutrients within the soil system is essential for the plant succession on Surtsey, and the soil microbial community plays a key role in this process. Microbial biomasses and activity have increased markedly during the succession from bare soil to the complex plant community established in the bird colonies. Parallel to the changes in plant cover, fungi have gained increasing importance in the soil microbial community. Today about 250 pairs of gulls nest on the southern part of the island, and the single main event stimulating succession at present probably is the nutrients deposited by these birds as droppings etc. The microbes in the soil from the bird colony inhabit an unusually nutrient rich environment where a carbon addition without supplementary nutrients will stimulate growth and thereby aid the conservation of nutrients within the system. There are still areas on the island where no plants grow, and here the microbial biomass is very low. The microbial growth in these bare soils takes place at a high rate when nutrients are available, and this could be an adaptive mechanism to retain nutrients in the soil for subsequent plant growth and thereby to mediate the primary succession from bare soil to plant cover.

INTRODUCTION

The island of Surtsey was created by a series of volcanic eruptions in the period from November 1963 until 1967 (Fridriksson 1994), and during the following decades life became established on the bare volcanic surface. Some of the first colonisers on Surtsey were bacteria and blue-green algae (Schwabe 1970), and already in 1965 the first plants were observed (Fridriksson 1966). The question arises why some areas of the island at present have dense vegetation while others are still mostly without vegetation.

Nitrogen available for the establishment of plant growth on Surtsey may have originated from atmospheric deposition, sea spray and nitrogen fixing microorganisms, but nitrogen from organic matter washed unto the shore and bird droppings is probably more important (Fridriksson 1987). In 1985, seagulls, primarily *Larus fuscus* and *Larus argentatus,* began nesting on the lava-fields of the southern part of the island (Fridriksson 1994). As a consequence, nutrients such as nitrogen and phosphorus from the bird droppings, fish debris and dead gull chicks dramatically increased soil fertility near the nesting sites (Frederiksen *et al.* 2000).

Today the numbers of plant species are much higher and the average plant cover much denser in the bird colony than in the areas under limited influence of birds. Vegetation analyses from 1994 to 1995 (Magnússon *et al.* 1996) showed that plants covered approximately 4% of the area in the surveyed plots outside the colony. Inside the bird colony 30% of the area was covered by plants.

Many of the plants on Surtsey have produced seeds which have spread over most of the island, but in some areas they have been unable to ger-

minate and become established as plants (Fridriksson 1992). The low success of the seeds is probably due to a combination of the sandy tephra being unstable, of the low water retention capacity and low nutrient status of the soil (Fridriksson 1992). Nitrogen and phosphorus were low in these areas due to a small and/or infrequent input, but the soil may also have a low capacity to retain nutrients from the few occasional bird droppings that actually occur in these areas. The microbial community established in these soils must be tolerant to severe food limitations. But when nutrients are introduced into the soil through bird droppings, the microbial biomass must be able to assimilate the nutrients extremely fast in order efficiently to prevent the nitrogen and phosphorus input from leaching. Magnússon (1992) measured the soil respiration, and different microbial activities were found within the different types of plant cover. Soil respiration was low in the bare soil and only slightly higher in soil with *Honkenya peploides* cover, but 50-200% higher in soil with *Elymus arenarius* cover.

The aim of this study was to study which nutrient deficits limited the microorganisms in soil during the primary succession on Surtsey, in three areas that differed in quantity and quality of plant cover, and hence illustrate three stages in the succession. We wanted to study the ability of the microbes in the bare soil to retain and utilise a sudden nutrient input, and thereby to improve the nutrient status of the soil for plant growth. Moreover we wanted to clarify whether the functional differences in the soil microbial communities occurred in parallel to differences in plant cover.

MATERIALS AND METHODS

Study area

In the summer of 1995, six plots (3x3 m) were established for survey of the soil fauna. The sites were chosen in order to obtain a succession gradient of plant communities of increasing complexity. In July 1996, soil samples were collected in the bare soil plot (J4), in the *Honkenya* plot (J3) and in the bird colony (J5) (Fig. 1).

