Variation in the chlorophyll content index (CCI) in pioneer plants on Surtsey

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ABSTRACT

A plant community, dominated by *Leymus arenarius* and *Honckenya peploides* ssp. *diffusa*, has formed a relatively stable successional sere on most of the Surtsey island. A handheld instrument for measuring Chlorophyll Content Index (CCI) was tested in July 2012 on both species at 23 permanent study plots found on all the main surface types of the island. By grouping the plots based on the conditions of their surroundings, it could be derived how differences in water availability, nutrient availability and soil depth affected the CCI of those two species. Both had significantly higher CCI values ($p = 0.004$) when they grew on plots that received additional runoff water from nearby impermeable palagonite tuff surfaces, indicating that water availability could be an important limiting factor. Increased depth of the rooting substrate also significantly enhanced the CCI values for both species ($p = 0.001$), indicating again that soil resources (water and nutrients) were indeed limiting for both species. Plots with allochthonous nutrient inputs (located within a seagull colony) also had a strong interaction with the depth of the rooting substrate (<0.001), yielding the highest CCI values where both conditions were met. It is concluded that chlorophyll content meters have the potential to enable rapid assessment of the relative resource acquisition of pioneer plant species, giving valuable insights into their adaptations to different environmental conditions.

INTRODUCTION

Surtsey is the youngest island of the Vestmannaeyjar archipelago, which is located on an insular shelf 32 km off the south coast of Iceland. The island surfaced during an eruption in 1963-1967 and was protected already by 1965 to serve as a laboratory of how life establishes on an isolated volcanic island. With time it has become one of most studied ecosystems in Iceland (Baldursson & Ingadóttir 2007).

A plant community, dominated by *Leymus arenarius* and *Honckenya peploides* ssp. *diffusa*, has formed a relatively stable successional sere on most of the Surtsey island (Magnússon & Magnússon 2020, Magnússon 2022). It is only less dominant within a seabird colony on its southern part, where it has been partly replaced by different heathland and grassland species and on the palagonite tuff surfaces, where no vascular plants can colonize due to a lack of loose substrate for root growth.

Most terrestrial biology studies on Surtsey have focused on the colonization and community changes in flora, fauna and microbes (e.g. Fridriksson 1992, Ilieva-Makulec *et al.* 2015, Marteinsson *et al.* 2015, Magnússon S. *et al.* 2022, Magnússon B. *et al.* 2023, Ólafsson & Alfreðsson 2025) and only a few have been on the underlying ecophysiological and ecosystem processes (*e.g.* Sigurdsson 2009, Leblans *et al.* 2014, Sigurdsson & Stefánsdóttir 2015, Sigurdsson *et al.* 2022).

The Chlorophyll Content Index (CCI) is a non-destructive, relative measure of the amount of chlorophyll in a plant tissue, often used to explain variations in plant nutrient status or aboveground net primary production (Liu *et al.* 2019). It is calculated using a device that measures the ratio of light transmittance at a near-infrared wavelength (around 930 nm) to that in the red region (around 653 nm). Higher CCI values indicate greater chlorophyll content (Cate & Perkins 2003, Parry *et al.* 2014). The

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CCI is a unitless value, usually within the range of 1.0 (no pigment) to about 70.0 (very high pigment content), depending on instrument make and model (Cate & Perkins 2003).

The Chlorophyll Content Index has not been studied before on Surtsey, but Sigurdsson *et al.* (2022) did a study on three other vegetation indices and related them to variation in soil water availability, net photosynthesis rates and vegetation cover. Those were Normalized Difference Vegetation Index (NDVI), Photochemical Reflectance Index (PRI) and Clorophyll/Carotenoid Index (CCI). The last index mentioned is not the same as studied in this paper, albeit the same abbreviation (CCI), which here will only be applied to the Chlorophyll Content Index. The Clorophyll/Carotenoid Index uses different reflected wavelengths (around 532 nm and 630 nm) than the CCI.

The following hypotheses were put forward when the study was designed:

I. *Morphological differences*. Many plant species growing where light availability is a limiting factor, such as within mixed canopies of different species, distribute chlorophyll unevenly in space, and increase its contents where it is more likely that the leaf will receive higher light levels (top of canopy and upper surface of thicker leaves) (Chapin *et al.* 2011). As both studied species are pioneer species where light competition is normally not strong, I did not expect CCI to differ much between upper and lower leaf surfaces.

