Master's thesis

NTNU
Norwegian University of Science and Technology
Faculty of Natural Sciences
Department of Biology

Halvor Røssum

Winter gardening at 78° North:

measuring extreme warm spell impacts on above- and below-ground biomass of vascular plant communities

Master's thesis in Biology
Supervisor: Brage Bremset Hansen
Co-supervisor: Mathilde Le Moullec, Laura Bartra Cabré
June 2022

Photos: INSYNC project collection

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Abstract

Global warming is most pronounced in the high Arctic. This is likely to impact tundra vegetation communities, in which most of the biomass is located below ground. The below-ground biomass is important for both the dynamics of the vegetation communities themselves as well as for the global carbon cycle. However, it is often only the above-ground biomass, or more typically proxies of it, that is monitored. We often lack basic knowledge about how these proxies relate to each other and to the below-ground biomass, as well as how the below- versus above-ground biomass ratios may respond to environmental stress. This master thesis utilizes data from a vegetation transplant experiment conducted at Svalbard to contribute to filling these knowledge gaps. The experiment simulated extreme winter weather events in two different vegetation communities over three winters, following which all vascular plant biomass was harvested. Two types of extreme events were simulated: rain-on-snow events, causing basal icing, and thaw-freeze events, exposing the soil and vegetation to above-zero and subsequent freezing temperatures. The results showed that two above-ground biomass proxies, Normalized Difference Vegetation Index (NDVI) and the point intercept method (PIM) correlated positively with each other (r = 0.74 [0.59 – 0.84]). Both the above-ground biomass, below-ground biomass and total biomass was reflected better by NDVI (r = 0.78 [0.65 – 0.87], r = 0.70 [0.53 – 0.82] and r = 0.74 [0.58 – 0.84], respectively) than by PIM (r = 0.73 [0.57 – 0.83], r = 0.55 [0.33 – 0.71] and r = 0.59 [0.39 – 0.74], respectively) at the community level. At the species level, PIM reflected above- and below-ground biomass better than NDVI. While basal icing had only small effects on vegetation, the community-level ratio between below- and above-ground biomass increased under winter thaw-freeze treatment in the wet community. This was not the case in the drier community. Interestingly, although the species-level biomass ratios largely responded similarly, the treatments affected the above- and below-ground biomass of the species differently, which could be related to their growth forms. These results provide novel insight into the effects of extreme winter climatic events on above- and below-ground biomass and suggest that both NDVI (vascular plant community-level) and PIM (species level) are useful proxies to study impacts of environmental change on low-productive high-arctic tundra vegetation.

Samandrag

Global oppvarming gjer dei arktiske vintrane varmare og våtare, noko som fører til ei auke i ekstreme vêrfenomen på vinteren. Døme på slike vêr-hendingar er regn som frys på og dannar eit islag som «kapslar inn» tundraen (is-dannande vinterregn), samt mildvêr som smeltar snøen og tiner eit jordlag før det blir kaldt og frys på att (tine-fryse-hendingar). I dei arktiske vegetasjonssamfunna finn ein mest biomasse under bakken. Den er ikkje berre viktig for dynamikken i vegetasjonssamfunnet, men òg for den globale karbonsyklusen. Likevel er det hovudsakleg biomassen over bakken som har vorte studert i Arktis, ofte ved hjelp av ulike estimeringsmetodar (t.d. normalisert differanse-vegetasjonsindeks (NDVI) og «point intercept»-metoden (PIM)). Vi manglar grunnleggjande kunnskap om korleis desse estimeringsmetodane reflekterer biomassen under bakken i arktiske vegetasjonssamfunn, samt om korleis biomassen under bakken reagerer på ei auke i ekstreme vêr-hendingar på vinteren. For å vere med å tette desse kunnskapshola nyttar denne oppgåva seg av resultata frå eit fleirårig eksperiment utført på Svalbard der planter frå to ulike vegetasjonssamfunn vart utsett for eksperimentelle ekstreme vêrfenomen (is-dannande vinterregn og tine-fryse-hendingar) tre vintre på rad, før all biomassen vart hausta. Resultata viser at NDVI og PIM korrelerte positivt med kvarandre (r = 0.74 [0.59 – 0.84]). På samfunnsnivå reflekterte NDVI biomassen over bakken, biomassen under bakken og total biomasse (r = 0.78 [0.65 – 0.87], r = 0.70 [0.53 – 0.82] og r = 0.74 [0.58 – 0.84], i same rekkjefølgje) noko betre enn PIM (r = 0.73 [0.57 – 0.83], r = 0.55 [0.33 – 0.71] og r = 0.59 [0.39 – 0.74], i same rekkjefølgje), medan PIM reflekterte biomassen til den enkelte art betre enn NDVI. I det våtaste vegetasjonssamfunnet vart det relativt sett meir biomasse under bakken etter tine-fryse-hendingar, medan dette forholdet endra seg ikkje i det tørraste vegetasjonssamfunnet. Dei enkelte artane responderte, stort sett, på same måte som samfunnet, til trass for at dei hadde ulike måtar å endre forholdstalet mellom biomasse under og over bakken på. Desse resultata gir ny innsikt i korleis ekstreme vêr-hendingar påverkar biomasse under og over bakken, og syner samstundes at både NDVI og PIM er nyttige verkty for å undersøkje dette vidare.

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Introduction

The Arctic winters are becoming warmer and wetter (Bintanja & Andry, 2017; Graham et al., 2017). It is predicted that this change in climate will lead to more frequent rain-on-snow (ROS) episodes in the future (Hansen et al., 2014). ROS events may cause rain to permeate the snowpack and freeze on the ground underneath the snow, causing a basal ice layer to cover the ground (Putkonen & Roe, 2003). There are indications that such icing from ROS events can affect both reproduction, growth and phenological timing in the high Arctic vegetation (Le Moullec et al., 2019; Milner et al., 2016). On the other hand, warm winter periods and ROS can also melt away the snow layer and thaw the vegetation before colder weather comes and refreezes the vegetation, without the insulating snow layer. It is also documented that such thaw-freeze events affect the vegetation, yet only from studies conducted in the low Arctic, and only for the above-ground biomass (Bjerke et al., 2017; Bokhorst et al., 2011; Bokhorst et al., 2009) In general, however, the impacts of warmer and rainier winters on Arctic vegetation, and especially the below-ground biomass, remain largely unexplored.

Studies point out that the tundra, in general, is becoming greener (Arctic 'greening'), and that a warmer climate can be one of the drivers behind this (Epstein et al., 2012; Frost et al., 2020; Myers-Smith et al., 2011). However, there is also evidence that the trend of Arctic 'greening' has been slowed down, and even reversed in some areas (Bhatt et al., 2013; De Jong et al., 2011). Such Arctic 'browning' can be caused by different reasons (Myers-Smith et al., 2020), such as damage to photosynthetic tissue due to extreme winter climate events, e.g. thaw-freeze (Bjerke et al., 2017; Bokhorst et al., 2008, 2011; Phoenix & Bjerke, 2016). A decreasing correlation between mean annual temperatures and maximum NDVI can also explain this phenomenon (Vickers et al., 2016). Investigating how icing and thaw-freeze events affect the above- and below-ground biomass is therefore a contribution to disentangling the drivers behind Arctic 'greening' and 'browning' even further.

Although most studies conducted on vegetation in the Arctic use above-ground biomass measurements, it is shown that most of the biomass in Arctic tundra ecosystems is located below ground, with an exception for polar deserts. (Bell & Bliss, 1978; Bliss et al., 1984; Campioli et al., 2009; Henry et al., 1990; Wallén, 1986). Below-ground biomass is known to play important roles in the Arctic tundra ecosystems: it is tightly linked with above-ground biomass traits, and it is important for carbon storage (Iversen et al., 2015; Schuur et al., 2008).

Yet, there are a lot of research gaps when it comes to the drivers – and importance – of changes in below-ground biomass in the Arctic (Iversen et al., 2015). To study how the above/below-ground biomass ratio changes in response to extreme climatic events is therefore interesting, both to understand how the tundra plant communities might change in the future, and for the future feedback of carbon from the tundra into the atmosphere (Euskirchen et al., 2009).

Different 'tools' can be used when investigating the above- and below-ground biomass. The exact biomass can be measured by harvesting, weighing and drying the above- and below-ground biomass (as done in Van Der Wal & Stien (2014)). Since this is a direct measure of the biomass, not a proxy, it makes it the most accurate measure. The destructive nature of harvesting the biomass makes this method unsuitable for providing time series of the biomass production at the sampling site, at least for perennial species.

We can also estimate the above-ground biomass production in a vegetation community by using proxies and/or indices of primary production. One of the most common indices of primary production is the Normalized Difference Vegetation Index (NDVI). This method uses spectral reflectance data to calculate vegetation indices. The NDVI value is calculated from the reflectance of the red portion of the spectrum (RED) which chlorophyll absorbs and the reflectance of the near-infrared portion (NIR) of the spectrum which chlorophyll does not absorb: $NDVI = (NIR - RED)/(NIR + RED)$ (Tucker, 1979). NDVI can be a good measure for photosynthetic tissue biomass production, both when using NDVI maps derived from satellite images, but also from handheld NDVI instruments (Epstein et al., 2012; Hogrefe et al., 2017; Walker et al., 2003).

Another method for estimating the above-ground biomass production is the point intercept method (PIM). The PIM consists of registering the number of intercepts between the tip of a lowering pin and the vegetation at a set number of positions in the vegetation area that is to be investigated (Bråthen & Hagberg, 2004; Jonasson, 1988)). Data collected with PIM can then be calibrated against destructive biomass data. The non-destructive nature of PIM means that the measurements can be repeated both in one growing season and across growing seasons, and hence result in time series that shows the estimated above-ground biomass production within and between growing seasons (Jonasson, 1983).

Some studies have compared how well NDVI (and similar spectroscopy methods) and PIM estimate the above-ground biomass (Byrne et al., 2011; Ónodi et al., 2017), but from tundra communities limited knowledge exists. The knowledge of how PIM and NDVI reflect the below-ground biomass is also limited. Therefore, it is of interest to compare NDVI and PIM as methods to estimate the total biomass production in different tundra communities, and test if they correlate with harvested above- and below-ground biomass. Thus, this master thesis aims to use data from an icing and thaw-freeze vegetation experiment in high Arctic Svalbard to answer the following research questions:

(1) How do different proxies of above-ground biomass (NDVI, PIM) relate to each other, and how well do they reflect measured above-ground and below-ground biomass, in high Arctic tundra vegetation communities?

(2) How is the below- versus above-ground biomass ratio affected by extreme climatic (icing and thaw-freeze) events?

Although it is shown that extreme climatic events can affect the above-ground biomass both when it comes to its phenological timing, tissue damage and biomass proxies, little is known about how such events affect the below-ground biomass (Bokhorst et al., 2011; Le Moullec et al., 2019, 2021; Milner et al., 2016). Hence, little is also known about how the below- versus above-ground biomass ratio is affected by extreme climatic events. However, knowing that below-ground biomass acts as storage organs for many tundra plants (Iversen et al., 2015), it is possible that compensatory plant responses after both changed phenological timing and tissue damage can lead to a decrease in the below-ground biomass after extreme climatic events, and therefore also affect the below- versus above-ground biomass ratio.

I expect both NDVI and PIM to be good estimators of, and thus positively correlated with, above-ground biomass at the vascular plant community level (Epstein et al., 2012; Hogrefe et al., 2017; Jonasson, 1988; Walker et al., 2003). Since NDVI is measuring the reflectance of the whole vegetation community, while PIM gives information about the abundance of each species, I expect NDVI to perform better than PIM at the community level, and PIM to perform better than NDVI at the species level. NDVI is known to saturate for high levels of above-ground biomass (Gao et al., 2000; Tucker, 1977), which is probably less likely for PIM. Therefore, given that a sufficient range of biomass is covered in the data, I expect the strength of correlation between biomass and NDVI, and PIM and NDVI, to decrease at high biomass. There is limited knowledge on how well NDVI/PIM reflects the below-ground biomass of the targeted vegetation communities. However, since both NDVI and PIM are proxies for above-ground biomass, one can expect that the two proxies reflect above-ground biomass better than below-ground biomass. Different tundra species have different below-/above-ground biomass ratios (Iversen et al., 2015), and therefore I expect the correlation between PI/NDVI and below-ground biomass to be dependent on the species composition of the different plant communities.

Methods

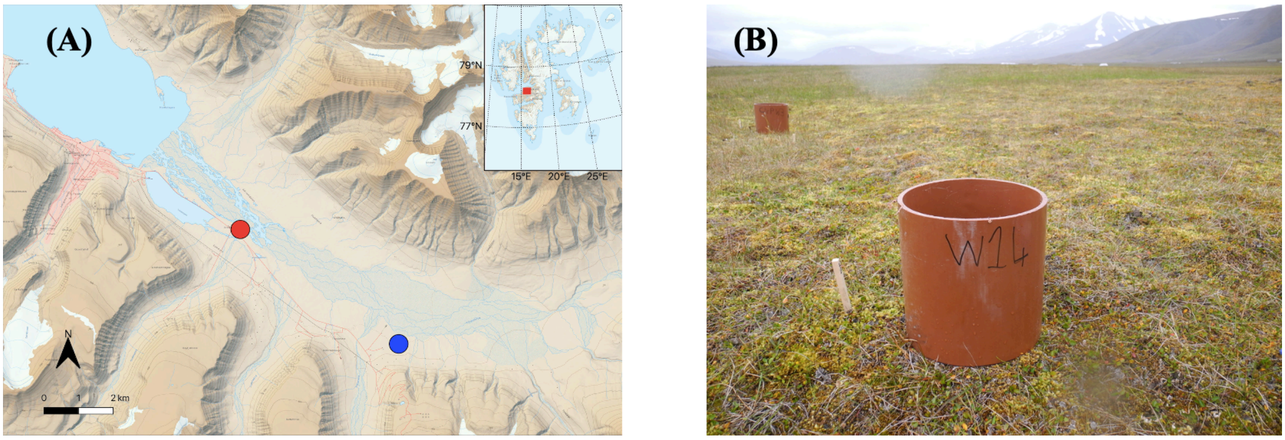

Figure 1. (A) Location of the study sites. The blue circle indicates the area where the plots were transplanted from. The red circle indicates the location of 'the garden'. © Norwegian Polar Institute. **(B)** Example of where one of the plots was transplanted from, as well as the plastic pipe the plots were transplanted in. Photo: INSYNC project collection.