The positions of the plots are noted in reference to the co-ordinate system which divides the island into quadrants of 100x100 m (Fridriksson 1992), and to plots established for botanical surveys by Magnússon *et al.* (1996) who investigated the plant-cover in the reference plots during 1994-1995.

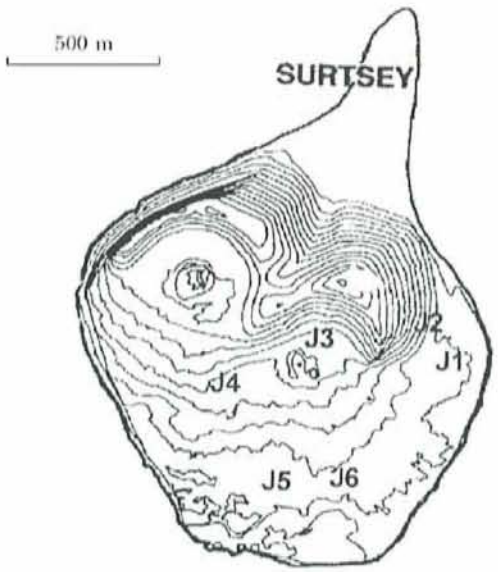

Figure 1. Map of Surtsey, which show the position of the three experimental plots. J3: *Honkenya* plot, J4: bare soil and J5: Bird Colony. No soil samples were colleted at the three other plots. Map from Jakobsson *et al.* (1992), with permission from S. Fridriksson. North is up in the figure.

The *Honkenya* patch (J3) was established in 1974, and positioned in quadrant L13; 36°-12 m south of plot 12 which had a plant cover of 19%. The smallest coastal distance was 550 m to the eastern beach, and the plot was located on a south facing slope (15°). The soil was tephra sand with *Honkenya peploides*, and some *Fulmarus glacialis* were nesting nearby.

The control with bare soil (J4) was positioned in quadrant O10 approximately 200 m northwest of plot 11 which had a plant cover of 4%. The smallest coastal distance was 300 m to the southern cliff. The soil was unvegetated tephra sand, but some root material was found in the soil samples.

The vegetation in the bird colony (J5) was established in 1983, and since 1986 gulls have been nesting. The plot was positioned in quadrant Q12; 318°-22 m south of plot 1 which had a plant cover of 70%. The smallest coastal distance was 250 m to the southern cliff. The soil was tephra sand with a dense vegetation cover primarily consisting of *Honkenya peploides, Poa pratensis, Puccinellia retroflexa, Cochlearia officinalis* and *Stellaria media. Larus fuscus* and *Larus argentatus* were nesting.

Sampling

On July 23rd 1996, bulk samples each consisting of five sub-samples (36 cm^2, 0-5 cm) were randomly collected from each plot. The samples

were placed in airtight plastic bags and stored at 5°C upon arrival in Reykjavik the following day.

Soil respiration

In order to investigate which nutrients limit the microbial growth, a respiration experiment was set up. 2 g samples of sieved soil (fresh weight, sieve mesh size: 2x2 mm) were placed in 116 ml serum bottles. Distilled water and nutrient solutions containing factorial combinations of C, N and P were added (i.e. $2^3 = 8$ treatments). Distilled water was added to a final liquid volume of 1.50 ml pr flask, and final concentrations in each flask were 0.278 M C as $C_6H_{12}O_6$; 0.163 M N as NH_4NO_3 and/or 0.073 M P as KH_2PO_4 + 0.088 M P as Na_2HPO_4. This was equal to 1.5 mg C, 0.34 mg N and/or 0.37 mg P per gram soil (fresh weight). Three replicates were prepared for each of the three soils. The serum bottles were sealed with rubber stoppers, and 10 ml atmospheric air was added in order to avoid partial vacuum during sampling. To prevent any oxygen limitations in the soil slurry, the flasks were shaken at moderate speed during the 48 hour incubation period at room temperature. Headspace gas samples (0.5 ml) were collected every 3-4 hours and analysed on a gas chromatograph equipped with a TCD and a 1.8 m x 3 mm Porapak Q column operated at 35°C.

Direct counting of bacteria and fungi

Three replicates from each plot were prepared for direct enumeration of bacteria and fungal hyphae by fixing 2 g fresh soil in 5 ml 0.4% formaldehyde.

