

# Vegetation cover, gross photosynthesis and remotely sensed vegetation indices in different aged sub-arctic volcanic islands in the Vestmannaeyjar archipelago

BJARNI D. SIGURDSSON<sup>1</sup>, ESTHER M. KAPINGA<sup>1</sup> AND BORGTHÓR MAGNUSSON<sup>2</sup>

<sup>1</sup>Agricultural University of Iceland, Hvanneyri 311 Borgarnes, Iceland (bjarni@lbhi.is)

<sup>2</sup>Icelandic Institute of Natural History, Urridaholtsstræti 6–8, 210 Gardabær, Iceland

## ABSTRACT

Surtsey and the older islands in the Vestmannaeyjar archipelago offer a unique possibility to study how sub-Arctic ecosystems develop from unvegetated mineral volcanic substrate to grasslands with thick Brown Andosol soils. The present study was carried out on 24 study plots distributed across six different ecosystems on Surtsey, Heimaey and Elliðaey islands and involved field measurements of soil volumetric water content (VWC), vascular plant cover (VPC) and instantaneous rate of gross primary production (GPP). Remote sensing was also used to determine the vegetation indices of normalized difference vegetation index (NDVI), photochemical reflectance index (PRI) and chlorophyll/carotenoid index (CCI) of each plot and find their relationships to the measured VPC and GPP. Nýjahraun on Heimaey and the area not affected by seabirds on Surtsey were not significantly different in any measured variable. During their initial 48–58 years of primary succession, they had reached ca. 3% (VPC) to 12–13% (GPP, VWC) of the measured variables in the 5900-year-old Lyngfellisdalur on Heimaey, which has negligible seabird nutrient inputs. However, the measured VPC and GPP had reached similar levels in only 58 years in the seabird-affected parts of Surtsey as measured on the 5900-year-old seabird-affected Elliðaey. This shows how seabirds can greatly speed up ecosystem development by oceanic nutrient inputs into terrestrial ecosystems. Significant relationships were found between NDVI and VPC and between CCI and GPP, which may become important tools to track ecosystem development in space and time on the islands.

## INTRODUCTION

Surtsey volcanic island, formed in an eruption during 1963–1967, is one of most studied ecosystems in Iceland (cf. Baldursson & Ingadóttir 2007). Most ecological studies on Surtsey have focused on community changes in flora, fauna and microbes (e.g. Magnusson *et al.* 2014, Ilieva-Makulec *et al.* 2015, Marteinsson *et al.* 2015) and only few have focused on the underlying ecosystem processes and soil development (e.g. Sigurdsson & Magnusson 2010, Sigurdsson 2011, Leblans *et al.* 2017, Sigurdsson *et al.* 2020). From these studies, it is clear that the establishment of a seabird colony on Surtsey in 1986 had a large impact on plant succession and ecosystem processes on the new island.

Now, almost 60 years after Surtsey emerged from

the ocean and after both plant succession and soil development are under way, comparison to older volcanic islands in the archipelago is of interest to clarify how far ecosystem structure and function on Surtsey has reached. In the past few years, papers have been published where plant communities (Magnusson *et al.* 2014), soil development (Leblans *et al.* 2017) and nutrient availability (Sigurdsson & Leblans 2020) has been compared between Surtsey and older neighboring islands. It is, however, noteworthy that no ecological studies have so far taken place on the younger lavafield of Nýjahraun on Heimaey. The lava is from an eruption in Jan–Jul 1973.

Multispectral remote sensing captures the spectral reflectance properties of surfaces caught by the

sensors that can be e.g. hand held or mounted on drones, airplanes or satellites. The reflectance can be related to plant function (e.g. Ustin *et al.*, 2009). Therefore, the use of remotely sensed vegetation indices as proxies of plant function can be exploited to parameterize relationships for estimating rates of GPP (Wong *et al.* 2019, 2020). Such relationships can then be used as means to extrapolate plot-level GPP data to larger areas.

The first aim of this study was to compare measurements in areas in the Vestmannaeyjar archipelago that differed both in age and if they had high seabird nutrient inputs (Surtsey, 58 years; Elliðaey, 5900 years) or not (Surtsey, 58 years; Nýjahraun, Heimaey, 48 years; Lyngfellisdalur, Heimaey, 5900 years: Table 1). By including all these sites we were interested to see how far the ecosystem parameters had reached in the younger lavafields, compared to the older islands where the grassland ecosystems can be considered fully developed. The second aim was to compare the Nýjahraun and Surtsey ecosystems. The third and final aim was to establish relationships between VPC and GPP and the measured vegetation indices (NDVI, PRI, CCI).