Study area

The field site was located in Adventdalen valley, 5 km east of Longyearbyen, on the west coast of the archipelago of Svalbard (78°12`N, 15°50`E) (Figure 1 A). Because of its proximity to the warm North Atlantic Current, the west coast of Svalbard is known to have an oceanic climate with relatively mild temperatures compared to other areas at the same latitude (Aagaard et al., 1987). In the period 2018 to 2021 (when the experiment was done) the mean temperature in the winter months (October – March) was -10.4 °C, the mean temperature in the summer months (April – September) was 1.7 °C and the average annual precipitation (for years 2018-2020) was 118.9 mm (data from Adventdalen weather station, available at seklima.met.no).

One can divide Svalbard into different bioclimatic zones, each with its own characteristic vegetation composition. Adventdalen is placed in the subzone middle Arctic tundra zone (MATZ) (Jónsdóttir, 2005). There is also a heterogeneity of ecosystems inside the subzones. In the MATZ, and hence also Adventdalen, the vegetation communities differ between dry areas in the valley side and on ridges, and more moist and productive areas on the valley floor (Johansen & Tømmervik, 2014). In the experiment, two different vegetation communities from the valley floor are in focus: one community from relatively dry areas and one community from wetter areas. The two vegetation communities were targeted to contain mainly the same species (e.g. *Salix polaris*, *Alopecurus borealis*, *Bistorta vivipara, Poa* *arctica, Luzula confusa, Dupontia fisheri* and *Equisetum arvense*), but moss was more dominant in the vegetation community of the wet habitat. The two vegetation communities are later referred to as *mesic* and *wet* habitats.

The experiment

A total of 54 turfs (diameter 19.5 cm, depth 20 cm) containing the targeted species *A. borealis*, *S. polaris*, *B. vivipara*, *P. arctica* and *L. confusa*, were in 2018 transplanted to the field site from an in-situ control site, about 10 km east of Longyearbyen (figure 1 A and B). The transplanting was done one year before treatments of the plants started, in order to let the vegetation acclimate to the new environment. The turfs were collected from two different habitats: mesic (n = 33) and wet (n = 21). Each turf was planted in a pipe (with an inner diameter of 19.5 cm and a length of 20 cm). The turfs in the pipes were transported to the field site ('the garden'), where 54 pots were planted in 6 rows with 60 cm between them. In each row, there was a minimum of 40 cm between each pot (figure 2 B). The placement of the plots in the garden was randomized. In addition to the 54 plots transplanted to the garden, control plots were established at the in-situ control sites, both with the pipe (mesic: n = 10, wet: n = 6) and without the pipe (mesic: n = 10, wet: n = 6). All plots in the garden were watered during the growing season. The wet plots were watered more than the mesic plots (wet plots approximately 1 L per plot per week, mesic plots approximately 0.5 L per plot per week).

Two different treatments were applied to the plots in the garden during the winters of 2019, 2021 and 2021: icing treatment (mesic: n = 13, wet: n = 8, 2019-2021) and thaw-freeze treatment (mesic: n = 10, wet: n = 5, 2020 and 2021) (figure 2 A, C and D). Some plots were also given no treatment (control plots, mesic: n = 10, wet: n = 8). The icing treatment consisted of placing a bottomless bucket over the plots, and filling it gradually with water until a 15 cm thick ice layer was established. The thaw-freeze treatment consisted of placing an electric heater (60 W) inside an insulated bucket, which again was placed on top of the plot (with the bottom up), for a week. The plot surface and subsurface (at 5 cm depth) temperature reached respectively around 6 – 10 °C and *-5 – 0 °C.* After applying the thaw-freeze treatment, a refreezing period followed, without the snow cover as protection for six days. Finally, the plots were covered with snow again. If rain occurred naturally during the winter a tarp was used to keep the garden dry and to make sure that no icing/thaw-freeze events happened naturally to any of the plots.

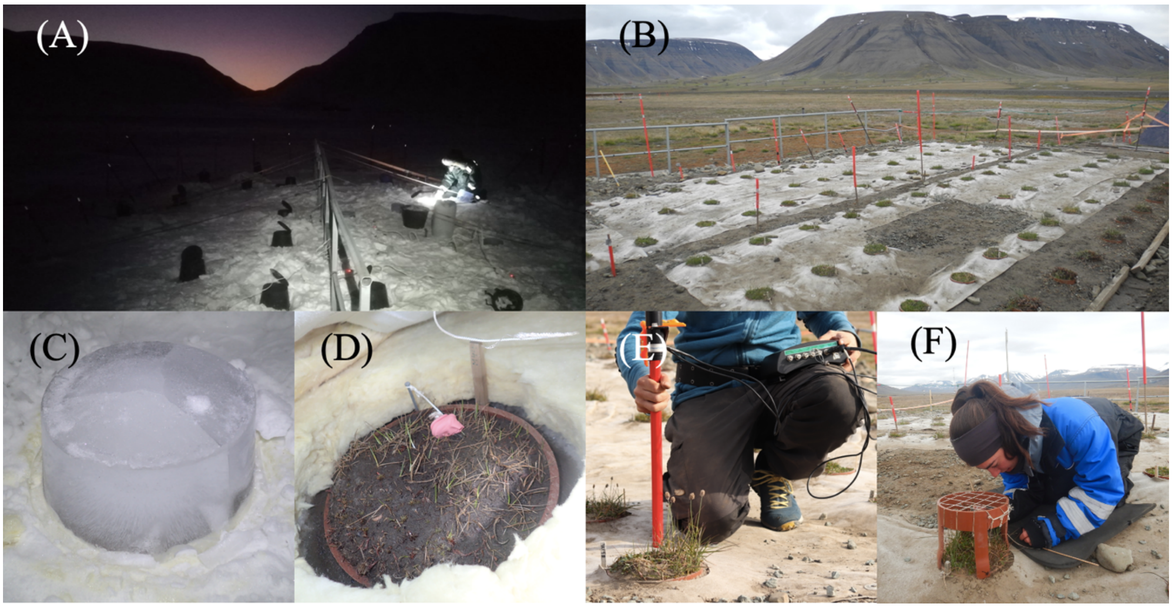

Figure 2. (A) An overview of the garden during treatment of the plots in January 2020. **(B)** An overview of the garden in July 2021. (**C)** Iced plot. **(D)** Thaw-freezed plot, before the refreezing period. Note the green shoots of *A. borealis.* **(E)** Measuring NDVI. **(F)** Performing the point intercept method. All photos: INSYNC project collection.

NDVI data

NDVI was measured for each plot approximately every fifth day during the growing season of 2021, until the plot was harvested. At the time of harvest, the NDVI was also measured. A handheld NDVI machine (SpectroSense 2+) was used to measure the NDVI of a circle (11 cm in diameter) centred in the middle of the plot (figure 2 E). NDVI can take values between -1 and 1, but negative values are only measured in unvegetated areas. The closer the NDVI is to 1, the greener is the area measured (Myneni et al., 1995).

Point intercept data

PIM was performed at the peak growing season of 2021. In each plot, the PIM was performed by placing a frame with a double string grid on it. The strings were aligned to help the observer lower the pin vertically from the cross while aiming from above. The double string grid made in total 16 crosses. At each cross, a wooden pin (diameter = 3 mm) was lowered until it hit the ground (figure 2 F). For each plot, it was recorded which species the pin intercepted on its way to the ground, as well as how many times each species was hit. When the pin hit the ground, the end-point of the plot was recorded as either moss, litter or packed sand. When using the PIM data in the data analysis two different subsets were used: either all recorded intercepts with moss, lichen and vascular plants in the plot (aPIM), or all recorded intercepts with vascular plants in the plot (vPIM).

Harvested biomass data

The total amount of biomass of different species was quantified in each plot, by harvesting, dissecting, washing, drying (48 hours at 60 degrees Celsius) and weighing (accuracy of +-0.0001 g) all above- and below-ground vascular plant biomass from all plots. The plots were harvested between the 24^{th} of July and the 5^{th} of August, at the peak of the growing season. When harvesting the plot, all of the soil and biomass in the plot cylinder was brought up of the ground (figure 3 A). The plot consists of three horizontal layers: (1) a lower layer consisting of soil, (2) a middle layer consisting of moss and (3) an upper layer mainly consisting of vascular plants (figure 3 B). The roots of the vascular plants grow in the moss layer as well as in the soil layer. In the harvest process, the soil and moss were carefully removed from the two lower layers, which left us with the vascular plants (figures 3 C, D and E). The parts of the vascular plants that were in the moss layer or the soil layer were sorted as *below-ground* biomass while the parts of the plants that came from the upper layer were sorted as *above-ground* biomass (figure 3 F). Although the top layer of the moss marked our dividing point, I will hereafter refer to it as above- and below-ground biomass. For most species, the transition between above- and below-ground biomass was characterized by a change in colour from green to brown. This is further elaborated in figure A1. Both the above- and below-ground parts of the plant were then washed, dried and weighed. A small amount of unidentified roots that were found in the soil/moss-layer of the plot were washed, dried and weighed as well, and identified as *free roots*. The free roots were also defined as below-ground biomass. The total biomass of the plot was defined as above-ground biomass + below-ground biomass. Most of the plots had an additional freezing step between the removal of soil/moss and the washing/dissecting process. This extra step was necessary because the plots had to be harvested during a limited time window. Since the washing/dissecting step required a lot of time, freezing down the biomass allowed us to focus on harvesting plots and removing the soil/moss, while postponing the washing/dissecting of the biomass until the harvest process was finished.

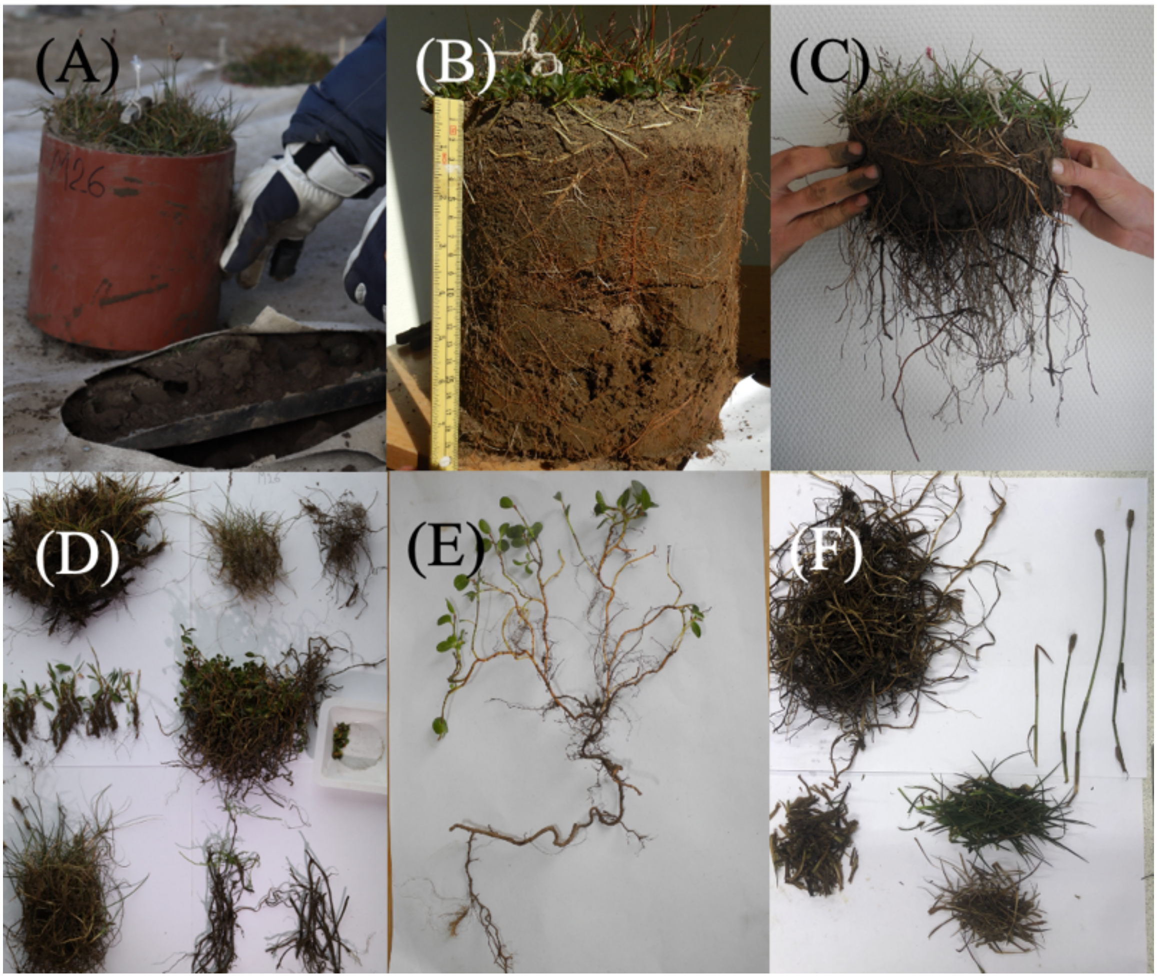

Figure 3. (A) Plot taken out of the ground. **(B)** Harvested plot seen from the side. **(C)** A plot with about half the soil layer removed. **(D)** Different species separated into different piles. **(E)** One harvested individual of *S. polaris*. **(F)** All *A. borealis* in one of the plots separated into different parts. All photos: INSYNC project collection.

Statistical analysis

All data analyses were performed in R version 4.1.2 (R Core Team, 2021). PIM data (count data) were natural log (ln) transformed, while biomass weight data were square-root transformed. NDVI data, which are continuous, were not transformed. All transformations were done in order to meet the assumption of normally distributed residuals of the linear regressions (Poole & O'Farrell, 1971; Warton et al., 2016).

Comparing two different proxies of biomass (NDVI, PIM)

The relationship between NDVI and PIM was modelled using a linear model, lm() function in "stats" package (R Core Team, 2021), with vPIM count data as the response variable, and NDVI data as the predictor variable. The original habitat of the plot as well as the treatment given was included as predictor variables in all possible combinations (interactions). Model selection with AICc (Burnham & Anderson, 1998) was used to see if habitat or treatment should be included in the final model.

The NDVI values used as the predictor variable in the model were the NDVI recordings closest to the day when the PIM data was collected for each plot. The subset of PIM data (aPIM or vPIM) that were used as the response variable in the model was the subset of PIM data that best reflected the harvested vascular biomass (above-ground biomass, below-ground biomass and total biomass) of the plots. This was found by fitting six linear models (aPIM/vPIM as predictor variable, and above-ground biomass/below-ground biomass/total biomass as response variable), and then ranking the models based on the second-order Aikake Information Criterion (AICc) (Burnham & Anderson, 1998).

How well do the two different proxies of biomass reflect the measured biomass?
To investigate how PIM and NDVI reflected the harvested vascular biomass six linear models were fitted. The models included either NDVI or vPIM as predictor variables and either above-ground biomass, below-ground biomass or total biomass as response variables. To find out which predictor variable that predicted the above-ground, below-ground and total biomass best, the two models with the same response variables were rated using AICc.