II. *Water availability:* There are certain permanent study plots located next to the impermeable palagonite tuff craters in Surtsey which receive lateral rainwater discharges and a significant increase in net photosynthesis per surface area has been documented there for the two pioneer species (Sigurdsson 2009, Sigurdsson & Stefánsdóttir 2015). If water is a strong limiting factor for the pioneer plants on the island I expected CCI to be higher on those plots for both species.

III. *Species differences.* Both species are pioneer species that invest mainly in belowground root growth, while maintaining relatively small but physiologically active aboveground parts (Leblans *et al.* 2014, Stefansdóttir *et al.* 2014). Therefore, I did not expect much difference in the CCI values for the two species, and that both would have relatively high CCI per unit leaf area.

IV. *Nutrient availability.* Many studies have documented how nutrient availability has increased within the seagull colony on the south part of Surtsey because of allochthonous nutrient inputs the birds have transferred from sea to land (Magnusson *et al.* 2000, Leblans *et al.* 2014, Aerts *et al.* 2020) and both photosynthetic rates per surface area and NDVI have been found to be significantly higher there (Sigurdsson *et al.* 2022). I expected that both species would invest in more chlorophyll content per leaf area on plots within the seagull colony.

V. *Depth of rooting media.* Leblans *et al.* (2014) showed that vegetation biomass accumulation and accumulation of soil organic matter (SOM) and nitrogen (N) was significantly different between plots established on lava with shallow depths of substrate for root growth, compared to plots established on deeper tephra sand areas. The reasons for this are likely partly related to H_{II} and H_{IV}. I expected that this would also be mirrored in the CCI of the plants growing on plots with contrasting "soil depth".

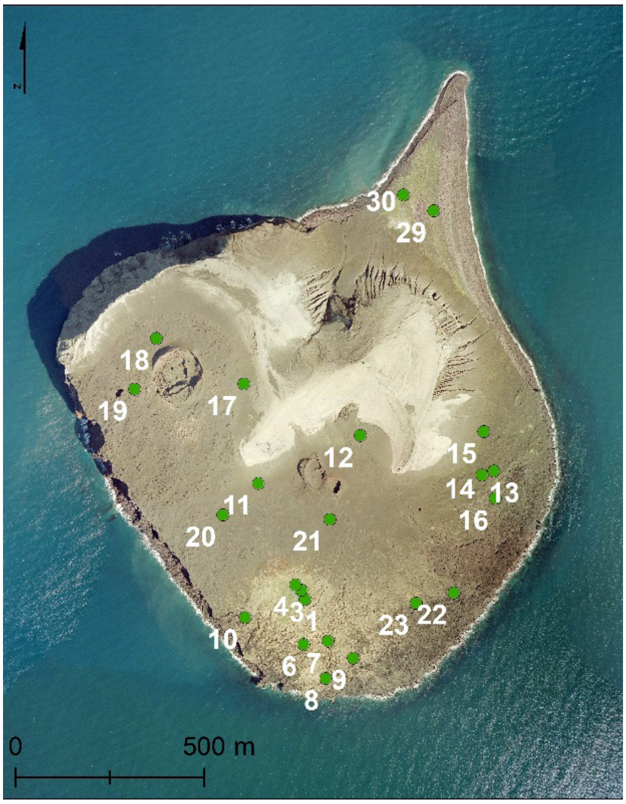

Figure 1. Location of the permanent study plots (dots and numbers) relevant to this study on Surtsey, shown on an aerial image from 2012 (© Surtsey Research Society)

VI. Interactions between factors. *L. arenarius* net photosynthesis has been shown to be less sensitive to drought than *H. peploides* (Sigurdsson 2009). Nutrient availability and "soil depth" has also been shown to strongly interact in its effects on vegetation growth (Leblans *et al.* 2014). I therefore expected that this would be the case for CCI in both species.

METHODS

Site description

Samples were collected on Surtsey (63°18´11 N, 20°36´17W) during 17-19 July 2012. The island has cool maritime climate, i.e. the annual temperature variation is dampened by the sea that cools the climate during summer and warms it during winter (Petersen & Jónsson 2020). During 2009-2019, the mean annual temperature was +6.6°C, with January (+3.2°C) and August (+11.3°C) as the coldest and warmest months, respectively. Total annual precipitation during the same period was on average 1009 mm, with Jun being driest (ca. 30 mm), while Sep-Feb typically receive >100 mm each (Petersen & Jónsson 2020). More information on the island's climate can be found in Petersen (2025).