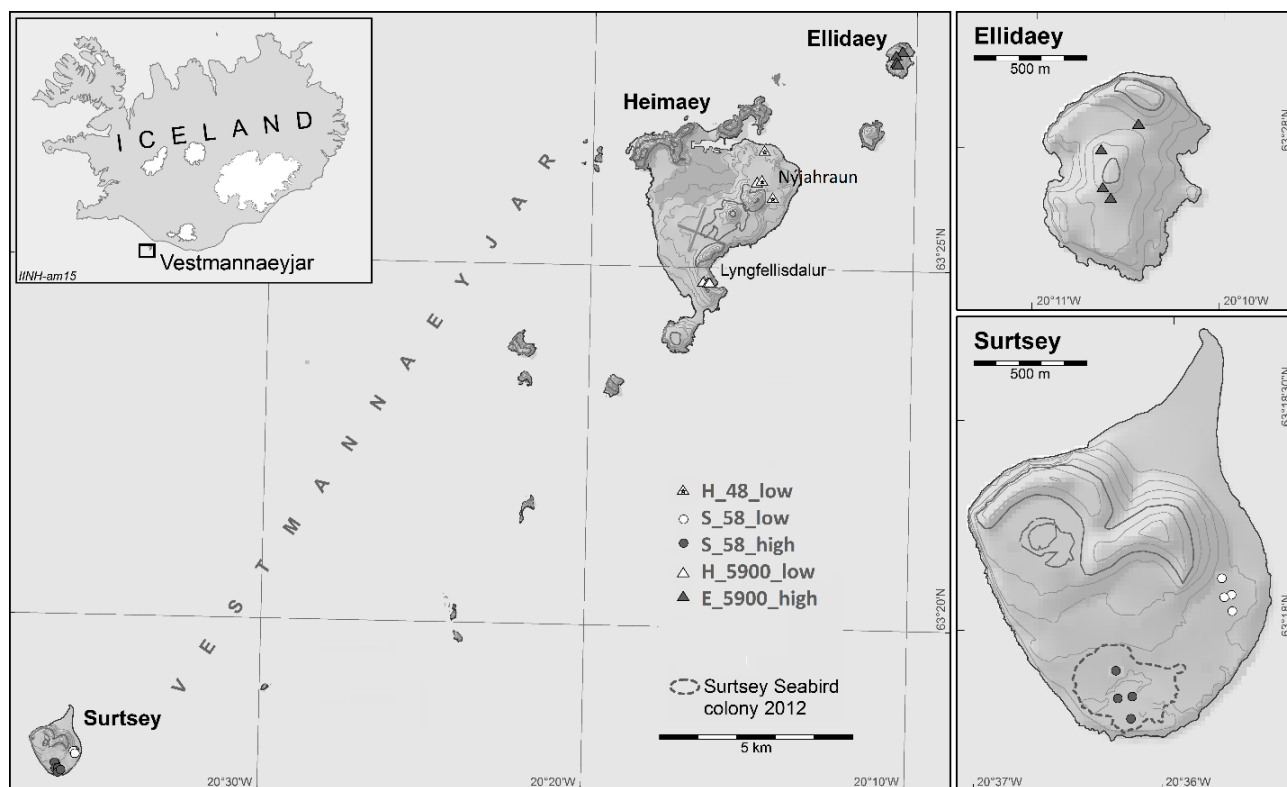
Such relationships can be of high value when using remote sensing to estimate ecosystem structure and function in space and time.

METHODS

Study area

This study was performed on three islands of the volcanic Vestmannaeyjar archipelago (63°250N, 20°170W; south Iceland; Fig. 1) in mid-July 2020 and 2021. The main vegetation type on the Vestmannaeyjar archipelago is lush grassland, except in areas that are unsuitable for seabird colonization, where heathlands, herb slopes or dry meadows can be found or where the surface is in early stages of primary succession after a volcanic eruption (Magnússon *et al.* 2014). Five sites were studied with low and high natural seabird inputs and of different age (Fig. 1).

At Surtsey and Nýjahraun on Heimaey the soils and vegetation were at an early successional stage (48 and 58 years old, respectively), but Lyngfellisdalur on Heimaey and Elliðaey have well-developed soils on bedrocks that both date from eruptions that took place ca. 5900 years ago. As Nýjahraun is located on the only inhabited island in the archipelago, Heimaey,



**Figure 1:** Location of the Vestmannaeyjar archipelago at the southwest coast of Iceland, including the three study islands, Surtsey, Heimaey and Elliðaey. The smaller two maps show the islands Elliðaey and Surtsey in a greater detail. Circles show study plots on Surtsey and triangles plots on the older Heimaey and Elliðaey. The number in the site label stands for age of site in 2021 (years) and “low” or “high” stand for relative seabird nutrient inputs. Map by Anette Th. Meier.

parts of it have been heavily influenced by human activities; especially the spread of the N-fixing exotic plant species *Lupinus nootkatensis* (Sims) Donn. Parts of it remain, however, relatively intact and those were used in the study. The soil profiles at Lyngfellisdalur, Heimaey and Elliðaey were undisturbed at least since 395 AD, which was determined from the presence of an ash layer from that time <1 m below the surface (Leblans *et al.* 2017). The Surtsey, Heimaey and Elliðaey sites have different vegetation communities, which reflect the differences in seabird influence (Magnússon *et al.* 2014, Leblans *et al.* 2017). The Lyngfellisdalur and Nýjahraun sites on Heimaey are not likely to have ever hosted a seabird colonies due to their topographical characteristics, while Elliðaey has served as breeding ground for seabirds from early times. The most common seabird species on Elliðaey is Atlantic puffin (*Fratercula arctica*) but on Surtsey it is mainly seagulls of different species (*Larus* sp.) and northern fulmar (*Fulmarus glacialis*). Appendix 1 gives an overview of the research activities that have taken place on the older islands.