Pearson's correlation tests, cor.test()-function, were performed to examine how well NDVI and PIM predicted the measured above-ground, below-ground and total biomass for each species. Correlation coefficients (Pearson's r) were calculated between the log-transformed vPIM plus one (log(vPIM + 1)) and square root transformed weight of harvested biomass (above-ground, below-ground and total biomass) for each vascular species and for all species combined. Adding one to the number of vascular plant point intercept hits before log transforming was done to avoid log transforming zero. Correlation coefficients were also calculated between the NDVI measure done at the time of harvest and the square root transformed weight of the harvested biomass (above-ground, below-ground and total biomass) for all species as well as for all species combined.

How is the BGB/AGB-ratio affected by extreme climatic events?
Linear mixed-effect models were fitted using the lmer() function from the lme4 package (Bates et al., 2015). Below-ground/above-ground biomass ratio (BGB/AGB-ratio) was the response variable in all models, while different combinations of habitat and treatment were

included as predictor variables. To investigate how the BGB/AGB-ratio changes for the whole community species was included as a random effect. This was done to account for the fact that observations from the same species were not independent. Model selection (model.sel() function in MuMin package (Bartoń, 2020)) was used to choose the best model using the AICc criteria.

In order to investigate how the harvested above-ground biomass and the below-ground biomass differed between treatments, two models were fitted. In one of the models, the response variable of the best-ranked model in the model selection above (BGB/AGB-ratio) was replaced with sqrt(harvested above-ground biomass), and in the other model, the response variable was replaced with sqrt(harvested below-ground biomass). Hence, we could investigate what was the driver behind the potential change in BGB/AGB-ratio.

A linear model with log-transformed BGB/AGB-ratio as the response variable and species, habitat and treatment as interacting predictor variables was made to find out what effect the treatments had on the BGB/AGB-ratio for the different species in the different habitats. Only the most abundant species were included in this analysis, and all graminoid species except *L. confusa* (*A. borealis, P. arctica, D. fisheri, Calamagrostis neglecta*) were analyzed as one. To further investigate the driver behind the potential change in BGB/AGB-ratio for each species, two new linear models were made. One with square-rooted above-ground biomass as the response variable and habitat, treatment and species as interacting predictor variables, and one with square-rooted below-ground biomass as the response variable and habitat, treatment and species as interacting predictor variables.

Results

Comparing two different proxies of biomass (NDVI, PIM)

NDVI and PIM were positively correlated to each other (Pearson's r = 0.74 [95 % confidence interval (CI) = 0.59 – 0.84]). The relation between NDVI and PIM did not differ with treatment (based on AICc, table A1). NDVI was chosen as the only predictor variable in the model. This was because model selection ranked the model with NDVI as the only predictor variable as the best (table A1). vPIM reflected the above-ground biomass, below-ground biomass and total biomass of the plots better than aPIM (based on AICc, table A2). Thus, vPIM was used as the response variable in the final model investigating the relationship between NDVI and PIM.

How well do the two different proxies of biomass reflect the harvested biomass?

Both NDVI and PIM captured the above-ground biomass, below-ground biomass and total biomass well at the community level (table 3). However, AICc testing showed that NDVI was a better predictor of both above-ground biomass, below-ground biomass and total biomass than PIM (table 2). NDVI showed a high correlation with both above-ground biomass, below-ground biomass and total biomass (table 2, figure 5), while PIM showed a lower (only slightly for above-ground biomass) correlation with all three measures of biomass (table 2, figure 5).

For most species, species-specific vPIM was a better predictor of the biomass (both above-ground, below-ground and total biomass) than the total NDVI of the plot. PIM did show a very high, positive correlation with both above-ground biomass, below-ground biomass and total biomass for all of the most abundant vascular species (table 3). For all species, except *B. vivipara*, the correlation was higher between PIM and above-ground biomass than between PIM and below-ground biomass (table 3). However, NDVI did also show a high correlation with the biomass of *S. polaris*, *A. borealis* and *P. arctica* (table 3). The correlation between NDVI and biomass of the other species was lower.

How is the BGB/AGB-ratio affected by extreme climatic events?

There were large differences in the BGB/AGB-ratio of the species (figure 6 B, table A4). *E. arvense*, which had the highest BGB/AGB-ratio, had on average more than 23 times more biomass below the ground than above (figure 6 B, table A4). *Stellaria sp.*, with the lowest ratio, had on average about the same amount of biomass above ground as below ground (table

A4). The two most abundant species, *S. polaris* and *A. borealis* (figure 6 A), had respectively almost 8 times and about 4 times more biomass below ground than above ground (table A4). There were also large differences in the total abundance (g/m^2) of the species (figure 6 A). The two most abundant species made up more than half of the total biomass of the plots (table A3). The total BGB/AGB-ratio, for all species combined, shows that there on average was about 5.5 times more biomass harvested from below ground than from above ground in our plots (table A4).

There was a difference in how the BGB/AGB-ratio of the two vegetation communities responded to treatments (table 4, figure 7). For plots originating from the wet habitat, there was strong evidence that the BGB/AGB-ratio increased after thaw-freeze treatment (table 4). The BGB/AGB-ratio was 60.7 % higher for plots that received thaw-freeze treatment compared to the control-treated plots (table A5). In the wet habitat, there was weak evidence of an increasing BGB/AGB-ratio in response to icing treatment, with a 21.4 % higher BGB/AGB-ratio in iced plots than in control plots from the same habitat (table 4, table A5). The treatments had no effect on the expected mean BGB/AGB-ratio for mesic plots (table 4, table A5). The expected means of the model, on the log scale, is visualized in figure 7.

Model selection showed that there was evidence of a treatment effect on the BGB/AGB-ratio at the community level (table A6). When ranking the linear mixed-effects models with different predictor variables against each other, the model with habitat and treatment in interaction as fixed effects was ranked as the best model followed by the model with only treatment as a fixed effect (ΔAICc = 1.12; table A6). Hence, treatment was included in both models with ΔAICc > 2. The random effect, species, explained more than 97 % of the variation in log(BGB/AGB-ratio) compared to the fixed effects (table 4). This was reflected in the visualization of the species random effects (figure A2).

Linear mixed-effect models with above-ground biomass and below-ground biomass as response variables showed that there was no evidence of a change in either above-ground biomass or below-ground biomass as a response to the treatments in any of the two habitat types (table A7, table A8). However, there was a very weak trend of the above-ground biomass decreasing for thaw-freezed plots (-22.1 %, p-value = 0.190) compared to control plots (table A8).

The treatments had a similar effect on the BGB/AGB-ratio of most species. There was no evidence of an effect of treatment on the BGB/AGB-ratio for any of the species in the mesic habitat (figure 8, table A9). In the wet habitat, there was strong evidence that the thaw-freeze treatment increased the BGB/AGB-ratio for all species, except *L. confusa*, compared to the control treatment (figure 8; table A9). The data also showed that there was evidence of icing increasing the BGB/AGB-ratio of *S. polaris*, but less than thaw-freeze treatment did. There was no evidence of the other species, except *L. confusa*, changing their BGB/AGB-ratio in response to icing treatment, although a small increase in BGB/AGB-ratio after icing treatment seemed to be a trend when inspecting the data visually (figure 8). *L. confusa* showed a different pattern than the other species: there was evidence that the BGB/AGB-ratio decreased in the iced plots (figure 8, table A9). There was also weak evidence of the BGB/AGB-ratio of *L. confusa* changing after thaw-freeze treatment (figure 8, table A9).

Despite the similarities in the how BGB/AGB-ratio of the species responded to treatments, the corresponding linear models with sqrt(above-ground biomass) and sqrt(below-ground biomass) as response variables showed that the driver behind the change of BGB/AGB-ratio in the wet habitat not was the same for all species (table 5). The drivers behind the significant BGB/AGB-changes are presented below.

S. polaris increased the BGB/AGB-ratio with 168.3 % in thaw-freezed plots compared to control plots in the wet habitat (control: 4.17 [3.06 – 5.69], thaw-freeze: 11.19 [7.55 – 16.57]; table A10), and this BGB/AGB-ratio change was driven by an increase in below-ground biomass (+73.4 %, p-value = 0.202; table 5, table A11) and a slight decrease in above-ground biomass (-21.4 %, p-value = 0.675; table 5, table A11). For the iced plots the BGB/AGB-ratio increased with 74.1 % (control: 4.17 [3.06 – 5.69], icing: 7.26 [5.32 – 9.90]; table A10), which was driven by an slight increase in below-ground biomass (+21.0 %, p-value = 0.659; table 5, table A11) and a slight decrease in above-ground biomass (-17.9 %, p-value = 0.693; table 5, table A11).

E. arvense increased the BGB/AGB-ratio in the thaw-freeze plots from wet habitat with 84.0 % compared to the control plots from wet habitat (control: 16.34 [11.98 – 22.29], thaw-freeze: 30.07 [18.11 – 49.92]; table A10). This change was driven by a bigger decrease in the above-ground biomass (-83.3 %, p-value = 0.383; table 5, table A11) than in the below-ground biomass (-73.9 %, p-value = 0.098; table 5, table A11).

B. vivipara increased the BGB/AGB-ratio of thaw-freezed plots with 82.4 % (control: 4.42 [3.24 – 6.03], thaw-freeze: 8.06 [5.44 – 11.94]; table A10) compared to the control plots. As for *E. arvense*, a bigger decrease in the above-ground biomass (-79.4 %, p-value = 0.109; table 5, table A11) than in the below-ground biomass (-58.4 %, p-value = 0.337; table 5, table A11) was the driver of this change.

For the graminoids, the thaw-freezed plots increased the BGB/AGB-ratio with 45.2 % (control: 3.56 [2.88 – 4.40], thaw-freeze: 5.17 [3.92 – 6.83]; table A10). This was a result of a bigger increase of the below-ground biomass (+54.9 %, p-value = 0.215; table 5, table A11) than of the above-ground biomass (+6.2 %, p-value = 0.870; table 5, table A11).

For *L. confusa,* the 53.9 % lower BGB/AGB ratio in the iced plots compared to the control plots (control: 5.05 [3.41 – 7.48], icing: 2.38 [1.54 – 3.69]; table A10) was driven by a bigger increase in above-ground biomass (+290.2 %, p-value = 0.006; table 5, table A11) than in below-ground biomass (+66.0 %, p-value = 0.451; table 5, table A11).

Table 1. Summary of a linear model with NDVI as the predictor variable and log-transformed number of point intercepts with vascular plant species (vPIM) as the response variable. Estimated intercept and slope with their 95 % confidence intervals are given. Significant p-values (alfa = 0.05) are marked in bold. R^2 gives the proportion of variance accounted for in the model, while R^2 adjusted gives the proportion of variance accounted for in the model after adjusting for the number of variables. Pearson's r gives the Pearson's product-moment correlation with the 95 % confidence interval in brackets.

Predictors	*Estimates*	*CI*	*p*
(Intercept)	1.14	0.61 – 1.67	**<0.001**
NDVI	3.22	2.41 – 4.04	**<0.001**
Observations	54		
R^2 / R^2 adjusted	0.546 / 0.537		

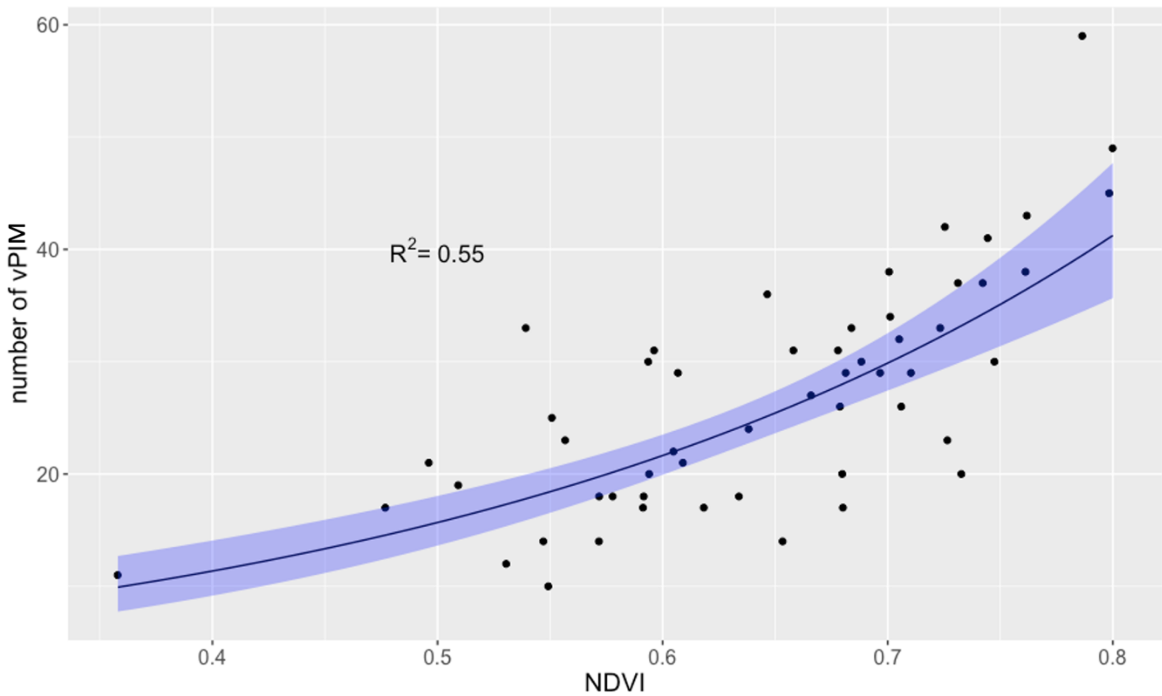

Figure 4. Predicted effect of NDVI on the number of point intercept hits with vascular plant species (vPIM). Observations plotted as black dots (n = 54 plots). The 95 % CI is shown with the shaded blue.