Bacteria were stained with Acridine-orange (Hobbie *et al.* 1977). A 100 µl sample of the fixed suspension was added to 5 ml diluted sterile filtered acetic acid (0.15 mM, pH=4). One ml Acridine-orange (0.5 mg/ml) was added to the bacterial suspension, which was left for two min. The suspension was filtered onto a black polycarbonate filter (pore-size: 0.2 µm). Bacteria numbers were determined by direct counting using an epifluorescence microscope equipped with an eyepiece graticule (graticules Ltd, Tonbridge, UK). The number of fields inspected per filter was 30-50, and a minimum of 200 cells were counted. The biovolumes (Jenkinson *et al.* 1976) of 20 cells per filter were estimated using a Porton G12 eyepiece graticule (Graticules Ltd, Tonbridge, UK). Bacterial biomass-carbon was calculated using 310 fgC μm^{-3} as biovolume conversion factor (Fry 1990).

The fungal hyphae were stained with Calcoflour-white (West 1988). A 800 µl sample of the fixed suspension was added to 5 ml sterile filtered, distilled water. To the hyphal suspension 1ml Calcofluor-white (6.0 mg/ml) was added, and the suspension was left for one hour at room temperature. The sample was filtered onto a black polycarbonate filter (pore-size: 0.8 µm). The hyphal length was mesured by the grid intersecting method (Olsen 1950) using an epifluorescence microscope equipped with a 10x10 squares eyepiece graticule (graticules Ltd, Tonbridge, UK). The length of a line in the grid, at 500x magnification, was 200 µm and 60 grids were inspected per filter. Fungal biomass-carbon was estimated assuming a diameter of 2 µm, and using 130 fgC μm^{-3} as conversion factor (Van Veen & Paul 1979).

Soil moisture and pH

Gravimetric water content was determined after drying 10–15 g soil for 24 hours at 105°C. pH was measured in a suspension with 5.0 g (fresh weight) soil and 10ml distilled water. The suspension was shaken for 30 min and left to settle for 30 min before pH was measured. pH was also measured in collected bird droppings.

Statistics

Data were analysed using a one-way ANOVA or Kruskal–Wallace ANOVA on ranks and Tukey's multiple range tests were used to analyse for significant differences between the three soils.

It is possible to use the linear increase in ln (respiration rates) during the exponential phase, as an estimate of the first order growth rate of the microbial biomass (Colores *et al.* 1996). The time interval where the regression has the highest r-square is used to find the growth rate as the slope with time. Growth rates, when calculated this way, may only be valid when the microbial growth yield does not change during the period analysed.

Significant difference between two regression lines was tested using the Tukey-Kramer test.

Results from the statistical analyses are presented at the appropriate figures and tables. Sigmastat for Windows, Version 2.03 from SPSS Inc. was used to perform the statistical analyses.

RESULTS

There was a significant difference in the water content in the three soils (Table 1). The bare soil had the least water, and the soil from the colony, with the largest plant biomass, had the

Table 1. Soil pH and content of soil water (dw), standard error in parenthesis. Means with different letters are significantly different (One-way ANOVA, $p<0.0001$).

	% Water	pH
Bare soil	4.42[a] (0.12)	7.9
Honkenya	6.64[b] (0.18)	7.5
Colony	12.73[c] (0.02)	6.5

most water. pH in the bare soil and in the *Honkenya* plot was 7.5 and 7.9 (Table 1). pH in the colony soil was 6.5 even though bird droppings alone had a pH of 8.0. The high content of ammonia in the guano (Bedard *et al.* 1980) probably resulted in a high nitrification activity that reduced the pH.

Initial respiration rates were very low in the bare soil and virtually unaffected by C, N and P amendments (Fig. 2a). In the *Honkenya* soil, similar respiration rates were slightly stimulated by the simultaneous addition of C and N, whereas added P had no effect (Fig. 2 b). The soil from the bird colony showed a marked increase in initial respiration rates upon C addition alone, whereas addition of N and P had no additional effect on the initial rate (Fig. 2c). This indicates that indigenous microbes in the *Honkenya* soil and the soil under the bird colony were capable of increasing their activity if supplied with a suitable substrate, in contrast to the organisms in the bare soil that showed no such response.