**Table 1.** Explanation for the different site names used in this study.

Site name	Island	Yrs of origin	Seabird influence	No of plots
H-48-low	Heimaey	1973	low	4
S-58-low	Surtsey	1963-67	low	4
S-58-high	Surtsey	1963-67	high	4
H-5900-low	Heimaey	5900 BP	low	4
E-5900-high	Elliðaey	5900 BP	high	4

The study took place in four permanent 10x10 m study plots at each site that were established at Nýjahraun in 2021, Lyngfellisdalur and Elliðaey in 2013 and on Surtsey in 1990 (Table 1, Fig. 2). The vegetation in the high nutrient inputs sites at Elliðaey and Surtsey was a grassland dominated with *Festuca richardsonii* Kartesz, *Poa* sp. and *Stellaria media* (L.) Vill. In the Lyngfellisdalur “old site” the vegetation community was dominated by *Anthoxantum odoratum* L., *Galium verum* L. and *Luzula multiflora* (Ehrh.) Lej., a herb rich heathland community representing lower fertility (Magnússon *et al.* 2014). The vegetation on Nýjahraun and outside the seabird colony on Surtsey was dominated by *Honckenya peploides* (L.) Ehrh. and *Leymus arenarius* (L.) Hochst, and also moss on Nýjahraun. Further information about the site conditions can be found in Sigurdsson & Leblans

(2020), Leblans *et al.* (2017) and Magnússon *et al.* (2014).

#### GPP and environmental parameters

Measurements took place in middle of July 2020 on Surtsey and in 2021 on Heimaey and Elliðaey with an EGM-4 portable gas analyzer and a transparent CPY5 cuvette (PP-Systems, Amesbury, MA, USA) in the permanent plots. Four measurements were done at 1, 4, 8 and 11 m along a diagonal line across each plot. First the net CO<sub>2</sub> flux (Net Ecosystem Exchange; NEE) was measured in light and thereafter the cuvette was covered and the measurement was repeated in darkness, yielding the ecosystem respiration rate (RE). Gross photosynthesis rate (GPP) was calculated as:

$$GPP = NEE + RE . \quad (1)$$

Other measurements recorded together with the GPP measurements included soil temperature at 10 cm depth and photosynthetically active radiation (PAR) in  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ . Also we measured volumetric water content (VWC;% ) in the 0-5 cm surface soil layer (Theta-probe, model ML3, Delta-T Devices Ltd, Cambridge, UK).

#### Remote sensed vegetation indices

Measurements were done in middle of July 2020 on Surtsey and 2021 on Heimaey and Elliðaey with multispectral sensors mounted on a 2 m long pole (Spectrosense 2+, model SKL910/4, Skye Instruments Ltd., Powys, UK). Each measurement covered 0.6 m<sup>2</sup> of surface. Five measurements were done above each plot, one in each corner and one in the middle. The instrument measures four spectral bands from which three vegetation indices were calculated:

$$NDVI = \frac{R_{800} - R_{630}}{R_{800} + R_{630}} , \quad (2)$$

$$PRI = \frac{R_{532} - R_{570}}{R_{532} + R_{570}} , \quad (3)$$

$$CCI = \frac{R_{532} - R_{630}}{R_{532} + R_{630}} , \quad (4)$$

where R indicates reflectance at the specific wavelengths in nm.

Normalized difference vegetation index (NDVI) is calculated from visible and near-infrared wave bands and relates to the density of chlorophyll per unit area (Myneni *et al.*, 2002). It is more related to vegetation cover and structure than plant physiological activity



**Figure 2:** Six out of the 20 study plots used in this study. Two study plots on Nýjahraun on Heimaey (a-b). a) In the most sheltered parts of Nýjahraun moss is dominating, b) but in the largest and more exposed part on Nýjahraun vascular plants dominate. c) Plot outside and inside d) the seagull colony on Surtsey. Plots on 5900 year old bedrock in e) Lyngfellisdalur on Heimaey where seabird influence is at minimum and f) on Elliðaey where seabird nutrient input is high. Photos BDS.

such as photosynthetic rates (GPP). Photochemical reflectance index (PRI) is responsive to the carotenoid pigment composition in leaf tissues (Peñuelas *et al.*, 2011). Those pigments are involved in regulating photosynthetic processes. It shows the leaf light use efficiency per unit leaf surface, rather than the

rate of photosynthesis per unit area (Peñuelas *et al.*, 1995); i.e. it needs to be scaled with both surface leaf area (vegetation cover) and photosynthetically active radiation (PAR) to give GPP. Chlorophyll/carotenoid index (CCI) is closely related to PRI, and is also related to the carotenoid pigment composition

(Gamon *et al.*, 2016). It is, however, also sensitive to the amount of chlorophyll pigments (Wong *et al.*, 2019). That means that it is more directly related to gross photosynthesis (GPP) than PRI is. Therefore it catches both physiological and structural features of plant canopies.