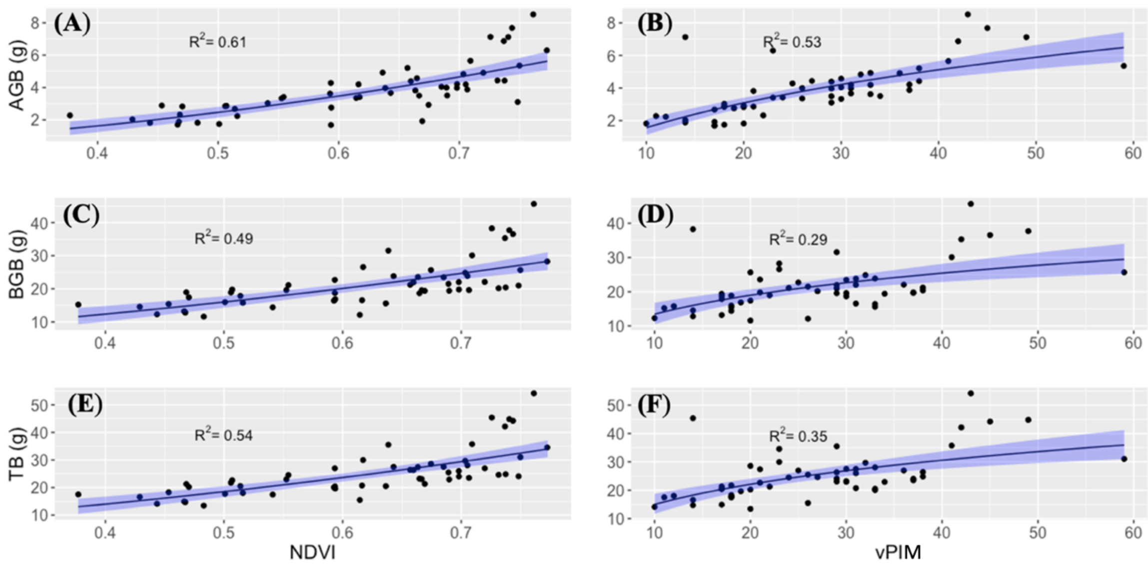

Figure 5. Predicted effect of: **(A)** NDVI on sqrt(harvested above-ground biomass (g) (AGB)), **(B)** log(number of point intercept hits with vascular plant species(vPIM)) on sqrt(AGB), **(C)** NDVI on sqrt(harvested below-ground biomass (g) (BGB)), **(D)** log(vPIM) and sqrt(BGB), **(E)** NDVI on sqrt(total harvested biomass (g) (TB)), **(F)** vPIM on sqrt(TB). All predicted effects are plotted on the back-transformed level. Raw data is plotted in the background. The 95 % CI is shown with the shaded blue. n = 54 plots for all models.

Table 2. Model selection table for linear models with the square-rooted amount of harvested biomass (above moss-layer biomass (AGB), below-moss layer biomass (BGB) and total biomass (TB)) (all in gram) as the response variable and with the number of point intercept method hits with vascular plant species (vPIM) and NDVI as the predictor variable. Both estimated intercept and estimated slope are given, with 95 % confidence intervals in parenthesis. R^2 gives the proportion of variance in the response variable explained by the model. Pearson's r gives Pearson's product-moment correlation between the response variable and the predictor variable. df gives the degrees of freedom in the model. n gives the number of observations (plots) in the model. The model with the lowest AICc score is marked in bold.

Response variable	Predictor variable	Estimate (Intercept)	Estimated slope (Predictor variable)	R^2	Pearson's r (95 % CI)	df	N	AICc	ΔAICc
sqrt(AGB)									
	~ NDVI	**0.10 (-0.31 – 0.51)**	**2.94 (2.29 – 3.60)**	**0.61**	**0.781 (0.649 – 0.867)**	**3**	**54**	**7.72**	**0**
	~ log(vPIM)	-0.43 (-1.05 – 0.19)	0.73 (0.54 – 0.92)	0.53	0.729 (0.573 – 0.834)	3	54	17.63	9.91
sqrt(BGB)									
	~ NDVI	**1.58 (0.72 – 2.45)**	**4.84 (3.46 – 6.21)**	**0.49**	**0.700 (0.532 – 0.815)**	**3**	**54**	**92.18**	**0**
	~ log(vPIM)	1.38 (-0.02 – 2.78)	0.99 (0.56 – 1.42)	0.29	0.540 (0.319 – 0.706)	3	54	111.07	18.89
sqrt(TB)									
	~ NDVI	**1.50 (0.60 – 2.40)**	**5.59 (4.17 – 7.03)**	**0.54**	**0.736 (0.584 – 0.839)**	**3**	**54**	**87.67**	**0**
	~ log(vPIM)	1.11 (-0.36 – 2.59)	1.20 (0.74 – 1.65)	0.35	0.592 (0.385 – 0.742)	3	54	105.40	17.73

Table 3. Pearson's product-moment correlation between (1) the number of point intercepts for the most abundant vascular species (vPIM) and harvested biomass (above-ground (AGB), below-ground (BGB) and total (TB)) for the same species (all in gram) and (2) NDVI of the plot and the harvested biomass (AGB, BGB, TB) of the given species. Pearson's product-moment correlation is given, with the 95 % confidence interval in brackets. Correlation coefficients from 0.50 and above are marked with four different shades of green, with stronger green color for every 0.10 interval.

	Correlation between above-ground biomass proxy and harvested biomass per species					
	log(1 + vPIM)			*NDVI*		
Species	*sqrt(AGB)*	*sqrt(BGB)*	*sqrt(TB)*	*sqrt(AGB)*	*sqrt(BGB)*	*sqrt(TB)*
S. polaris	0.78 [0.64 - 0.87]	0.63 [0.44 - 0.77]	0.67 [0.49 - 0.79]	0.64 [0.45 – 0.78]	0.48 [0.24 – 0.66]	0.51 [0.28 – 0.69]
B. vivipara	0.72 [0.56 - 0.83]	0.76 [0.62 - 0.86]	0.77 [0.63 - 0.86]	0.27 [0.00 – 0.50]	0.19 [-0.08 – 0.43]	0.21 [-0.06 – 0.43]
L. confusa	0.85 [0.75 - 0.91]	0.73 [0.57 - 0.83]	0.76 [0.62 - 0.85]	0.22 [-0.05 – 0.46]	0.34 [0.08 – 0.56]	0.33 [0.06 – 0.55]
E. arvense	0.86 [0.77 - 0.92]	0.74 [0.59 - 0.84]	0.75 [0.60 - 0.84]	-0.17 [-0.42 – 0.10]	-0.28 [-0.51 – 0.10]	-0.27 [-0.50 – 0.01]
A. borealis	0.72 [0.56 - 0.83]	0.67 [0.49 - 0.79]	0.69 [0.51 - 0.81]	0.59 [0.38 – 0.74]	0.52 [0.30 – 0.69]	0.54 [0.32 – 0.71]
P. arctica	0.64 [0.46 - 0.78]	0.57 [0.36 - 0.73]	0.60 [0.39 - 0.74]	0.61 [0.40 – 0.75]	0.60 [0.40 – 0.75]	0.60 [0.39 – 0.75]
All species	0.73 [0.57 - 0.83]	0.55 [0.33 - 0.71]	0.60 [0.40 - 0.75]	0.78 [0.65 – 0.87]	0.71 [0.55 – 0.82]	0.74 [0.59 – 0.84]
All species, free roots included	0.73 [0.57 - 0.83]	0.54 [0.32 - 0.71]	0.59 [0.39 - 0.74]	0.78 [0.65 – 0.87]	0.70 [0.53 – 0.82]	0.74 [0.58 – 0.84]

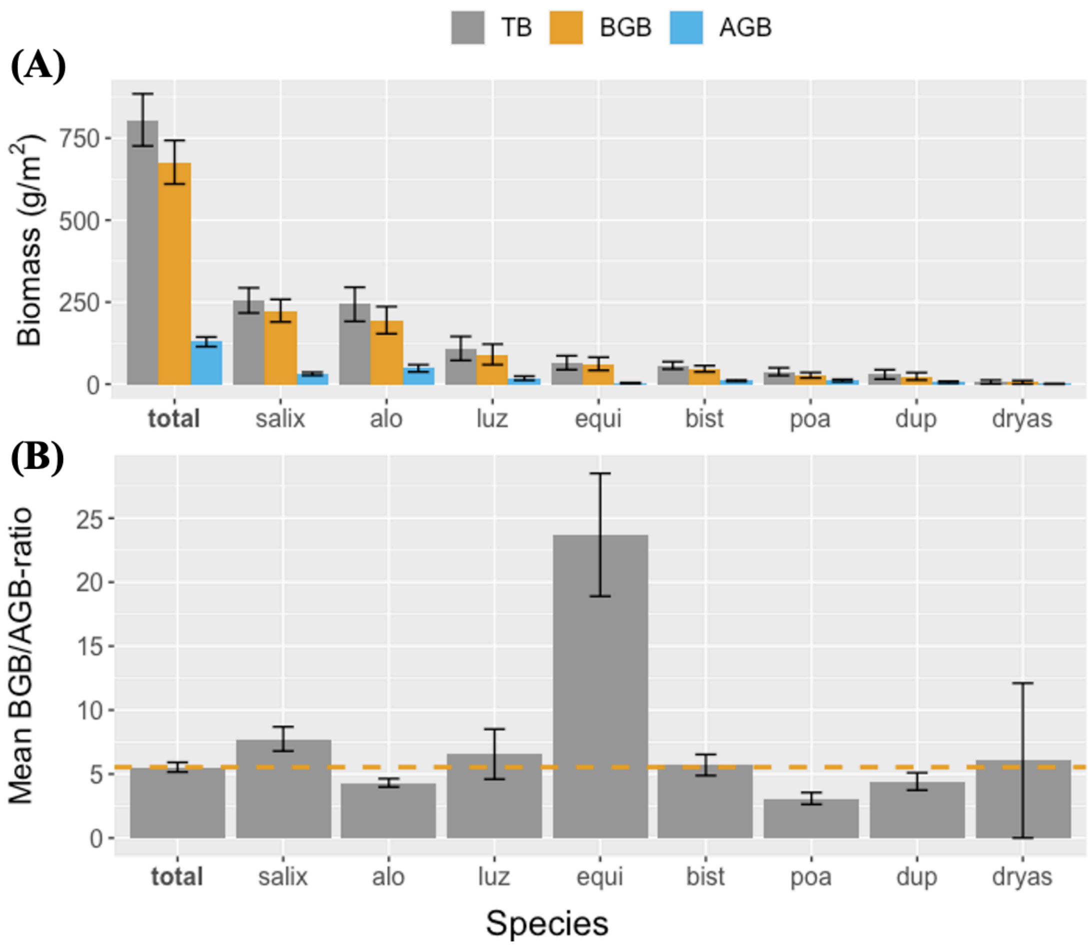

Figure 6. (A) Shows the mean amount of harvested biomass in the plots (converted to g/m^2) for the most abundant species. TB = total biomass. AGB = above-ground biomass. BGB = below-ground biomass. The whiskers correspond to the 95 % confidence interval. **(B)** Shows the mean below-ground biomass/above-ground biomass ratio (BGB/AGB-ratio) in the plots for the most abundant species. The whiskers correspond to the 95 % confidence interval. The dotted orange line corresponds to the mean BGB/AGB-ratio of all biomass in the plots. Total = all species combined, salix = *S. polaris*, alo = *A. borealis*, luz = *L. confusa*, equi = *E. arvense*, bist = *B. vivipara*, poa = *P. arctica*, dup = *D. fisheri*, dryas = *Dryas octopetala*.

Table 4. Summary of the linear mixed-effect model with log below-ground/above-ground biomass ratio (BGB/AGB-ratio) as a response variable, habitat and treatment as fixed predictor variables, and species as a random intercept effect. The p-value tells if the predictors change the estimates significantly compared to the intercept. Significant p-values (alpha = 0.05) are marked in bold. 95 % confidence interval given in the CI column. σ^2 represents the residual intercept variance within species. τ_{00} is the residual intercept variance, controlling for species. $N_{species}$ gives the number of different species included in the model. Marginal R^2 gives the proportion of variance explained by the fixed factors. Conditional R^2 gives the proportion of variance explained by both random and fixed effects. The number of observations is the number of different species found in each plot, added together.

*(Intercept)**	*Predictors*	*Estimates*	*CI*	*p*
Mesic, control		1.45	1.02 – 1.89	**<0.001**
	Icing	0.02	-0.14 – 0.19	0.789
	Thaw-freeze	0.07	-0.11 – 0.25	0.440
Wet, control		1.27	0.83 – 1.70	**<0.001**
	Icing	0.19	-0.00 – 0.39	0.055
	Thaw-freeze	0.47	0.24 – 0.70	**<0.001**
	Random Effects			
	σ^2	0.23		
	$\tau_{00\ species}$	0.50		
	$N_{species}$	12		
	Observations	310		
	Marginal R^2 / Conditional R^2	0.017 / 0.691		

**The levels of the habitat predictor variable were releveled to compare the effect of icing and thaw-freeze to the control in the different habitats.*

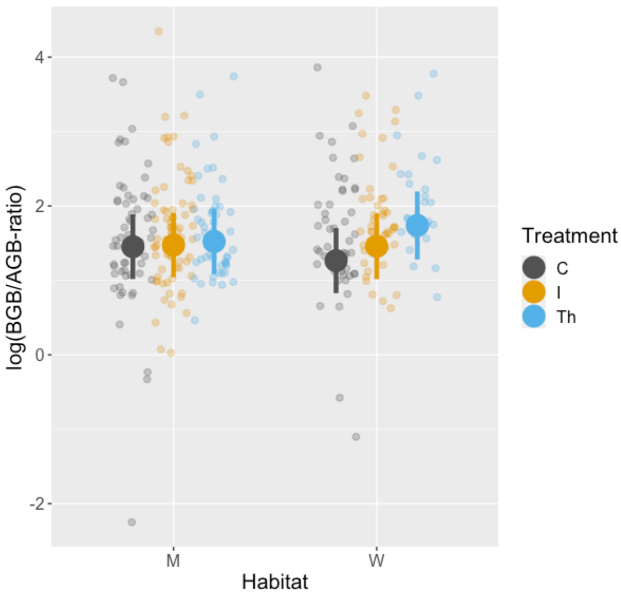

Figure 7. Effect plot visualizing the effect of treatment and habitat on log-transformed below-ground/above-ground biomass ratio (BGB/AGB-ratio), with species as a random intercept effect. Log transformed observations are plotted as dots of the corresponding treatment color (n = 310). The corresponding 95 % CI is represented as a vertical line. M = mesic habitat. W = wet habitat. C = control treatment. I = icing treatment. Th = thaw-freeze treatment.