The maximal initial substrate induced respiration rate (SIR) has been correlated with the microbial biomass (Anderson & Domsch 1978). Using the CNP amended respiration rates from the first 3-6 hours, the estimated respiration in the three soils were significantly different (Table 2). The initial respiration rate in the bird colony soil and the *Honkenya* soil were 24 and 6 times greater than in the bare soil, indicating a much lower active microbial biomass in the bare soil. The direct counting showed a significantly higher bacterial biomass in the colony soil compared with the *Honkenya* and the bare soil (Table 2). A significant increase was also found in the hyphal biomass, which correlated with the increase in vegetation cover. The difference in fungal biomass resulted in large differences in the ratios between bacteria and fungi. The ratio was 1:1.4 in the bare soil, but 1:34.3 in the *Honkenya* soil and 1:15.2 in the soil under the bird colony. Due to the extreme nature of the bare soil and the very low respiration rate, it was not appropriate to calculate the microbial biomass in accordance with the equation found by Anderson & Domsch (1978).

The addition of C, N and P resulted in the largest respiration rate increase (i.e. growth) for all three plots, but there were differences in the time elapsed before this effect became appar-

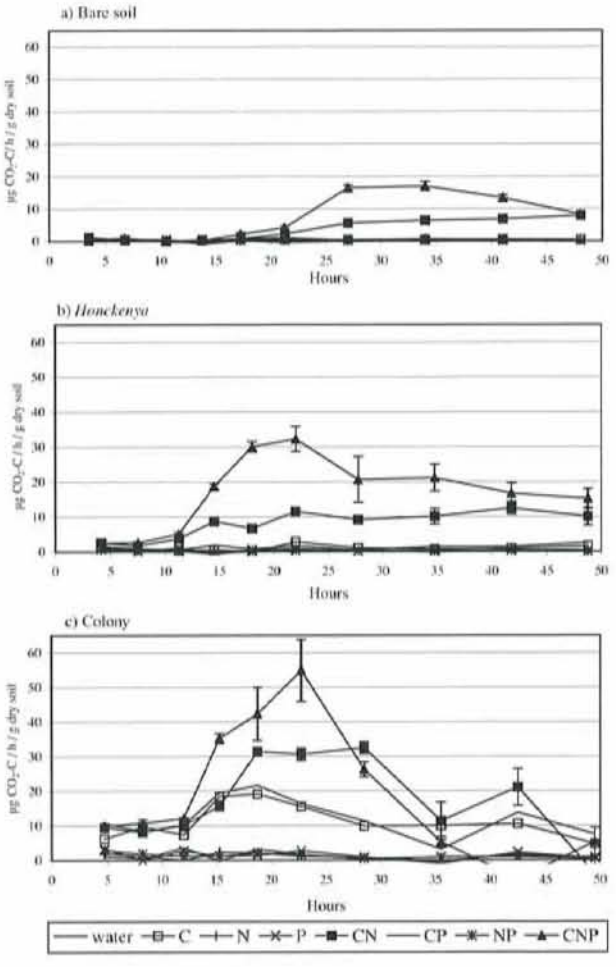

Figure 2. Substrate induced respiration rates in the bare soil plot (a), the *Honkenya* plot (b) and in the bird colony plot (c) for the following amendments: water, C, N, P, CN, CP, NP and CNP. ± standard error bars for the CN and CNP treatment.

Table 2. Initial substrate induced respiration rates after 3-6 hours of incubation with CNP, standard error in parenthesis. Means with different letters within a row are significantly different (*One-way ANOVA and **Kruskal-Wallis ANOVA on ranks, $p<0.005$).

	SIR* µg CO2-C/h/g (dw)	Bacteria* µg C/g (dw)	Fungal hyphae** µg C/g (dw)
Bare soil	0.41[a] (0.18)	3.72[a] (0.48)	5.23[a] (1.27)
Honkenya	2.55[b] (0.10)	2.28[a] (0.47)	78.21[b] (0.98)
Colony	9.90[c] (0.44)	9.51[b] (1.54)	144.36[c] (26.43)

Table 3. Growth rates and R-square (standard error in parenthesis), estimated from best-fit regressions see text for further explanation. Means with different letters are significantly different (Tukey-Kramer test, $p<0.05$).