#### Vegetation cover

A measurement tube was placed across the 10 x 10 m plots and the cover of both non-vascular and vascular plants was determined by line-intercept method (see Magnússon *et al.* 2014). Existing data was used from Surtsey (from 2018) and Lyngfellisdalur and Elliðaey (from 2010), whereas the measurements were done in July 2021 for Nýjahraun.

#### Data and statistical analyses

The site differences were tested with an one-way ANOVA. In case of significant ANOVA model, pairwise differences were tested by post hoc LSD tests, when the requirements of normality and homoscedasticity of the residuals were met. The latter was visually inspected. Linear regression was used to derive relationships between GPP and VPC and vegetation indices.

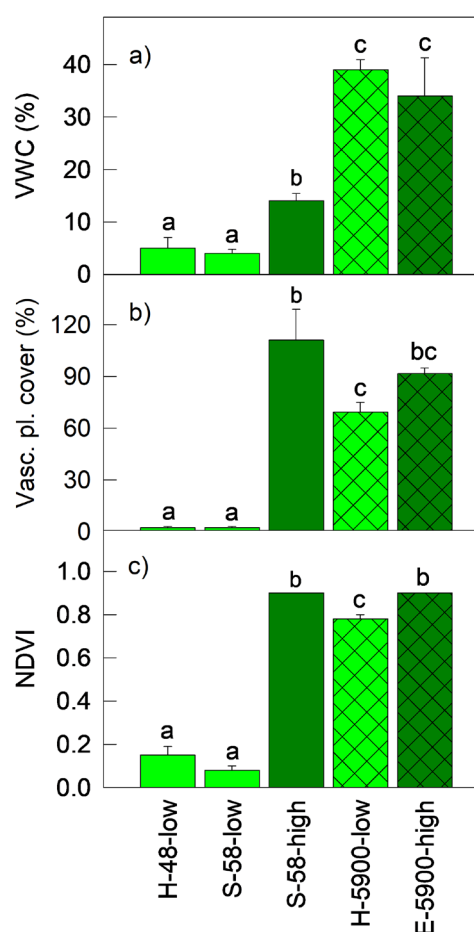
## RESULTS AND DISCUSSION

#### Soil water

Soil water content was significantly higher in the older soils of Elliðaey and Lyngfellisdalur, than in the younger Surtsey and Nýjahraun soils (Fig. 3a), but no difference was found between H-49-low and S-59-low. The seabird-affected soils on Surtsey contained intermediate amounts of water. The observed difference mirrored the differences in soil organic matter between the sites (Leblans *et al.* 2017) and is therefore indicative of improvements in water holding capacity as the soils develop.

#### Vegetation cover

Moss cover was highest on the old soils with low nutrient inputs in Lyngfellisdalur, but due to relatively high within-site variability, it was not significantly different across sites (Table 1). Vascular plant cover (VPC) was therefore a more sensitive parameter than total plant cover, both to age and to nutrient inputs (Fig. 3b and Table 2). It was noteworthy that the highest VPC was found within the 58 years old seagull colony on Surtsey ( $111\% \pm 18\%$ ), even if it was not significantly different from the seabird-affected



**Figure 3.** a) Volumetric water content (VWC), b) Vascular plant cover and c) Normalized Difference Vegetation Index (NDVI) on the 48 years old Nýjahraun on Heimaey (H-48-low), on the 58 year old Surtsey outside (S-58-low) and within a seabird affected area (S-58-high), in Lyngfellisdalur on Heimaey since 5900 BP without seabird influence (H-5900-low) and on Elliðaey (E-5900+high) where seabirds bring in nutrients from the sea. Vertical bars represent SE of n=4. Different letters above bars indicate significant differences ( $P < 0.05$ ) by post-hoc LSD tests.

Elliðaey ( $92\% \pm 3\%$ ). The old Lyngfellisdalur, with low seabird influence, had an intermediate vascular plant cover of 69%, but still the highest total plant cover, due to the high contribution of mosses there (Table 2). The difference in soil nitrogen (N) among four of the sites has the same pattern as the difference in VPC found here (Leblans *et al.* 2017).

That Surtsey (S-58-high) had already reached significantly higher VPC than was found in the 5900-year-old Lyngfellisdalur shows how the seabird nutrient inputs have greatly enhanced the plant succession rate, as has also been found by others (e.g. Magnusson *et al.* 2014). On the other young

**Table 2.** Moss cover and total plant cover, surface cover of vegetation in the cuvette used for GPP measurements, as well as mean soil temperature at 10 cm depth (Ts10), irradiance, net ecosystem exchange (NEE,  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ; note negative values indicate net uptake) and ecosystem respiration (RE,  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  on the 48 years old Nýjahraun on Heimaey (H-48-low), on the 58 years old Surtsey outside (S-58-low) and within a seabird affected area (S-58-high), in Lyngfellisdalur on Heimaey since 5900 BP without seagull influence (H-5900-low) and on Elliðaey (E-5900+high) where seabirds bring in nutrients. Different letters behind means indicate significant differences among sites ( $P < 0.05$ ) by post-hoc LSD tests.