The surface of the higher parts of Surtsey consists of palagonite tuff, whereas in lower parts it is made of basaltic lava or covered by deep tephra sands (Baldursson & Ingadóttir 2007). The island is still young and does not have well-developed soils (Möckel & Sigurdsson 2025). The lava is partly filled with tephra sand and silt, which originate from the eruption, erosion of the bedrock material and aeolian transport. The vegetation on these sandy areas is dominated by *Honckenya peploides* ssp. *diffusa* (Hornem.) Hultén ex V.V. Petrovsky and *Leymus arenarius* (L.) Hochst (Stefansdottir *et al.* 2014; Magnússon *et al.* 2022; plant nomenclature according to Wąsowicz 2020). Those two pioneer species were among the first vascular plants to successfully colonize Surtsey (Fridriksson 1992) and are now widely distributed all over the island (Magnússon *et al.* 2022), where they have formed a relatively stable successional sere.

In 1985, a seabird colony of lesser black-backed gulls (*Larus fuscus* L.) was established in an area on the south part of the island (Petersen 2009) and has been expanding in size ever since. Within the seagull colony, most pioneer plant species are gradually replaced by grasses, especially *Poa pratensis* L. and *Festuca richardsonii* Hook., except for the *L. arenarius* which continues to co-exist on deeper tephra sands (Magnússon *et al.* 2023).

Between 1990 and 2014, 37 permanent 10×10 m study plots were established on Surtsey to monitor the ongoing ecosystem changes at all the main occurring surface types found on the island. Today, 29 remain in the vegetation monitoring programme (Fig. 1). I selected 23 plots of those (Table 1), 9 inside and 14 outside the seabird colony. Both groups were placed

Table 1. Permanent study plots on Surtsey that were included in this work and how the basic environmental conditions vary among them. The conditions were if plots were located within the borders of the seagull colony on south and southwest Surtsey (Seagull), if they had deep (>30cm) tephra sand for rooting (Deep) and if they were located where they were likely to receive additional lateral rainwater discharges (Water).

Plot	Seagull	Deep	Water
01	1	1	0
03	1	1	0
04	1	1	0
06	1	0	0
07	1	0	0
08	1	0	0
09	1	0	0
22	1	0	0
23	1	0	0
10	0	0	0
11	0	1	0
12	0	1	1
13	0	0	0
14	0	0	0
15	0	1	1
16	0	0	0
17	0	1	0
18	0	0	0
19	0	0	0
20	0	1	0
21	0	1	0
29	0	1	1
30	0	1	1

on lava surfaces which most had some shallow tephra sand or on deep (≥30 cm) tephra sands.

Chlorophyll Content Index measurements

A portable, non-destructive and lightweight instrument (CCM-200 Chlorophyll Concentration Meter, Opti-Sciences, Hudson, NH, USA) was used to measure Chlorophyll Content Index (CCI) for six randomly chosen individuals of *L. arenarius* and *H. peploides* within or adjacent to each permanent plot. The measurements were done *in situ* on both above and below surfaces of the 3^{rd}-4^{th} and the 7^{th}-8^{th} leaf from the youngest emerging leaf of each plant for *L. arenarius* and *H. peploides*, respectively.

Data analysis

All analyses were done on average values for the six individuals measured at or adjacent to each plot, which were randomly selected. Distributions were first checked visually for normality before ANOVAs were used to test for differences in CCI between upward and downward sides of leaves of the two species (Two-Way), plots with additional lateral rainwater discharge inputs (Two-Way) and between the two species growing and on plots with contrasting soil depth (Deep) inside and outside the seagull colony (Three-Way).

RESULTS

There were no significant differences in CCI values between upward and downward facing leaf surfaces of either species (p = 0.99). The average CCI value across both leaf sides, both species and all plots was 16.1 (data now shown).

The average CCI values increased across both species from 14.1 to 19.2, or 37%, on permanent plots that received additional lateral rainwater discharges (Fig. 2; p = 0.004). There were no significant differences between the two species in this respect (Fig. 2).