	Growth h-1	Period h	R square*
CN-addition:			
Bare soil	0.196^{b} (0.022)	17.25-27.00	0.92
Honkenya	0.176^{ab} (0.010)	7.50-14.50	0.54
Colony	0.078^{a} (0.021)	3.50-17.25	0.61
CNP-addition:			
Bare soil	0.285^{b} (0.040)	10.50-27.00	0.84
Honkenya	0.281^{b} (0.029)	7.50-18.00	0.93
Colony	0.111^{a} (0.015)	6.75-21.25	0.84

* All regression lines were significant ($p<0.01$).

ent. The bare soil responded slowly, with a maximal respiration rate that occurred after 27-34 hours. In comparison, the *Honkenya* soil and the bird colony soil attained a maximum respiration rate after only 23 hours. Induction of growth required the addition of C as well as N in the bare soil and the *Honkenya* soil (Fig. 2a, 2b), whereas growth was induced by C addition alone, to a lower but comparable level as found with addition of C, N and P in the soil under the bird colony (Fig. 2c).

Estimating first order growth rate of the microbial biomass (Table 3) for CN and CNP addition showed that growth at a detectable level began after 3-7 hours in the soil from the bird colony, and after 8 hours in the *Honkenya* soil. Growth in the bare soil began after 10-11 hours with CNP addition, and after 17 hours when only CN was added. The growth rates were significantly lower for the microbes in the soil from the bird colony, compared with the microbes in the other two plots (Table 3). The addition of P increased growth rates by 40-60% in these soils.

Assuming that a minimum of 40% of the assimilated carbon had been respired into the headspace, it is possible to calculate the maximal percentage of glucose-C that had been mineralised by the microbes (Voroney & Paul 1984). The microbes in the colony soil were able to utilise 90% of the added glucose-C within 24 hours when C, N and P were added (Table 4). In the *Honkenya* soil, 52% were mineralised, whereas the microbes in the bare soil only managed to mineralise 4% of the added glucose-C during 24 hours. This indicates that the microbes in the fully amended incubations from the bird colony were carbon limited after 24 hours.

DISCUSSION

In the early stages of primary succession the build-up of soil fertility requires that plant nutrients are retained within the system. The nutrients can be stored in the soil system by sorption to the organic matter or within the microorganisms. In the sandy tephra soils of Surtsey, the content of organic matter was extremely low, as 3% carbon and 0.3% nitrogen were found in the bird colony soil, in contrast to 0.2% carbon and no detectable nitrogen in soil without vegetation (Frederiksen *et al.* 2000).

There was a significant increase in the total microbial biomass determined as direct counts or as SIR during the succession. The sum of bacterial and fungal biomass in the bird colony and the *Honkenya* soils were 17 and 9 times, respectively, larger than in the bare soil. Thus there is accordance between the variation in SIR and microscopical biomass estimates between the sites. The direct estimates of fungal and bacterial biomass showed that fungi totally dominated the microbial communities in the plots with vegetation, whereas bacteria comprised 40% of the microbial biomass in the bare soil. The input of plant debris favours fungal decomposition as in the *Honkenya* soil, but the addition of easy decomposable matter such as bird droppings also facilitates bacterial growth. This could explain the relatively lower bacterial:fungal ratio in the bird colony soil

Table 4. Estimated % of glucose-C mineralised in the different treatments after 24 hours, assuming 40% of the assimilated carbon is respired into the headspace, standard error in parenthesis. Means with different letters within a row are significantly different (One-way ANOVA, $p<0.001$).

	C - addition	CN - addition	CP - addition	CNP - addition
Bare soil	0.13^{a} (0.18)	1.87^{a} (0.31)	1.44^{a} (0.28)	4.10^{a} (0.41)
Honkenya	2.46^{b} (0.18)	19.27^{b} (0.43)	3.79^{b} (0.29)	52.00^{b} (2.97)
Colony	42.49^{c} (0.55)	60.34^{c} (1.37)	48.76^{c} (0.66)	90.91^{c} (2.57)

(1:15.2) compared with the *Honkenya* plot (1:34.3), whereas the fungal:bacterial ratio in the bare soil was much lower (1:1.4).