Ecosystem	Moss cover	Total pl cover	Cuvette surface. cover	Ts10	PAR	NEE	RE
H-48-low	7%	9.2% a	23% a	16.7 a	349 a	-0.06	0.06 a
S-58-low	0%	2.3% a	8% a	13.9 b	285 a	-0.13	0.07 a
S-58-high	0%	111% c	94% b	12.5 c	765 b	-0.80	1.32 c
H-5900-low	73%	142% b	100% b	12.2 c	470 ab	-0.56	0.69 b
E-5900-high	0.3%	92% c	100% b	13.0 bc	620 b	+0.23	3.33 d
ANOVA P	n.d.	<0.001	<0.001	<0.001	0.03	0.08	<0.001

sites, where seabird nutrient inputs had not affected the succession, the VPC remained at only 2% after 48-58 years (Fig. 3b). The pattern in VPC more or less reflects the reported differences in accumulated soil nitrogen (N) stocks among the sites (Leblans et al. 2017).

*NDVI and its relationship to vegetation cover*

The site differences in measured NDVI had very similar relative differences as were seen in vascular plant cover (Fig. 3b and c). The two seabird-influenced sites on Surtsey and Elliðaey had significantly highest NDVIs of 0.90, while Lyngfellisdalur site had an

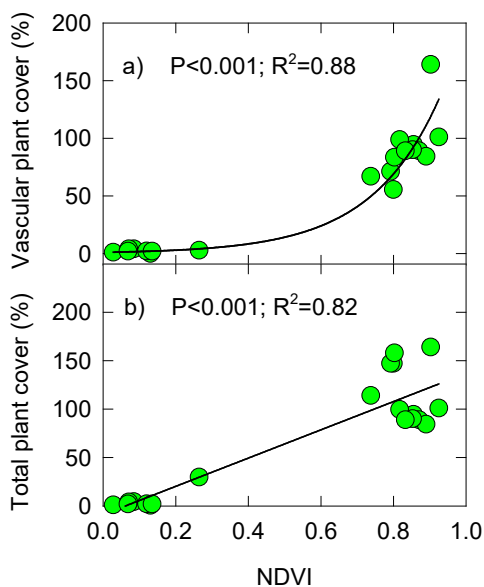
intermediate NDVI of 0.78 and Nýjahraun and most of Surtsey, not affected by seabirds, lowest of 0.11 on average.

Two other studies have reported NDVI of Surtsey, one based on high-resolution satellite data around the permanent study plots on Surtsey (Magnússon et al. 2020) and another using a coarser resolution but mapping the long-term annual changes in the NDVI across the whole island (Magnússon et al. 2022). The present close-to ground NDVI measurements of the permanent plots gave comparable NDVI values inside and outside the seabird-affected area as the Magnússon et al. (2020) study, but somewhat higher NDVI values inside the seabird-affected area than Magnússon et al. (2022) reported. The low spatial resolution used in that study will, however, include more exposed unvegetated lava surfaces within each pixel than measured within or just around the permanent plots, which likely explains this difference.

There was a highly significant exponential relationship between NDVI and vascular VPC across the sites in the present study, shown in Fig. 4a and with Eq. 5:

$$VPC = e^{5.2948 \times NDVI}, \quad (5)$$

where VPC is in % (summed cover of all vascular plant species) and NDVI is a unitless index of 0-1. Eq. 5 explained 88% of the observed variation in VPC among all plots on the three islands. This relationship is of the same form as has been reported between NDVI and aboveground vegetation biomass in Surtsey (Magnússon et al. 2020) (Table 2).

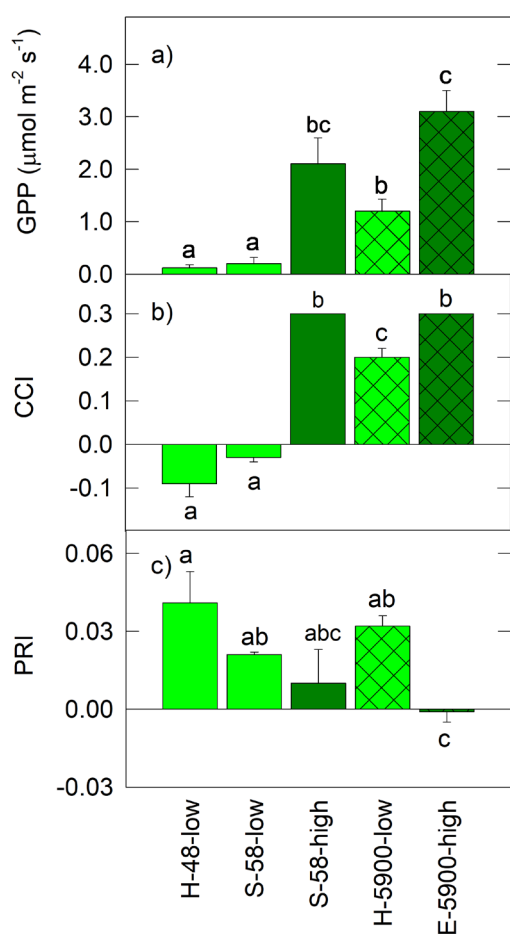


**Figure 4.** The relationship NDVI and (a) vascular plant cover (VPC) and (b) total plant cover (TPC) including mosses and lichens. The two calibration curves are shown in Eqs. 5 and 6.