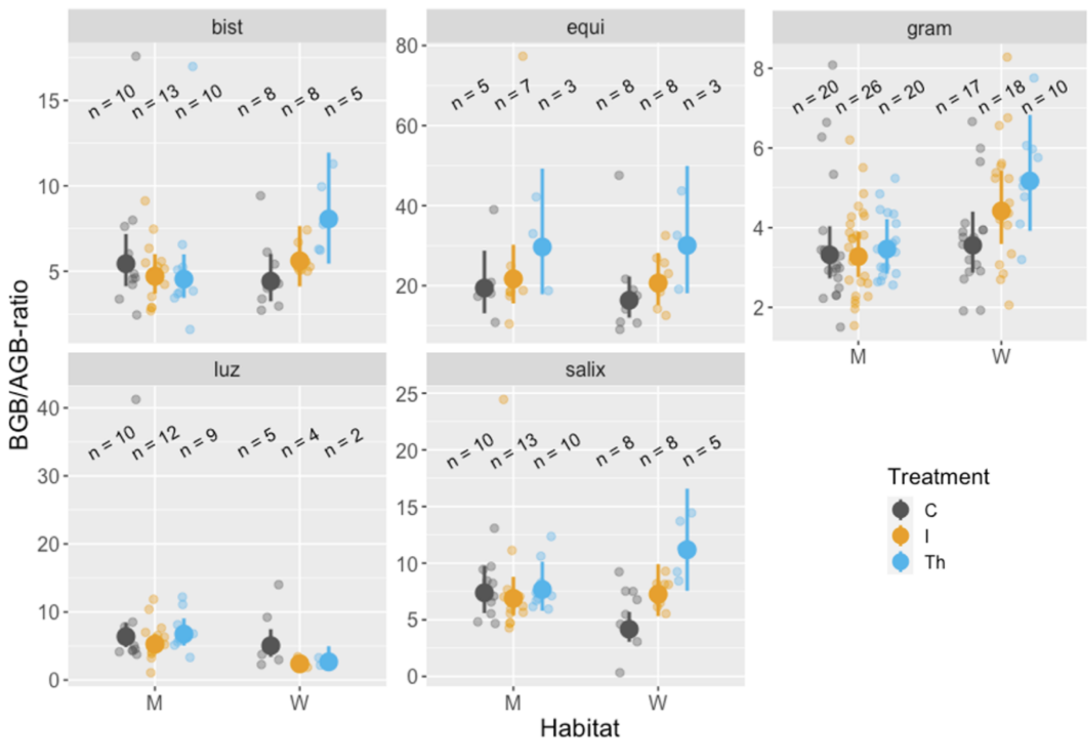

Figure 8. Effect plots visualizing the estimated effect of habitat and treatment on the below-ground/above-ground biomass ratio (BGB/AGB-ratio) of the most abundant species. The effect plots are showing the back-transformed data. The corresponding 95 % CI is represented as a vertical line. All graminoid species, except Luzula confusa, were pooled in the “gram” category. M = mesic habitat. W = wet habitat. C = control treatment. I = icing treatment. Th = thaw-freeze treatment. bist = *B. vivipara*. equi = *E. arvense*. gram = *A. borealis*, *P. arctica*, *C. neglecta*, *D. fisheri*. luz = *L. confusa*. salix = *S. polaris*.

Table 5. Summary of the linear model with above-ground biomass (g) (square root transformed) as a response variable and habitat, treatment and species as interacting predictor variables, and the linear model with below-ground biomass (g) (square root transformed) as a response variable and habitat, treatment and species as interacting predictor variables. M = mesic habitat. W = wet habitat. C = control treatment. I = icing treatment. Th = Thaw-freeze treatment. Salix = *S. polaris*. Gram = *A. borealis, P. arctica, D. fisheri* and *C. neglecta*. Bist = *B. vivipara*. Luz = *L. confusa*, Equi = *E. arvense*. CI gives the 95 % confidence interval. Significant p-values (alpha = 0.05) are marked in bold.

*(Intercept)**	*Predictors*	*sqrt(Above-ground biomass)* *Estimates*	*CI*	*p*	*sqrt(Below-ground biomass)* *Estimates*	*CI*	*p*
Salix : C : M		1.09	0.87 – 1.30	**<0.001**	2.95	2.48 – 3.42	**<0.001**
	I	0.01	-0.27 – 0.30	0.925	-0.14	-0.77 – 0.48	0.652
	Th	-0.09	-0.39 – 0.21	0.561	-0.16	-0.83 – 0.51	0.634
Salix : C : W		0.75	0.51 – 0.98	**<0.001**	1.68	1.15 – 2.20	**<0.001**
	I	-0.07	-0.40 – 0.27	0.693	0.17	-0.58 – 0.91	0.659
	Th	-0.08	-0.46 – 0.30	0.675	0.55	-0.30 – 1.40	0.202
Gram : C : M		0.95	0.80 – 1.10	**<0.001**	1.72	1.38 – 2.05	**<0.001**
	I	0.04	-0.16 – 0.24	0.683	0.15	-0.30 – 0.59	0.514
	Th	0.02	-0.19 – 0.23	0.875	0.12	-0.35 – 0.59	0.622
Gram : C : W		0.81	0.64 – 0.97	**<0.001**	1.54	1.18 – 1.90	**<0.001**
	I	-0.24	-0.47 - -0.02	**0.036**	-0.35	-0.86 – 0.15	0.168
	Th	0.02	-0.24 – 0.29	0.870	0.38	-0.22 – 0.97	0.215
Bist : C : M		0.53	0.32 – 0.75	**<0.001**	1.17	0.70 – 1.64	**<0.001**
	I	-0.03	-0.31 – 0.26	0.854	-0.08	-0.71 – 0.55	0.803
	Th	-0.01	-0.31 – 0.29	0.924	-0.08	-0.75 – 0.59	0.818
Bist : C : W		0.58	0.35 – 0.82	**<0.001**	1.17	0.64 – 1.70	**<0.001**
	I	-0.08	-0.42 – 0.25	0.622	0.01	-0.74 – 0.75	0.984
	Th	-0.31	-0.69 – 0.07	0.109	-0.42	-1.27 – 0.44	0.337
Luz : C : M		0.63	0.42 – 0.84	**<0.001**	1.58	1.10 – 2.05	**<0.001**
	I	0.01	-0.27 – 0.30	0.923	-0.01	-0.64 – 0.63	0.988
	Th	0.09	-0.22 – 0.40	0.559	0.36	-0.32 – 1.05	0.298
Luz : C : W		0.64	0.35 – 0.94	**<0.001**	1.26	0.60 – 1.93	**<0.001**
	I	0.64	0.19 – 1.09	**0.006**	0.36	-0.58 – 1.31	0.451
	Th	0.11	-0.45 – 0.67	0.703	0.04	-1.21 – 1.29	0.952
Equi : C : M		0.35	0.05 – 0.65	**0.023**	1.50	0.83 – 2.17	**<0.001**
	I	0.05	-0.34 – 0.44	0.797	0.27	-0.60 – 1.14	0.544
	Th	-0.07	-0.56 – 0.42	0.774	-0.08	-1.17 – 1.01	0.882
Equi : C : W		0.35	0.12 – 0.59	**0.004**	1.48	0.95 – 2.00	**<0.001**
	I	0.08	-0.26 – 0.41	0.659	0.41	-0.33 – 1.16	0.279
	Th	-0.20	-0.65 – 0.25	0.383	-0.72	-1.57 – 0.13	0.098
Observations		295			298		
R^2		0.370			0.341		

* The levels of the habitat and species predictor variables were releveled in total ten times per model to easier compare the estimated effect of the icing and thaw-freeze against the control treatment in the different habitats for each species.

Discussion

This study found evidence that experimental thaw-freeze treatment in a high-arctic, low-productive tundra community increased the below-ground biomass/above-ground biomass ratio (BGB/AGB-ratio) at the community level. At the species level, the thaw-freeze treatment increased the BGB/AGB-ratio for virtually all species in the wet habitat. No evidence of a treatment effect was seen in the drier habitat, neither at the community nor the species level (table 4, figure 7, figure 8). However, the species had different patterns of change in above- and below-ground biomass as the driver behind the ratio change (table 5). This also means that the applicability of different proxies of above-ground biomass will depend on species, as well as scale and type of study. As expected, however, there were strong inter-correlations of PIM, NDVI, and above-ground biomass at the community level (table 3). NDVI was also a suitable estimator of the below-ground biomass of the community, and PIM was a reliable estimator of the species-specific below-ground biomass for most species (table 2, table 3, figure 5).

Thaw-freeze increased the BGB/AGB-ratio at both community and species level

My findings suggest that increased frequency of extreme climatic events could change the BGB/AGB-ratio at both community and species levels, and more drastically for the thaw-freeze than the icing treatment. These results can partly be explained by the activation of growth hormones due to a temperature increase in the plant tissue initiating the growth process, which makes the plants spend energy stored for the growing season prematurely (Sundberg, 2000). Both icing and thaw-freeze treatments can increase the soil, and thus plant tissue, temperature (Putkonen & Roe, 2003). However, this temperature increase was greater and lasted longer for the thaw-freezed plots than the iced plots. The thaw-freezed plots were heated for 6 days raising the sub-surface soil temperature (at 5 cm depth) by approximately 6 - 8 °C compared to the pre-treatment temperature, while the latent heat released in icing events lasts for only a few days on average with an increase of sub-surface soil temperature of 4 - 6 °C (Detampel, 2021; Le Moullec et al., 2021). This explanation is supported by observations of green shoots of *A. borealis* emerging in some plots after thaw-freeze treatment (figure 2 D).

Also, the thaw-freeze treatment caused the vegetation to refreeze after the thawing period without an insulating layer of snow, which can cause damage to the plants due to e.g. cellular dehydration (Pearce, 2001). Stressful abiotic conditions, e.g. freezing, can change the growth strategy of plants into portioning more biomass to root systems (Qi et al., 2019). In addition, icing events maintain soil temperatures low in spring by isolating the ground from the air temperatures (Le Moullec et al., 2019). However, this period of ice isolating the ground may have been shortened in this experiment, due to the ice only covering a relatively small area (a circle with a diameter of 19.5 cm), and hence melting earlier than it would have done if the ice cover were larger and more connected. Therefore, the effect of the icing treatment might have been dampened compared to a naturally occurring icing event where large areas would be covered by ice.

Even though the effect of thaw-freeze on the BGB/AGB-ratio was bigger than the effect of icing, a non-significant tendency for increasing BGB/AGB-ratio after icing events was also seen in the wet habitat, both at the community and species level, for some species. This is in accordance with other studies that suggests that ROS episodes and associated icing may affect negatively both the above- and below-ground growth of *S. polaris*, the most abundant species in our community (Le Moullec et al., 2020; Opała-Owczarek et al., 2018; Owczarek & Opała, 2016). If this decrease in above-ground biomass is bigger than the decrease in below-ground biomass, this could affect the BGB/AGB-ratio negatively at the community level.

The increase in BGB/AGB-ratio found in the wet community can occur due to either (1) an increase in below-ground biomass a decreased/unchanged amount of above-ground biomass, (2) a bigger increase in below-ground biomass than in above-ground biomass or (3) a smaller reduction in the below-ground biomass than the above-ground biomass. The same holds at the species level. A decrease in above-ground biomass in the thaw-freeze plots originating from the wet habitat could be the driver behind the significant change in BGB/AGB-ratio at the community level. This would be in accordance with earlier studies showing that thaw-freeze events can cause damage to the photosynthetic tissue of the vascular plants (Bjerke et al., 2017; Bokhorst et al., 2008, 2011; Phoenix & Bjerke, 2016).

However, at the species level, it seemed that the driver behind the significant BGB/AGB-ratio changes differed between functional groups. The BGB/AGB-ratio increased due to pattern 1 (see paragraph above) for *S. polaris* (shrub), due to pattern 2 for the graminoids, except *L. confusa*, and due to pattern 3 for *B. vivipara* (forb) and *E. arvense* (fern). Such heterogeneity in how different functional groups change their above-ground biomass and below-ground biomass in response to extreme climatic events has previously been reported in a study of drought events in a meadow step vegetation community in northeastern China (Wang et al., 2018). It is important to notice that the changes in above-ground biomass and below-ground biomass changes mostly were non-significant, even if they resulted in a significant BGB/AGB-ratio change. However, the clear trend of a similar treatment effect on the BGB/AGB-ratio across species/functional groups suggests that the small and non-significant changes in above-ground biomass and below-ground biomass were consistent between plots. Still, the different changes in above-ground biomass and below-ground biomass all resulted in a larger proportion of biomass, and hence carbon, being allocated below-ground. It is suggested that such investment in below-ground biomass is related to the harsh environment of the tundra, like low temperatures and high soil moisture, and can be useful to store energy and nutrients (Chapin & Slack, 1979; Webber, 1977). My results suggest that making the environment even more extreme, by simulating ROS and thaw-freeze events, can increase the relative investment in the storage of energy and nutrients compared to investment in above-ground biomass.

Also, habitat modified the responses to the treatments. According to my results, the BGB/AGB-ratio in the mesic vegetation community remained unchanged after both icing and thaw-freeze treatments at the community and species level (for most species), while the wet vegetation community increase their BGB/AGB-ratio in response to treatments. The wet plant community was characterized by a thicker moss layer than the mesic plant community, thus more of the vascular plant organs were located in the moss layer in the wet habitat compared to the mesic habitat. The moss layer is known to reduce both the temperature and the thaw depth of the soil layer beneath (Gornall et al., 2007), but in the wet habitat, the plant organs were a part of this insulating cover rather than beneath it. This caused a bigger increase in experienced temperature after treatment for the plants in the wet plots compared to mesic plots (pers. obs.). In turn, plants in the wet habitat could experience more stressful conditions than plants in the mesic habitat, which again can lead to a bigger increase in BGB/AGB-ratio (Qi et al., 2019).

In addition, the wet and mesic plots might have been exposed to different winter conditions before the transplantation. The wet community is often being found on the valley floor in areas with little drainage of water, while the mesic community often is located on small slopes with more water drainage. Therefore, the vegetation communities might have been exposed to different snow depths and/or water conditions during winter. In theory, this could have caused one of the habitats to be exposed to either thaw-freeze or icing with a higher frequency, and give the plant individuals in this habitat a bigger resilience towards this extreme climatic event. However, the complex mechanisms behind natural icing and thaw-freeze events, as well as our mesic and wet community being exposed to relatively similar snow depths during winter, makes it hard to conclude how previous winter conditions might have caused different treatment response for the habitats.

Lastly, the pipe the plots were transplanted in prevented lateral water flow through the soil, which is an important source of water (from snow-melt and permafrost melt), particularly for the wetter tundra communities (Johansen & Tømmervik, 2014). Hence, the plants in the wet plots might have been more exposed to drought stress than the plants in the mesic plots. Drought stress can cause plants to increase their BGB/AGB-ratio in order to maximize the water absorption (Wang et al., 2018). Time limitations prevented us from exploring the transplanting effect (i.e., from harvesting control plots transplanted in a pipe kept in their in-situ environments). However, a future analysis could explore the impact of the transplanting process on the above-ground biomass proxies (NDVI and PIM).

Species-specific BGB/AGB-ratio: fundamental knowledge found

The time-consuming and destructive nature of below-ground biomass proxies makes estimation of below-ground biomass through less time-demanding and non-destructive above-ground biomass proxies, e.g. satellite NDVI measurements, preferred (Berner et al., 2018; Gang & Bao, 2013). In turn, this can lead to a low-effort and precise estimation of the above- and below-ground carbon stock in large areas, especially if using satellite-derived NDVI, which proved to be a useful above-ground biomass proxy (Hogrefe et al., 2017). However, the estimation of below-ground biomass from such proxies depends on both the proxy being representative of the above-ground biomass, as well as precise knowledge of (1) which vegetation communities the NDVI is measured for and (2) the BGB/AGB-ratio of this community especially. Comparing BGB/AGB-ratios found in this study with earlier findings from similar vegetation communities is therefore interesting.