The average CCI across all the plots for *L. arenarius* and *H. peploides*, was 16.4 and 15.7, respectively. This difference was not significant (S, p = 0.62; Table 2), and neither was there a significant interaction in how *L. arenarius* and *H. peploides* responded at plots at different environmental conditions (S×D, p = 0.22; S×G, p = 0.52; Table 2). When, however, the CCI values of both species together were compared across all plots, a significant 40% positive effect was found if they were located on deep tephra sands (18.8 vs. 13.4; D, p = <0.001; Table 2).

When the CCI values of both species were compared on plots inside the seagull colony compared to outside, only a weakly significant 20% increase was observed (17.6 vs 14.6; G, p = 0.03; Table 2). However, plants that grew on plots within the seabird colony on deep tephra sands had 40%

Figure 2. The CCM-200 Chlorophyll Content Meter next to *Leymus arenarius* (straws) and *Honckenya peploides* ssp. *diffusa* (forbs) next to Plot 13 on Surtsey in July 2012. Photo: B.D. Sigurdsson.

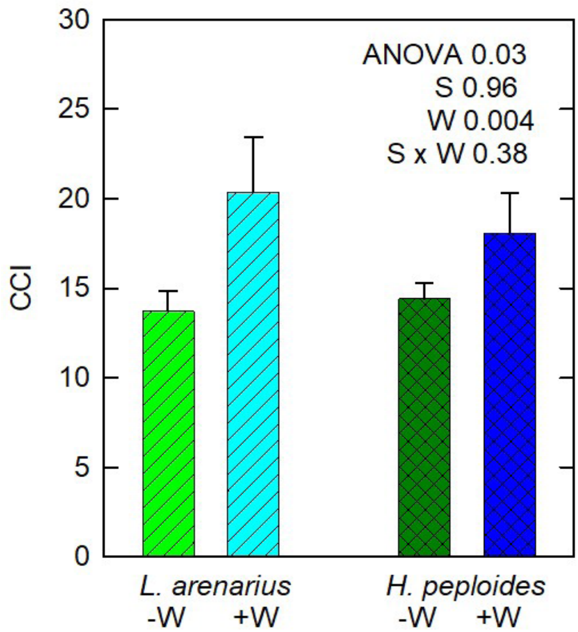

Figure 3. Mean (±SE) values of Chlorophyll Content Index (CCI) of *Leymus arenarius* and *Honckenya peploides* ssp. *diffusa* plants without (green colours) and with additional rainwater inputs by lateral rainwater discharges (blue colours) on Surtsey. Also shown are p-values of 2-Way ANOVA on species (S) and plots with additional water (W) and their interaction (S x W).

Table 2. Mean (±SE) values of Chlorophyll Content Index (CCI) of the two species (S), *Leymus arenarius* and *Honckenya peploides* ssp. *diffusa*, on permanent study plots on lava or on deep (>30cm) tephra sands (D) inside and outside the seagull colony (G) on Surtsey. Also shown are the p-values for 3-Way ANOVA on those three factors. Significant values are shown in bold format.

Outside seagull colony		Inside seagull colony	
Shallow	Deep	Shallow	Deep
L. arenarius			
14.4 ±1.1	14.5 ±2.1	11.3 ±1.0	25.5±1.8
H. peploides			
13.9 ±1.1	15.5 ±1.7	13.9 ±1.5	19.7 ±2.5
3-Way ANOVA p-values			
Model	**<0.001**		
S	0.62		
G	**0.03**		
D	**<0.001**		
S × G	0.52		
S × D	0.22		
G × D	**0.001**		
G × D × S	0.07		

and significantly higher CCI values across the two species (G×D, p = 0.001; Table 2). It was noteworthy that *L. arenarius* had somewhat stronger positive G×D reaction than *H. peploides*, or +125% (11.3 vs 25.4 CCI) compared to +41% for *H. peploides* (13.9 vs. 19.6 CCI), but the species, gull colony and depth interaction was not quite significant (S×G×D p = 0.07; Table 2).

DISCUSSION

The H_I was confirmed, the CCI values did not vary between upper and lower leaf surfaces of the *L. arenarius* and *H. peploides* plants. As both species are pioneers and commonly grow on sandy areas with low vegetation cover along coasts in Iceland (Kristinsson *et al.* 2018), where light competition is not strong, this was expected. They also both form a relatively sparse single layer canopy, where leaves are typically not placed fully laterally (Figs. 2 and 4), so an even distribution of chlorophyll along all leaf surfaces can receive some solar light and yield higher total net photosynthesis per surface area.