The exponential growth rates with CNP additions were significantly lower in the colony soil than in the two other plots. This implies that the microbial cells in the colony soil were relatively slow in assimilating the added nutrients, compared with the equivalent microbial biomass in the *Honkenya* plot and in the bare soil. This indicates that the microbial community had a different structure in the different sites, since it is considered unlikely that micronutrients are more limiting to microbial growth in the bird colony soil than in the bare soil and *Honkenya* soil.

Communities, which are dominated by bacteria would be able to perform exponential growth in response to a sudden input of nutrients and thus exhibit a faster response than would a community dominated by fungal hyphae with a more linear growth pattern. The bird colony soil, with the highest fungal biomass, also had the lowest growth rate as compared with the two simpler communities. This could indicate that the microbial communities in the *Honkenya* soil and in the bare soil were dominated by r-strategists, whereas the bird colony soil was dominated by a mixture of r- and K- strategy microbes, which corresponds well with the theories on succession (Odum 1962).

Carbon was the primary limiting factor for microbial activity and growth in both the *Honkenya* soil and the bird colony soil communities at Surtsey, as in most decomposer communities (Swift *et al.* 1979). Carbon was able to stimulate activity but not growth in the bare soil community, and the overall respiration rate was very low in the bare soil as compared with both the colony soil and the *Honkenya* soils. The level of available nutrients was unusually high in the bird colony soil, since addition of carbon alone could induce an initial growth response similar to the response when carbon and nitrogen were added. The effect of N and in part also P was secondary, and addition of N and P resulted in an increased and prolonged growth response, but only when these nutrients were supplied in addition to C.

A depletion of the organic nutrient source could explain the decrease in growth rate at late stages of the inoculation (Stotzky & Norman 1964). In the colony soil and *Honkenya* soil with C, N and P addition, 52-90% of the added C mineralised after 24 hours. Growth also decreased in the bare soil during the late stages of incubation with C, N and P, but in this case less than 5% of the added C was mineralised. Therefore, other explanations than reduced carbon supply, for example production of inhibitory substances and/or depletion of micronutrients, were probably involved in the reduced growth rates in the bare soil.

The capacity of a soil community to utilise and store a sudden supply of nutrients has been important for the development of the Surtsey ecosystem. The ability to do so depends on the specific growth rate of the microorganisms combined with the response time and the standing biomass of the microbial community. The high growth rate of the microbes in the bare soil shows a great capacity of the cells to retain nutrients when available, and this adaptation is probably important for the accumulation of nutrients in the bare soil. But despite the higher growth rate, the microbial community in the bare soil may only be able to utilise a minor fraction of a sudden nutrient input such as a bird dropping. The long time intervals between occasional bird droppings or inputs from other nutrient sources prevent the formation of a sufficient microbial biomass, allowing the bare soil to efficiently immobilise the nutrients in a bird dropping before the nutrients are lost. In spite of the lower growth rate, the microbes in the colony soil have a great potential for utilising a sudden nutrient input as this community has a much higher standing biomass, and therefore a higher net-production rate. However, here the microbial capacity to store nutrients may be less important, due to the high concentration of soluble nutrients available for the plants.

During the more than 30 years that have elapsed since the eruptions began, a new ecosystem has evolved on Surtsey. Bacteria were established early on the island, even before the eruptions ceased (Ponnamperuma *et al.* 1967). In the following years life forms colonised the moist areas near the thermal vents and in craters, in what Schwabe (1971) called the oases of ecogenesis. Our investigations indicate that the birds currently may be the single most important factor for the further development of the ecosystem, as the level of microbial activity is significantly higher compared with the simpler communities.

The potentially fast growth of the microbial community in the bare soil is a mechanism evolved to retain introduced nutrients within the system for eventual use in plant growth. The

small biomass of microbes in the bare soil and the low ability to store nutrients result in a very slow accumulation of organic matter in the bare soil, however. These results show that the establishment of plants in the bare areas on Surtsey is still strongly limited by the low nutrient status of the soil.

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