In the plots, the amount of below-ground biomass was approximately five times higher than the above-ground biomass. This ratio is comparable to those found in other studies conducted in other high-Arctic vegetation communities; Henry et al. (1990) found a BGB/AGB-ratio of 5.3 [2.9 – 9.4] in a high-Arctic sedge meadow community, Hollister & Flaherty, (2010) found a BGB/AGB-ratio of 6.9 [5.2 – 10.6] in a high-Arctic mesic tundra community, while Mokany et al. (2006) reported that the mean BGB/AGB-ratio found for tundra communities to be 4.8 [0.9 – 15.2]. Most species-specific BGB/AGB-ratios in my study were novel findings for high-Arctic mesic habitats. The combined BGB/AGB-ratio of graminoid species spanned from 2 (*P. arctica*) to 5 (*L. confusa*), which is somewhat lower than the findings of an earlier study conducted in a high Arctic Alaska tundra vegetation community, which found a mean BGB/AGB-ratio of around 7 for graminoids (Hollister & Flaherty, 2010). The BGB/AGB-ratios found for *D. octopetala*, *Peduncularis sp.*, and *Ranunculus sp.* also deviates from earlier reported BGB/AGB-ratios of these species (Iversen et al., 2015), but this could be due to few observations of these species in the study.

Above-ground biomass proxies reflected the absolute biomass well, while showing different qualities

My results from this common garden experiment quantified the applicability of NDVI and PIM in the estimation of above- and below-ground biomass. Both NDVI and PIM were effective estimators of the above-ground biomass of the plots in both studied community types. In addition, PIM proved to estimate the above- and below-ground biomass of each species with high accuracy, and hence also the species composition of the community. It is expected that NDVI saturates for high values (Gao et al., 2000; Tucker, 1977), however, my results did not show a lower correlation between PIM and NDVI at high values of biomass. This might be caused by the values of measured NDVI not reaching high enough levels (the highest NDVI measured was 0.80), due to less vegetation being abundant than in e.g. the tropics, and hence not reaching the point of saturation. The correlation between the proxies and the below-ground biomass was similar both when including and not including the free roots. Hence, this potential methodological issue with some unidentifiable small roots did not influence my results.

Other studies have contrasting findings when it comes to whether PIM or spectroscopy measures, e.g. NDVI, reflect above-ground biomass the best. A study comparing spectroscopy measures in the semi-arid grasslands of Hungary compared how well NDVI and PIM reflected above-ground biomass (Ónodi et al., 2017), while a study conducted in the grasslands of Colorado investigated how well greenness index (GI), another spectroscopic measure, and PIM reflected the above-ground biomass (Byrne et. al, 2011). The study comparing NDVI and PIM found that NDVI reflected the above-ground biomass better, while the opposite was the case in the study comparing GI and PIM. The contrasting findings might be because the NDVI formula, unlike the GI formula, includes the incident radiation. Hence, NDVI will be less affected by current light and weather conditions than GI, and give a more precise estimation of the productivity of the community, and hence also the above-ground biomass.

Conclusion

In conclusion, the results of this thesis provide novel insight and fundamental knowledge into how and why the BGB/AGB-ratios of the communities, and their species, might change due to an increased frequency of extreme winter climatic events. The thesis also shed light on how different above-ground biomass proxies reflect above- and below-ground biomass in two high-Arctic tundra vegetation communities. Therefore, this study also provides a tool for future studies aiming to estimate the below-ground biomass from non-destructive and more time-efficient above-ground biomass proxies. Hence, this study represents a step, or maybe even two steps, towards a greater understanding of the dynamics of high Arctic vegetation communities under a new climate regime.

References

Aagaard, K., Foldvik, A., & Hillman, S. R. (1987). The West Spitsbergen Current: disposition and water mass transformation. *Journal of Geophysical Research: Oceans*, *92*(C4), 3778–3784.

Bartoń, K. (2020). MuMIn: Multi-Model Inference. *R Package Version 1.43.17*.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Bell, K. L., & Bliss, L. C. (1978). Root growth in a polar semidesert environment. *Canadian Journal of Botany*, *56*(20), 2470–2490.

Berner, L. T., Jantz, P., Tape, K. D., & Goetz, S. J. (2018). Tundra plant above-ground biomass and shrub dominance mapped across the North Slope of Alaska. *Environmental Research Letters*, *13*(3), 35002.

Bhatt, U. S., Walker, D. A., Raynolds, M. K., Bieniek, P. A., Epstein, H. E., Comiso, J. C., Pinzon, J. E., Tucker, C. J., & Polyakov, I. V. (2013). Recent declines in warming and vegetation greening trends over pan-Arctic tundra. *Remote Sensing*, *5*(9), 4229–4254.

Bintanja, R., & Andry, O. (2017). Towards a rain-dominated Arctic. *Nature Climate Change*, *7*(4), 263–267.

Bjerke, J. W., Treharne, R., Vikhamar-Schuler, D., Karlsen, S. R., Ravolainen, V., Bokhorst, S., Phoenix, G. K., Bochenek, Z., & Tømmervik, H. (2017). Understanding the drivers of extensive plant damage in boreal and Arctic ecosystems: Insights from field surveys in the aftermath of damage. *Science of the Total Environment*, *599*, 1965–1976.

Bliss, L. C., Svoboda, J., & Bliss, D. I. (1984). Polar deserts, their plant cover and plant production in the Canadian High Arctic. *Ecography*, *7*(3), 305–324.

Bokhorst, S., Bjerke, J. W., Bowles, F. W., Melillo, J., Callaghan, T. V., & Phoenix, G. K. (2008). Impacts of extreme winter warming in the sub-Arctic: Growing season responses of dwarf shrub heathland. *Global Change Biology*, *14*(11), 2603–2612. https://doi.org/10.1111/J.1365-2486.2008.01689.X

Bokhorst, S., Bjerke, J. W., Street, L. E., Callaghan, T. V, & Phoenix, G. K. (2011). Impacts of multiple extreme winter warming events on sub-Arctic heathland: phenology, reproduction, growth, and CO2 flux responses. *Global Change Biology*, *17*(9), 2817–2830.

Bokhorst, S. F., Bjerke, J. W., Tømmervik, H., Callaghan, T. V., & Phoenix, G. K. (2009). Winter warming events damage sub-Arctic vegetation: Consistent evidence from an experimental manipulation and a natural event. *Journal of Ecology*, *97*(6), 1408–1415. https://doi.org/10.1111/J.1365-2745.2009.01554.X

Bråthen, K. A., & Hagberg, O. (2004). More efficient estimation of plant biomass. *Journal of Vegetation Science*, *15*(5), 653–660.

Burnham, K. P., & Anderson, D. R. (1998). Information Theory and Log-Likelihood Models: A Basis for Model Selection and Inference. *Model Selection and Inference*, 32–74. https://doi.org/10.1007/978-1-4757-2917-7_2

Byrne, K. M., Lauenroth, W. K., Adler, P. B., & Byrne, C. M. (2011). Estimating aboveground net primary production in grasslands: a comparison of nondestructive methods. *Rangeland Ecology & Management*, *64*(5), 498–505.

Campioli, M., Michelsen, A., Demey, A., Vermeulen, A., Samson, R., & Lemeur, R. (2009). Net primary production and carbon stocks for subarctic mesic–dry tundras with contrasting microtopography, altitude, and dominant species. *Ecosystems*, *12*(5), 760–776.

De Jong, R., de Bruin, S., de Wit, A., Schaepman, M. E., & Dent, D. L. (2011). Analysis of monotonic greening and browning trends from global NDVI time-series. *Remote Sensing of Environment*, *115*(2), 692–702.

Detampel, J.-P. (2021). *Effects of warmer and rainier Arctic winters on a widespread herb: Bistorta vivipara*. Freie Universität.

Epstein, H. E., Raynolds, M. K., Walker, D. A., Bhatt, U. S., Tucker, C. J., & Pinzon, J. E. (2012). Dynamics of aboveground phytomass of the circumpolar Arctic tundra during the past three decades. *Environmental Research Letters*, *7*(1), 15506.

Euskirchen, E. S., McGuire, A. D., Chapin III, F. S., Yi, S., & Thompson, C. C. (2009). Changes in vegetation in northern Alaska under scenarios of climate change, 2003–2100: implications for climate feedbacks. *Ecological Applications*, *19*(4), 1022–1043.

Frost, G. V, Bhatt, U. S., Epstein, H. E., Myers-Smith, I., Phoenix, G. K., Berner, L. T., Bjerke, J. W., Forbes, B. C., Goetz, S. J., & Kerby, J. T. (2020). *Arctic Report Card 2020: Tundra Greenness*.

Gang, B., & Bao, Y. (2013). Remotely sensed estimate of biomass carbon stocks in Xilingol grassland using MODIS NDVI data. *Proceedings 2013 International Conference on Mechatronic Sciences, Electric Engineering and Computer (MEC)*, 676–679.

Gao, X., Huete, A. R., Ni, W., & Miura, T. (2000). Optical–biophysical relationships of vegetation spectra without background contamination. *Remote Sensing of Environment*, *74*(3), 609–620.

Gornall, J. L., Jónsdóttir, I. S., Woodin, S. J., & Van der Wal, R. (2007). Arctic mosses govern below-ground environment and ecosystem processes. *Oecologia*, *153*(4), 931–941.

Graham, R. M., Cohen, L., Petty, A. A., Boisvert, L. N., Rinke, A., Hudson, S. R., Nicolaus, M., & Granskog, M. A. (2017). Increasing frequency and duration of Arctic winter warming events. *Geophysical Research Letters*, *44*(13), 6974–6983.

Hansen, B. B., Isaksen, K., Benestad, R. E., Kohler, J., Pedersen, Å. Ø., Loe, L. E., Coulson, S. J., Larsen, J. O., & Varpe, Ø. (2014). Warmer and wetter winters: characteristics and implications of an extreme weather event in the High Arctic. *Environmental Research Letters*, *9*(11), 114021.

Henry, G. H. R., Svoboda, J., & Freedman, B. (1990). Standing crop and net production of sedge meadows of an ungrazed polar desert oasis. *Canadian Journal of Botany*, *68*(12), 2660–2667.

Hogrefe, K. R., Patil, V. P., Ruthrauff, D. R., Meixell, B. W., Budde, M. E., Hupp, J. W., & Ward, D. H. (2017). Normalized Difference Vegetation Index as an estimator for abundance and quality of avian herbivore forage in Arctic Alaska. *Remote Sensing*, *9*(12), 1234.

Hollister, R. D., & Flaherty, K. J. (2010). Above-and below-ground plant biomass response to experimental warming in northern Alaska. *Applied Vegetation Science*, *13*(3), 378–387.

Iversen, C. M., Sloan, V. L., Sullivan, P. F., Euskirchen, E. S., McGuire, A. D., Norby, R. J., Walker, A. P., Warren, J. M., & Wullschleger, S. D. (2015). The unseen iceberg: plant roots in arctic tundra. *New Phytologist*, *205*(1), 34–58.

Johansen, B., & Tømmervik, H. (2014). The relationship between phytomass, NDVI and vegetation communities on Svalbard. *International Journal of Applied Earth Observation and Geoinformation*, *27*, 20–30.

Jonasson, S. (1983). The point intercept method for non-destructive estimation of biomass. *Phytocoenologia*, 385–388.

Jonasson, S. (1988). Evaluation of the point intercept method for the estimation of plant biomass. *Oikos*, 101–106.

Jónsdóttir, I. S. (2005). Terrestrial ecosystems on Svalbard: heterogeneity, complexity and fragility from an Arctic island perspective. *Biology and Environment: Proceedings of the Royal Irish Academy*, 155–165.

Le Moullec, M., Hendel, A.-L., Bon, M. P., Jónsdóttir, I. S., Varpe, Ø., van der Wal, R., Beumer, L. T., Layton-Matthews, K., Isaksen, K., & Hansen, B. B. (2021). Towards rainy Arctic winters: experimental icing impacts tundra plant productivity and reproduction. *BioRxiv*, 2021.06.10.447955. https://doi.org/10.1101/2021.06.10.447955

Le Moullec, M., Isaksen, K., Petit Bon, M., Jónsdóttir, I. S., Varpe, Ø., Hendel, A.-L., Beumer, L. T., & Hansen, B. B. (2019). *Towards rainy Arctic winters: effects of experimental icing on tundra plants and their soil conditions*. Norwegian Meteorological Institute.

Le Moullec, M., Sandal, L., Grøtan, V., Buchwal, A., & Hansen, B. B. (2020). Climate synchronises shrub growth across a high-arctic archipelago: contrasting implications of summer and winter warming. *Oikos*, *129*(7), 1012–1027.

Milner, J. M., Varpe, Ø., Wal, R. van der, & Hansen, B. B. (2016). Experimental icing affects growth, mortality, and flowering in a high Arctic dwarf shrub. *Ecology and Evolution*, *6*(7), 2139–2148. https://doi.org/10.1002/ECE3.2023

Mokany, K., Raison, R. J., & Prokushkin, A. S. (2006). Critical analysis of root: shoot ratios in terrestrial biomes. *Global Change Biology*, *12*(1), 84–96.

Myers-Smith, I. H., Forbes, B. C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K. D., Macias-Fauria, M., Sass-Klaassen, U., & Lévesque, E. (2011). Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters*, *6*(4), 45509.

Myers-Smith, I. H., Kerby, J. T., Phoenix, G. K., Bjerke, J. W., Epstein, H. E., Assmann, J. J., John, C., Andreu-Hayles, L., Angers-Blondin, S., & Beck, P. S. A. (2020). Complexity revealed in the greening of the Arctic. *Nature Climate Change*, *10*(2), 106–117.

Myneni, R. B., Hall, F. G., Sellers, P. J., & Marshak, A. L. (1995). The interpretation of spectral vegetation indexes. *IEEE Transactions on Geoscience and Remote Sensing*, *33*(2), 481–486.

Ónodi, G., Kröel-Dulay, G., Kovács-Láng, E., Ódor, P., Botta-Dukát, Z., Lhotsky, B., Barabás, S., Garadnai, J., & Kertész, M. (2017). Comparing the accuracy of three non-destructive methods in estimating aboveground plant biomass. *Community Ecology*, *18*(1), 56–62.

Opała-Owczarek, M., Pirożnikow, E., Owczarek, P., Szymański, W., Luks, B., Kępski, D., Szymanowski, M., Wojtuń, B., & Migała, K. (2018). The influence of abiotic factors on the growth of two vascular plant species (Saxifraga oppositifolia and Salix polaris) in the High Arctic. *Catena*, *163*, 219–232.