The relationship between NDVI and total plant cover (TPC) across the three islands, including moss cover, was however of different form, linear instead of exponential and somewhat weaker ( $R^2 = 0.82$ , Fig. 4b):

$$TPC = 145.91 \times NDVI - 8.86, \quad (6)$$

This observed difference in the form of the relationship and its lower  $R^2$  may indicate an issue when NDVI is used to estimate vegetation cover across variable plant communities or communities where moss is an important component. A vegetation community with a moss layer has more layering in the vegetation canopy. It may therefore not be so



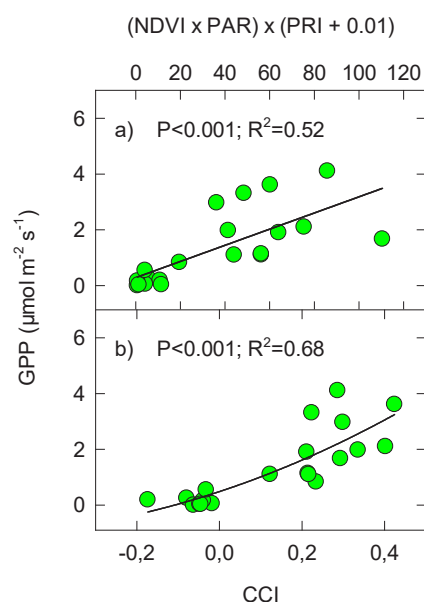
**Figure 5.** Gross Primary Production (GPP), chlorophyll/carotenoid index (CCI) and photochemical reflectance index (PRI) in the 48 years old Nýjahraun on Heimaey (H-48-low), on the 58 years old Surtsey outside (S-58-low) and within a seabird-affected area (S-58-high), Lyngfellisdalur since 5900 BP on Heimaey (H-5900-low) without seabird influence and Elliðaey (E-5900-high) where seabirds bring in nutrients from the sea. Vertical bars represent SE of  $n=4$ . Different letters above bars indicate significant differences ( $P < 0.05$ ) by post-hoc LSD tests.

surprising that VPC was more strongly related to remote sensed NDVI. Further work is needed to develop robust methods to estimate moss biomass or cover from multispectral measurements for subarctic ecosystems.

#### GPP, CCI and PRI

How much energy and carbon enter the ecosystem annually is mainly a function of three things: i) amount of leaf area, ii) photosynthetic activity of the plants and iii) length of the growing season (Chapin *et al.* 2002). In this study we have measurements of plant cover and remote sensed NDVI that both are closely related to i) and measurements of gross photosynthetic rate (GPP) and the remote sensed plant indices PRI and CCI that all are related to ii).

The measured GPP was significantly lowest in Nýjahraun on Heimaey and in areas outside the seabird colony on Surtsey (Fig. 5a), where the plant cover and NDVI was also lowest (Fig. 3). The significantly highest GPPs were measured in the seabird-affected sites, where the nutrient availability was highest (Leblans *et al.* 2017). This pattern of GPP was the same as was reported in an earlier study on Surtsey, Elliðaey, Álsey and Heimaey (Sigurdsson 2011). The GPP of Lyngfellisdalur was significantly lower than of the fertile grassland of Elliðaey (Fig. 5a), which was in line with significantly lower chlorophyll per unit area (NDVI) there (Fig. 3c), even



**Figure 6.** The relationship between (a) uncalibrated GPP (calculated from measured NDVI, PRI and PAR) and measured GPP and (b) between chlorophyll/carotenoid index (CCI) and measured GPP. The two calibration curves are shown in Eqs. 7 and 8.

if it had the highest total plant cover (Table 2)

PRI estimates light use efficiency of plants at the level of PAR that occurs when measurements are taken (Wong *et al.* 2019). PRI did not change significantly across the sites, except between the Nýjahraun and Elliðaey, where the PRI was significantly lower in the dense vegetation community of the latter (Fig. 5c). It should, however, be noted that the PAR was somewhat lower when the Nýjahraun and Surtsey seabird-colony plots were measured (Table 2), which makes a direct comparison of the PRI values across the sites problematic.

When we tried to use PRI to model the measured GPP across the islands, the best relationship also included information about NDVI and PAR (Fig. 6a):

$$GPP = 0.029 \times ((NDVI \times PAR) \times (PRI + 0.1)) + 0.287, \quad (7)$$

where GPP is measured gross photosynthesis in  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  and PAR is photosynthetically active radiation in  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$  and NDVI and PRI are vegetation indices. This relationship is similar to what Wong *et al.* (2020) developed for forest ecosystems. Even if Eq. 7 significantly simulated the measured GPP, it only explained 52% of the observed variation in GPP (Fig. 6a). Therefore, a better model would be preferred for remote sensing of GPP.