The H_{II} was confirmed, that CCI would be higher on plots adjacent to palagonite tuff surfaces. Sigurdsson (2009) and Sigurdsson and Stefánsdóttir (2015) had already shown that soil water availability and net-photosynthesis rates were higher in such plots. However, the summer 2012 when this study took place had a long dry-spell which severely affected the island's vegetation (Schrenk *et al.* 2022), and the apparent "drought response" may therefore have been especially strong this year.

The CCI values did not significantly differ between *L. arenarius* and *H. peploides* per unit leaf area, so H_{III} was also confirmed. Neither were the S×G, S×D or S×G×D interactions significant, indicating that both species responded similarly to changes in nutrient availability and "soil depth". The H_{VI} was therefore not confirmed. Sigurdsson (2009) found that *L. arenarius* maintained higher net photosynthesis rates per surface area than *H. peploides* on drier plots. There, it was hypothesized that this was due to the *L. arenarius*' deeper and more extensive root systems which could then partly alleviate water stress. Higher soil water contents were also measured later in those same plots (Stefánsdóttir *et al.* 2014). Plants with the same chlorophyll content can have different

Figure 4. *Leymus arenarius* and *Honckenya peploides* ssp. *diffusa* plants close to Plot 30 in July 2012, where lateral rainwater discharges from the palagonie tuff craters on Surtsey increases soil moisture. Photo: B.D. Sigurdsson.

photosynthetic rates during water stress, if stomates partly close for the species which experiences more water stress (Chapin *et al.* 2011). These contrasting findings may therefore not contradict each other.

It has been observed that *L. arenarius* is less sensitive to competition from other vascular plants when nutrient availability has improved after it had colonized than *H. peploides* (Magnússon 2023). *L. arenarius*, with its long straws and leaves, can form taller canopy and more leaf area per unit surface area than *H. peploides* can (Fig. 4). That is probably why it persists longer in competition with other species on deeper soils.

The CCI averaged as 16.1 across both species on Surtsey. It was highest for both species on deep soils within the seagull colony, 19.6 and 25.4 for *H. peploides* and *L. arenarius*, respectively. Parry *et al.* (2014) stated that the highest CCI values recorded are ca. 70 for vascular plants with exceptionally thin leaves with high chlorophyll contents. However, Cate and Perkins (2003) found maximum CCI of 25 in fertilization experiments on sugar maple (*Acer saccharum* Marsh.) and Rex Immanuel and Miruna (2024) found it to vary between 10 and 33 in rice leaves (*Oryza sativa* L.) with contrasting N contents. Values of 20-25 in the present study may therefore be relatively high, especially for plant species with thick leaves, as both *L. arenarius* and *H. peploides* have. More measurements of CCI need to be done for different plant species in Iceland to get a good comparison for what is “normal”.

It came as a surprise that the higher CCI values per unit leaf area inside and outside the seagull colony were only weakly significantly different across both species. The higher net photosynthesis and NDVI that have been found within the seagull colony for surfaces where these two species are at least co-dominating (Sigurdsson *et al.* 2022) may therefore rather be a product of denser canopies (more leaf area) per surface area rather than more activity per unit leaf area. However, the dry summer of 2012 (Schrenk *et al.* 2022), may also have reduced the difference between plots inside and outside the gull colony on the shallower soils, which would have reduced the overall difference (see later). The H_{IV} was still confirmed as the difference was still significant ($p = 0.03$; Table 2).

The CCI was significantly higher across both species on deeper tephra sands than on plots on lava with shallow depths of substrate for root growth (Table 2), and H_V was therefore confirmed. Leblans *et al.* (2014) also found that plant productivity and SOC accumulation was higher in plots with deeper rooting substrates, both inside and outside the seagull colony. However, the strongly significant G×D interaction in Table 2 was also noteworthy, caused by plants on plots within the seagull colony growing on “deep soil” having the highest CCI values recorded. It is possible that this strong G×D interaction was also partly caused by the exceptionally dry 2012 summer (Schrenk *et al.* 2022), so the expected strong positive impact of enhanced nutrient availability within the seagull colony (H_{IV}) was only realized where soils were deeper with higher water availability.

Chlorophyll content meters have the potential to enable rapid assessment of the relative condition of leaf chlorophyll in a variety of plant species, giving valuable insights into their adaptations to different environmental conditions.

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