Owczarek, P., & Opała, M. (2016). Dendrochronology and extreme pointer years in the tree-ring record (AD 1951–2011) of polar willow from southwestern Spitsbergen (Svalbard, Norway). *Geochronometria*, *43*(1), 84–95.

Pearce, R. S. (2001). Plant freezing and damage. *Annals of Botany*, *87*(4), 417–424.

Phoenix, G. K., & Bjerke, J. W. (2016). Arctic browning: extreme events and trends reversing arctic greening. *Global Change Biology*, *22*, 2960–2962.

Poole, M. A., & O'Farrell, P. N. (1971). The assumptions of the linear regression model. *Transactions of the Institute of British Geographers*, 145–158.

Putkonen, J., & Roe, G. (2003). Rain-on-snow events impact soil temperatures and affect ungulate survival. *Geophysical Research Letters*, *30*(4).

Qi, Y., Wei, W., Chen, C., & Chen, L. (2019). Plant root-shoot biomass allocation over diverse biomes: A global synthesis. *Global Ecology and Conservation*, *18*, e00606. https://doi.org/https://doi.org/10.1016/j.gecco.2019.e00606

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.r-project.org/

Schuur, E. A. G., Bockheim, J., Canadell, J. G., Euskirchen, E., Field, C. B., Goryachkin, S. V, Hagemann, S., Kuhry, P., Lafleur, P. M., & Lee, H. (2008). Vulnerability of permafrost carbon to climate change: Implications for the global carbon cycle. *BioScience*, *58*(8), 701–714.

Stuart Chapin, F., & Slack, M. (1979). Effect of defoliation upon root growth, phosphate absorption and respiration in nutrient-limited tundra graminoids. *Oecologia*, *42*(1), 67–79.

Sundberg, B. (2000). Cambial growth and auxin gradients. *Cell and Molecular Biology of Wood Formation*, 169–188.

Tucker, C. J. (1977). Asymptotic nature of grass canopy spectral reflectance. *Applied Optics*, *16*(5), 1151–1156.

Tucker, C. J. (1979). Red and photographic infrared linear combinations for monitoring vegetation. *Remote Sensing of Environment*, *8*(2), 127–150.

Van Der Wal, R., & Stien, A. (2014). High-arctic plants like it hot: A long-term investigation of between-year variability in plant biomass. *Ecology*, *95*(12), 3414–3427.

Vickers, H., Høgda, K. A., Solbø, S., Karlsen, S. R., Tømmervik, H., Aanes, R., & Hansen, B. B. (2016). Changes in greening in the high Arctic: insights from a 30 year AVHRR max NDVI dataset for Svalbard. *Environmental Research Letters*, *11*(10), 105004.

Walker, D. A., Epstein, H. E., Jia, G. J., Balser, A., Copass, C., Edwards, E. J., Gould, W. A., Hollingsworth, J., Knudson, J., & Maier, H. A. (2003). Phytomass, LAI, and NDVI in northern Alaska: Relationships to summer warmth, soil pH, plant functional types, and extrapolation to the circumpolar Arctic. *Journal of Geophysical Research: Atmospheres*, *108*(D2).

Wallén, B. O. (1986). Above and below ground dry mass of the three main vascular plants on hummocks on a subarctic peat bog. *Oikos*, 51–56.

Wang, Y., Meng, B., Zhong, S., Wang, D., Ma, J., & Sun, W. (2018). Aboveground biomass and root/shoot ratio regulated drought susceptibility of ecosystem carbon exchange in a meadow steppe. *Plant and Soil*, *432*(1), 259–272.

Warton, D. I., Lyons, M., Stoklosa, J., & Ives, A. R. (2016). Three points to consider when choosing a LM or GLM test for count data. *Methods in Ecology and Evolution*, *7*(8), 882–890.

Webber, P. J. (1977). Belowground tundra research: A commentary. *Arctic and Alpine Research*, *9*(2), 105–111.

Appendix

Figure A1. Illustrations of how the biomass was separated into above- and below-ground biomass for the harvested vascular species. **(A)** The leaves of *S. polaris* was separated as above-ground biomass, while the roots and shoots were separated as below-ground biomass. For B-H: The red line indicates where the above- and below-ground biomass was separated for **(B)** *D. octopetala*, **(C)** *P. arctica*, **(D)** *D. fisheri*, **(E)** *A. borealis*, **(F)** *E. arvense*, **(G)** *B. vivipara*, **(H)** *L. confusa*. **(I)** illustrates that the rest of the species were separated in the transition between brown and green, here represented by *Stellaria sp*. All photos: INSYNC project collection.

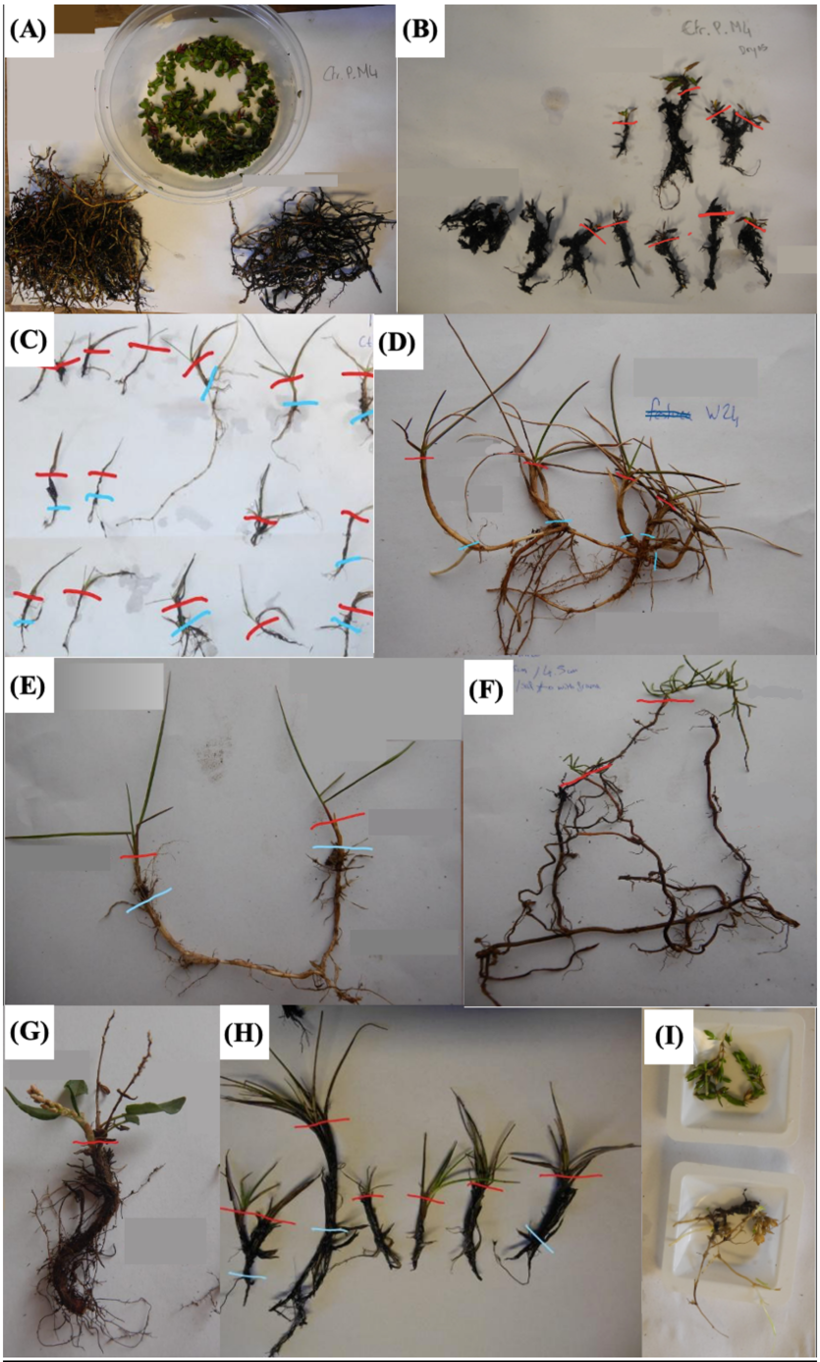

Table A1. Model selection table for the number of vascular species point intercept hits (vPIM) with different combinations of NDVI, habitat and treatment as predictor variables. df gives the degrees of freedom for each model. AICc gives the Second-order Akaike Information Criterion, while ΔAICc gives the difference in AICc value to the model with the lowest AICc. The model with the lowest AICc score is marked in bold.

Response variable	*Predictor variable(s)*	*df*	*AICc*	*ΔAICc*
log(vPIM)				
	NDVI	**3**	**15.69**	**0.00**
	NDVI+habitat	4	15.96	0.27
	NDVI*habitat	5	18.40	2.70
	NDVI+treatment	5	19.19	3.50
	NDVI+habitat+treatment	6	20.49	4.80
	NDVI*treatment	7	21.07	5.37
	NDVI*habitat+treatment	7	23.14	7.44
	NDVI*treatment+habitat	8	23.20	7.51
	NDVI*treatment*habitat	13	30.92	15.22
	1	2	56.09	40.40

Table A2. Model selection table for linear models with the square-root transformed amount of harvested biomass (g) as response variables, and with log-transformed number of point intercepts of vascular plant species (vPIM) and the number of point intercepts for lichens, moss and vascular species (aPIM) as predictor variables. Both estimated intercept are given. n gives the number of observations in the model. df gives the degrees of freedom in the model. R^2 gives the proportion of variance explained by the model. Pearson's r gives Pearson's product-moment correlation coefficient with a 95 % confidence interval. AICc gives the Second-order Akaike Information Criterion, while ΔAICc gives the difference in AICc value to the model with the lowest AICc for each pair of compared models. The model with the lowest AICc score for each pair of compared models is marked in bold. Only the models with the same response variables are compared against each other.

Response variable	*Predictor variable*	*Estimate (Intercept)*	*Estimated slope (Predictor variable)*	*n*	*df*	*AICc*	*ΔAICc*	*R^2*	*Pearson's r (95 % CI)*
sqrt(Above-ground biomass)									
	log(vPIM)	**-0.43**	**0.73**	**54**	**3**	**17.63**	**0**	**0.53**	**0.73 (0.57 – 0.83)**
	log(aPIM)	-0.33	0.66	54	3	41.35	23.72	0.27	0.52 (0.30 – 0.69)
sqrt(Below-ground biomass)									
	log(vPIM)	**1.38**	**0.99**	**54**	**3**	**105.40**	**0**	**0.29**	**0.54 (0.32 – 0.71)**
	log(aPIM)	1.94	0.77	54	3	117.67	12.28	0.11	0.33 (0.072 – 0.55)
sqrt(Total biomass)									
	log(vPIM)	**1.11**	**1.20**	**54**	**3**	**111.07**	**0**	**0.34**	**0.59 (0.39 – 0.74)**
	log(aPIM)	1.66	0.97	54	3	125.95	14.88	0.14	0.38 (0.13 – 0.59)

Table A3. Shows the mean amount of biomass (g/m^2) in the plots for all species. 95 % confidence interval is given in brackets. The below-ground/above-ground ratio (BGB/AGB-ratio) is calculated by dividing the mean below-ground biomass by the mean above-ground biomass and hence it gives the total BGB/AGB-ratio for all harvested biomass of each species. "Free roots" means unidentifiable vascular roots found in the moss/soil-layer of the plots. The first value in the "Number of observations" column corresponds to the number of different plots above-ground biomass of the species was found in. The second value in the "Number of observations" column corresponds to the number of different plots below-ground biomass of the species was found in. The number of observations in the "Total biomass"-column is equal to the biggest of the two numbers in the "Number of observations"-column.

Species	*Above-ground biomass (g/m²)*	*Below-ground biomass (g/m²)*	*Total biomass (g/m²)*	*Total BGB/AGB-ratio*	*Number of observations*
Bistorta vivipara	10.2 [8.0 - 12.4]	46.9 [37.3 - 56.4]	57.0 [45.6 - 68.5]	4.60	54/54
Poa arctica	10.8 [7.1 - 14.5]	27.2 [18.9 - 35.5]	38.0 [26.2 - 49.9]	2.52	37/37
Alopecurus borealis	48.3 [37.3 - 59.3]	195.1 [153.7 - 236.4]	243.4 [191.3 - 295.4]	4.04	53/53
Luzula confusa	18.1 [11.9 - 24.4]	90.7 [59.4 – 122.0]	108.8 [72.3 - 145.3]	5.00	42/43
Dupontia fisheri	5.83 [2.78 - 8.89]	23.9 [12.5 - 35.2]	29.7 [15.4 – 44.0]	4.09	20/20
Salix polaris	31.3 [26.5 - 36.1]	224.0 [189.6 - 258.5]	255.3 [217.0 - 293.6]	7.17	54/54
Equisetum arvense	3.34 [2.07 - 4.61]	62.0 [42.0 - 82.1]	65.4 [44.2 - 86.6]	18.6	34/36
Dryas octopetala	0.683 [0.080 - 1.29]	5.88 [0.52 - 11.24]	6.6 [0.8 - 12.4]	8.60	5/8
Stellaria sp.	0.113 [0.011 - 0.214]	0.0963 [0.009 - 0.183]	0.209 [0.029 - 0.389]	0.852	6/6
Peduncularis sp.	0.0277 [-0.0153 - 0.0706]	0.0907 [-0.0464 - 0.2279]	0.118 [-0.062 - 0.298]	3.27	2/2
Calamagrostis neglecta	0.290 [-0.292 - 0.872]	0.787 [-0.791 - 2.365]	1.08 [-1.09 - 3.24]	2.71	1/1
Ranunculus sp.	0.0103 [-0.0082 - 0.0288]	0.0584 [-0.0478 - 0.1646]	0.0687 [-0.0560 - 0.1934]	5.67	2/2
Free roots	-	43.5 [33.5 - 53.4]	43.5 [33.5 - 53.4]	-	- /54
Total	129.0 [114.4 - 143.7]	676.6 [610.2 - 743.1]	805.7 [726.3 - 885.0]	5.25	54/54

Table A4. Shows the mean below-ground biomass/above-ground biomass (BGB/AGB-ratio) in the plots for all species. 95 % confidence interval is given in brackets. n gives the number of plots with observations of both below-ground biomass and above-ground biomass for the respective species.