The chlorophyll/carotenoid index (CCI) was developed later than NDVI and PRI indices (Gamon *et al.*, 2016) and it has been identified as more directly related to gross photosynthesis than PRI (Wong *et al.*, 2019). Indeed, the measured differences in CCI more-or-less mirrored the relative differences in measured GPP (Fig. 5b). It sensed the two sites with high nutrient inputs with the significantly highest CCI values, the Lyngfjellisdalur plant community with intermediate values and the Nýjahraun and Surtsey outside the seagull colony with the significantly lowest CCI values.

When we used CCI to estimate GPP across all the sites, the following curvilinear relationship was found (Fig. 6b):

$$GPP = 0.4867 + 4.8824 \times CCI + 3.8384 \times CCI^2. \quad (8)$$

This relationship explained 68% of the observed variability in GPP, which is a promising finding. It is therefore clear that the use of the CCI index for estimating GPP is to be preferred method to the more traditional way of using both NDVI and PRI for

such modelling. However, further measurements of GPP and CCI at contrasting PAR conditions should be done to better test how sensitive the CCI is to variations in light compared to GPP.

## CONCLUSIONS

### *Nýjahraun versus Surtsey*

This was the first study of primary succession on the Nýjahraun lavafield on Heimaey to our knowledge. We did not find any significant differences in the measured variables between the intact parts of Nýjahraun and the plots outside the seabird colony in Surtsey. As colonization of N-fixing plants has been found to be an important driver of primary succession on other volcanos and cause similar shifts as the seabirds on Surtsey (del Moral & Magnusson 2014), it would be interesting to add more plots to the Nýjahraun study to also include the areas covered by *Lupinus nooktatensis* there.

### *How far has Surtsey come compared to the older islands?*

This study shows once again how the plant community and plant-derived process in the seabird-affected area in Surtsey have in less than 60 years reached similar levels as observed on a 5900-year-old island in the Vestmannaeyjar archipelago. However, when the areas outside the seagull colony of Surtsey were compared to Lyngfjellisdalur the ecosystem development had only reached 3% (VPC) to 12-13% (GPP, VWC) in the first 48-58 years.

### *How important are seabirds for ecosystem development?*

This study adds to the older existing studies from Surtsey in showing how the seabirds greatly speed up the ecosystem development with their nutrient inputs from the ocean to the terrestrial ecosystem. Especially the plant processes are maximized within decades, while soil development, here represented by VWC, responds more slowly.

### *Remote sensing and other planned research*

The estimation of aboveground plant biomass for the whole area of Surtsey by Magnússon *et al.* (2020) was the first remote sensing application used in ecological research on the island. The present study adds to this work and is an important step towards using such tools to track vegetation development and GPP in space and time on the island.



## REFERENCES

- Baldursson, S. & Á. Ingadóttir (Eds.), 2007. Nomination of Surtsey for the UNESCO World Heritage List. Reykjavik: Icelandic Institute of Natural History.
- Chapin III, F.S., P.A. Matson & H.A. Mooney, 2002. Principles of terrestrial ecosystem ecology. New York, Berlin, London: Springer.
- del Moral, R. & B. Magnússon, 2014. Surtsey and Mount St. Helens: a comparison of early succession rates. *Biogeosciences*, 11(7), 2099-2111.  
<https://doi.org/10.5194/bg-11-2099-2014>
- Gamon, J.A., K.F. Huemmrich, C.Y.S. Wong, I. Ensminger, S. Garrity, D.Y. Hollinger, Aþ Noormets & J. Peñuelas, 2016. A remotely sensed pigment index reveals photosynthetic phenology in evergreen conifers. *Proceedings of the National Academy of Sciences, USA* 113: 13087-13092.
- Ingimundardóttir, G.V., N. Cronberg & B. Magnússon, 2022. Bryophytes of Surtsey, Iceland: Latest developments and a glimpse of the future. *Surtsey Research*, 15, 61-87.  
<https://doi.org/10.33112/surtsey.15.6>
- Leblans, N.I.W., B.D. Sigurdsson, R. Aerts, S. Vicca, B. Magnússon & I.A. Janssens, 2017. Icelandic grasslands as long-term C sinks under elevated organic N inputs. *Biogeochemistry*, 134(3), 279-299.  
<https://doi.org/10.1007/s10533-017-0362-5>
- Magnússon, B., S.H. Magnússon, E. Ólafsson & B.D. Sigurdsson, 2014. Plant colonization, succession and ecosystem development on Surtsey with reference to neighbouring islands. *Biogeosciences*, 11(19), 5521-5537.  
<https://doi.org/10.5194/bg-11-5521-2014>
- Magnússon, B., G.A. Gudmundsson, S. Metúsalemsson & S.M. Granquist, 2020. Seabirds and seals as drivers of plant succession on Surtsey. *Surtsey Research*, 14, 115-130.  
<https://doi.org/10.33112/surtsey.14.10>
- Magnússon, B., P. Wasowicz & B. Magnússon, 2022. Vascular plant colonisation, distribution and vegetation development on Surtsey during 1965–2015. *Surtsey Research*, 15, 9-29.  
<https://doi.org/10.33112/surtsey.15.2>
- Myneni R.B., S. Hoffman, Y. Knyazikhin, J.L. Privette, J. Glassy, Y. Tian, Y. Wang, X. Song, Y. Zhang, G.R. Smith, A. Lotsch, M. Friedl, J.T. Morisette, P. Votava, R.R. Nemani & S.W. Running, 2002. Global products of vegetation leaf area and fraction absorbed PAR from year one of MODIS data. *Remote Sens. Envir.* 83: 214-231.  
[https://doi.org/10.1016/S0034-4257\(02\)00074-3](https://doi.org/10.1016/S0034-4257(02)00074-3)
- Peñuelas, J., I. Filella & J.A. Gamon, 1995. Assessment of photosynthetic radiation-use efficiency with spectral reflectance. *New Phytol.* 131: 291-296.  
<https://doi.org/10.1111/j.1469-8137.1995.tb03064.x>
- Peñuelas J., M.F. Garbulsky, & I. Filella I., 2011. Photochemical reflectance index (PRI) and remote sensing of plant CO<sub>2</sub> uptake. *New Phytol.* 191: 596-599.  
<https://doi.org/10.1111/j.1469-8137.2011.03791.x>
- Ustin, S.L., A.A. Gitelson, S. Jacquemoud, M. Schaepman, G.P. Asner, J.A. Gamon & P. Zarco-Tejada, 2009. Retrieval of foliar information about plant pigment systems from high resolution spectroscopy. *Remote Sens. Envir.* 113: S67-S77.  
<https://doi.org/10.1016/j.rse.2008.10.019>
- Sigurðsson, B.D., 2011. Mælingar á virkni vistkerfa í Surtsey og nálægum eyjum Vestmannaeyja. *Rit Fræðapings landbúnaðarins*, 8, 396-399.
- Sigurðsson, B.D., & N.I.W. Leblans, 2020. Availability of plant nutrients and pollutants in the young soils of Surtsey compared to the older Heimaey and Elliðaey volcanic islands. *Surtsey Research*, 14, 91-98.  
<https://doi.org/10.33112/surtsey.14.8>
- Wong, C.Y.S., P. D'Odorico, Y. Bhatena, M.A. Arain, & I. Ensminger, 2019. Carotenoid based vegetation indices for accurate monitoring of the phenology of photosynthesis at the leaf-scale in deciduous and evergreen trees. *Remote Sens. Envir.* 233: 111407.  
<https://doi.org/10.1016/j.rse.2019.111407>
- Wong, C.Y.S., P. D'Odorico, M.A. Arain & I. Ensminger, 2020. Tracking the phenology of photosynthesis using carotenoid-sensitive and near-infrared reflectance vegetation indices in a temperate evergreen and mixed deciduous forest. *New Phytol.*, 226(6), 1682-1695.  
<https://doi.org/10.1111/nph.16479>

## APPENDICES

Appendix 1. Overview over research excursions to the older islands in the Vestmannaeyjar archipelago, who were primarily responsible for measurements and publications from this work so far.

Date	Who	Main research activities and publications
<i>Álsey</i>		
10 Jul 2010	BM, BDS, Erling Ólafsson, <i>et al.</i>	Vegetation and invertebrate survey, C-fluxes (Sigurðsson, 2011)
<i>Ellidæy</i>		
11 Jul 2010	BM, BDS, Erling Ólafsson, <i>et al.</i>	Vegetation and invertebrate survey, C-fluxes (Sigurðsson, 2011)
15-24 Jul 2013	BDS, Járngerður Grétarsdóttir, Hafðís Hanna Ægisdóttir, <i>et al.</i>	Permanent plots established, vegetation survey (Magnússon <i>et al.</i> , 2014)
15-24 Jul 2013	BDS, Niki Leblans, <i>et al.</i>	Soil sampling, vegetation harvest (Thuys, 2014; Leblans <i>et al.</i> , 2017) and PRS probes (Sigurdsson & Leblans, 2020).
19-20 Jul 2018	Gróa Valgerður Ingimundardóttir, Nils Cronberg <i>et al.</i>	Bryophyte survey (Ingimundardóttir <i>et al.</i> , 2022)
28 Jul 2021	BDS, EMK	Soil fauna sampling, NDVI and C-fluxes on permanent plots
<i>Lyngfellisdalur - Heimaey</i>		
15-24 Jul 2013	BDS, Járngerður Grétarsdóttir, Hafðís Hanna Ægisdóttir, <i>et al.</i>	Permanent plots established, vegetation survey (Magnússon <i>et al.</i> , 2014)
15-24 Jul 2013	BDS, Niki Leblans, <i>et al.</i>	Soil sampling, vegetation harvest (Thuys, 2014; Leblans <i>et al.</i> , 2017) and PRS probes (Sigurdsson & Leblans, 2020).
29 Jul 2021	BDS, EMK	Soil fauna sampling, NDVI and C-fluxes on permanent plots
<i>Nýjahraun - Heimaey</i>		
29 Jul 2021	BDS, EMK	Soil fauna sampling, soil sampling, NDVI and C-fluxes on permanent plots

## REFERENCES

Not found in the paper

Thuys, R., 2014. Hoe veranderen plant traits langsheen een bodemchronosequentie op IJslandse eilanden? (M.Sc. thesis). University of Antwerp, Antwerp, Belgium.