	Mean BGB/AGB-ratio	*95 % CI*	*n*
Bistorta vivipara	5.71	[4.88 - 6.53]	54
Poa arctica	3.09	[2.63 - 3.55]	37
Alopecurus borealis	4.32	[3.99 - 4.64]	53
Luzula confusa	6.56	[4.60 - 8.51]	43
Dupontia fisheri	4.42	[3.74 - 5.10]	20
Salix polaris	7.74	[6.80 - 8.69]	54
Equisetum arvense	23.7	[18.9 - 28.5]	36
Dryas octopetala	6.05	[0.00 - 12.10]	8
Stellaria sp.	1.07	[0.24 - 1.90]	6
Peduncularis sp.	3.42	[-0.37 - 7.21]	2
Calamagrostis neglecta	2.71	-	1
Ranunculus sp.	5.40	[0.99 - 9.81]	2
Total	5.54	[5.16 - 5.91]	54

Table A5. The table shows the back-transformed expected mean and the 95 % confidence interval for the log(below-ground biomass/above-ground biomass ratio) with habitat and treatment as fixed effects and species as random intercept effect. The values in the table were extracted by releveling the order of the fixed effects so that all six combinations of habitat and treatment were the intercept and then reading out the back-transformed expected mean and the 95 % confidence intervals for all six possible intercepts.

	BGB/AGB-ratio	
(Intercept)	*Expected mean*	*95 % CI*
Mesic, control	4.27	2.77 – 6.60
Mesic, icing	4.37	2.84 – 6.73
Mesic, thaw freeze	4.59	2.96 – 7.11
Wet, control	3.54	2.95 – 4.27
Wet, icing	4.30	2.76 – 6.69
Wet, thaw-freeze	5.69	3.60 – 8.98

Table A6. Model selection table for below-ground biomass divided by above-ground biomass with different combinations of habitat and treatment as fixed predictor variables. Species were included as a random effect (random intercept) in all models. df gives the degrees of freedom for each model. logLik gives the log-likelihood for each model. AICc gives the Second-order Akaike Information Criterion, while ΔAICc gives the difference in AICc value to the model with the lowest AICc.

Response variable	*Fixed effects*	*Random effects*	*df*	*logLik*	*AICc*	*ΔAICc*
log(below/above-ground biomass ratio)						
	habitat*treatment	(1|species)	8	-233.81	484.10	0.00
	treatment	(1|species)	5	-237.51	485.23	1.12
	habitat + treatment	(1|species)	6	-237.44	487.16	3.06
		(1|species)	3	-242.16	490.41	6.30
	habitat	(1|species)	4	-241.96	492.05	7.95

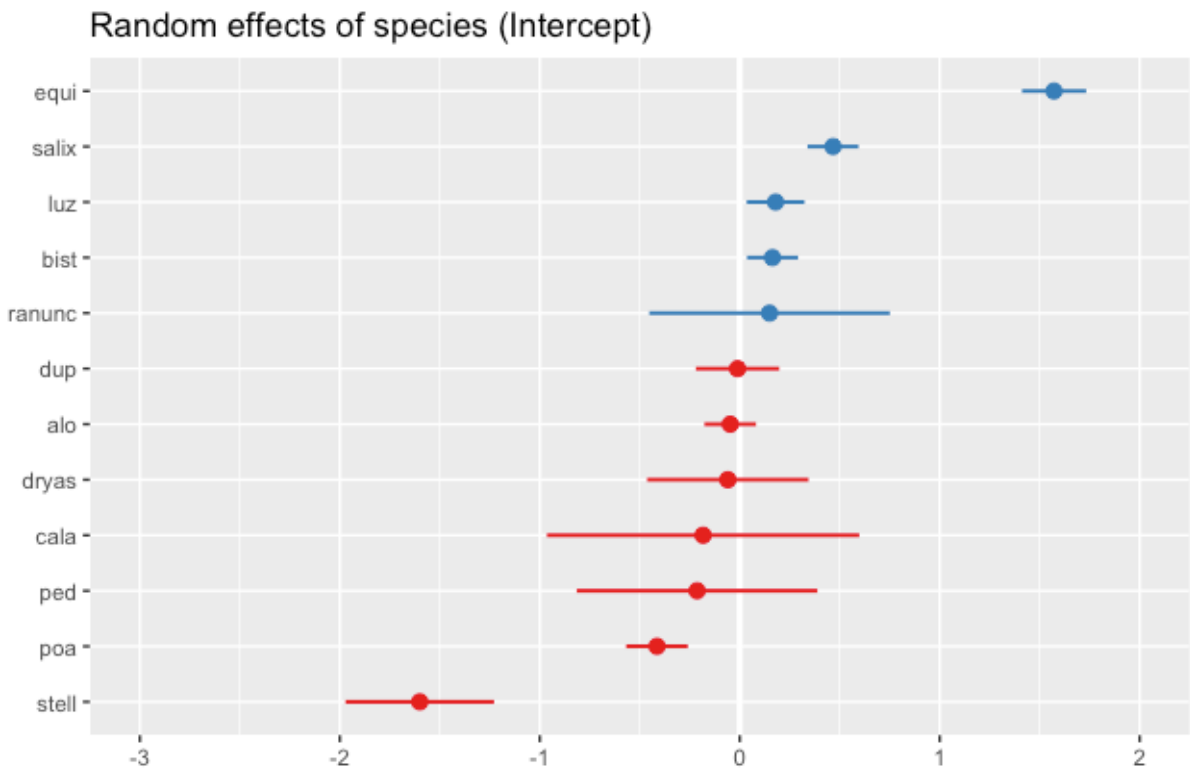

Figure A2. The plotted random effect on the below-ground/above-ground biomass ratio of the different species (equi = *E. arvense*, salix = *S. polaris,* luz = *L. confusa,* bist = *B. vivipara,* ranunc = *Ranunculus sp.,* dup = *D. fisheri,* alo = *A. borealis,* dryas = *D. octopetala,* cala = *C. neglecta,* ped = *Peduncularis sp.,* poa = *P. arctica,* stell = *Stellaria sp.).*

Table A7. Summary of the linear mixed-effect model with below-ground biomass (g) (square root transformed) as a response variable, habitat and treatment as fixed predictor variables, and species as a random intercept effect. The p-value tells if the predictors change the estimates significantly compared to the intercept. Significant p-values (alpha = 0.05) are marked in bold. The intercept was changed by releveling the treatment variable. 95 % confidence interval is given in the CI column. σ^2 represents the residual intercept variance within species. τ_{00} is the residual intercept variance, controlling for species. ICC (intraclass correlation coefficient) gives the proportion of variance accounted for by species. $N_{species}$ gives the number of different species included in the model. Marginal R^2 gives the proportion of variance explained by the fixed factors. Conditional R^2 gives the proportion of variance explained by both random and fixed effects. The number of observations is the number of different species with below-ground biomass in each plot, added together. M = mesic habitat. W = wet habitat. C = control treatment. I = icing treatment. Th = thaw-freeze treatment.

(Intercept)	*Predictors*	*Estimates*	*CI*	*p*
M : C		1.36	0.89 – 1.82	**<0.001**
	I	0.07	-0.15 – 0.30	0.521
	Th	0.09	-0.16 – 0.33	0.491
	W	-0.37	-0.63 – -0.11	**0.006**
W : C	I	-0.01	-0.28 – 0.26	0.955
	Th	0.00	-0.31 – 0.31	0.993
	Random Effects			
	σ^2		0.44	
	$\tau_{00\ species}$		0.53	
	ICC		0.54	
	$N_{species}$		12	
	Observations		316	
	Marginal R^2 / Conditional R^2		0.043 / 0.564	

Table A8. Summary of the linear mixed-effect model with sqrt(above-ground biomass (g)) as a response variable, habitat and treatment as fixed predictor variables, and species as a random intercept effect. The p-value tells if the predictors change the estimates significantly compared to the intercept. Significant p-values (alpha = 0.05) are marked in bold. The intercept was changed by releveling the treatment variable. 95 % confidence interval is given in the CI column. σ^2 represents the residual intercept variance within species. τ_{00} is the residual intercept variance, controlling for species. ICC (intraclass correlation coefficient) gives the proportion of variance accounted for by species. $N_{species}$ gives the number of different species included in the model. Marginal R^2 gives the proportion of variance explained by the fixed factors. Conditional R^2 gives the proportion of variance explained by both random and fixed effects. The number of observations is the number of different species with below-ground biomass in each plot, added together. M = mesic habitat. W = wet habitat. C = control treatment. I = icing treatment. Th = thaw-freeze treatment.

(Intercept)	*Predictors*	*Estimates*	*CI*	*p*
M : C		0.62	0.42 – 0.81	**<0.001**
	I	0.02	-0.09 – 0.13	0.713
	Th	0.00	-0.11 – 0.12	0.943
	W	-0.11	-0.23 – 0.02	**0.089**
W : C	I	-0.06	-0.18 – 0.07	0.394
	Th	-0.10	-0.25 – 0.05	0.190
	Random Effects			
	σ^2		0.10	
	$\tau_{00\ species}$		0.09	
	ICC		0.48	
	$N_{species}$		12	
	Observations		310	
	Marginal R^2 / Conditional R^2		0.034 / 0.497	

Table A9. Summary of the linear model with log(below-ground biomass/above-ground biomass (BGB/AGB-ratio)) as a response variable and habitat, treatment and species as interacting predictor variables. The predictor variables in the model were releveled in total 10 times in order to easier compare the estimated effect of the treatment in the different habitats for different species. M = mesic habitat. W = wet habitat. C = control treatment. I = icing treatment. Th = Thaw-freeze treatment. Salix = *S. polaris*. Gram = *A. borealis, P. arctica, D. fisheri* and *C. neglecta*. Bist = *B. vivipara*. Luz = *L. confusa*, Equi = *E. arvense*. CI gives the 95 % confidence interval. Significant p-values (alpha = 0.05) are marked in bold. The number of observations corresponds to the number per species per plot summed together for all plots.

(Intercept)	*Predictors*	*Estimates*	*CI*	*p*
Salix : C : M		2.00	1.72 – 2.28	**<0.001**
	I	-0.07	-0.44 – 0.30	0.708
	Th	0.04	-0.36 – 0.43	0.851
	W	-0.57	-0.99 - -0.16	**0.007**
Salix : C : W	I	0.55	0.12 – 0.99	**<0.001**
	Th	0.99	0.49 – 1.49	**<0.001**
Gram : C : M		1.20	1.00 – 1.40	**<0.001**
	I	-0.01	-0.27 – 0.25	0.921
	Th	0.04	-0.23 – 0.32	0.762
	W	0.07	-0.22 – 0.36	0.636
Gram : C : W	I	0.22	-0.08 – 0.51	0.152
	Th	0.37	0.02 – 0.72	**0.036**
Bist : C : M		1.69	1.42 – 1.97	**<0.001**
	I	-0.14	-0.51 – 0.22	0.442
	Th	-0.18	-0.57 – 0.21	0.366
	W	-0.21	-0.62 – 0.21	0.327
Bist : C : W	I	0.24	-0.20– 0.68	0.286
	Th	0.60	0.10 – 1.10	**0.019**
Luz : C : M		1.85	1.58 – 2.13	**<0.001**
	I	-0.19	-0.57 – 0.18	0.312
	Th	0.06	-0.35 – 0.46	0.785
	W	-0.23	-0.72 – 0.25	0.337
Luz : C : W	I	-0.75	-1.34 - -0.16	**0.013**
	Th	-0.64	-1.37 – 0.10	0.089
Equi : C : M		2.97	2.57 – 3.36	**<0.001**
	I	0.11	-0.40 – 0.63	0.671
	Th	0.42	-0.22 – 1.07	0.194
	W	-0.17	-0.67 – 0.33	0.500
Equi : C : W	I	0.23	-0.20 – 0.67	0.294
	Th	0.61	0.02 – 1.20	**0.044**
Observations	295			
R^2 / R^2 adjusted	0.643 / 0.604			

Table A10. The table shows the back-transformed expected mean and the 95 % confidence interval for the log(below-ground biomass/above-ground biomass ratio) with habitat, treatment and species as interacting predictor variables. The values in the table were extracted by releveling the order of the fixed effects so that all combinations of habitat, treatment and species were the intercept, and then reading out the back-transformed expected mean and the 95 % confidence intervals for all 30 possible intercepts. n gives the number of observations for the 30 different combinations of species, habitat and treatment. M = mesic habitat. W = wet habitat. C = control treatment. I = icing treatment. Th = Thaw-freeze treatment. Salix = *S. polaris*. Gram = *A. borealis*, *P. arctica*, *D. fisheri* and *C. neglecta*. Bist = *B. vivipara*. Luz = *L. confusa*, Equi = *E. arvense*.

	BGB/AGB-ratio		
(Intercept)	*Expected mean*	*95 % CI*	*n*
Salix : M : C	7.39	5.60 – 9.75	10
Salix : M : I	6.89	5.40 – 8.79	13
Salix : M : Th	7.67	5.81 – 10.13	10
Salix : W : C	4.17	3.06 – 5.69	8
Salix : W : I	7.26	5.32 – 9.90	8
Salix : W : Th	11.19	7.55 – 16.57	5
Gram : M : C	3.32	2.73 – 4.04	20
Gram : M : I	3.28	2.76 – 3.89	26
Gram : M : Th	3.46	2.85 – 4.22	20
Gram : W : C	3.56	2.88 – 4.40	17
Gram : W : I	4.42	3.59 – 5.44	18
Gram : W : Th	5.17	3.92 – 6.83	10
Bist : M : C	5.44	4.12 – 7.18	10
Bist : M : I	4.71	3.69 – 6.01	13
Bist : M : Th	4.54	3.44 – 5.99	10
Bist : W : C	4.42	3.24 – 6.03	8
Bist : W : I	5.61	4.11 – 7.65	8
Bist : W : Th	8.06	5.44 – 11.94	5
Luz : M : C	6.38	4.84 – 8.43	10
Luz : M : I	5.26	4.08 – 6.78	12
Luz : M : Th	6.75	5.04 – 9.05	9
Luz : W : C	5.05	3.41 – 7.48	5
Luz : W : I	2.38	1.54 – 3.69	4
Luz : W : Th	2.67	1.43 – 4.96	2
Equi : M : C	19.41	13.10 – 28.74	5
Equi : M : I	21.69	15.56 – 30.22	7
Equi : M : Th	29.66	17.86 – 49.25	3
Equi : W : C	16.34	11.98 – 22.29	8
Equi : W : I	20.66	15.15 – 28.18	8
Equi : W : Th	30.07	18.11 – 49.92	3

Table A11. The table shows the back-transformed expected mean and the 95 % confidence interval for the sqrt(above-ground biomass (g)) with habitat, treatment and species as interacting predictor variables., and for the sqrt(below-ground biomass (g)) with habitat, treatment and species as interacting predictor variables The values in the table were extracted by releveling the order of the fixed effects so that all combinations of habitat, treatment and species were the intercept, and then reading out the back-transformed expected mean and the 95 % confidence intervals for all 30 possible intercepts. n gives the number of observations for the 30 different combinations of species, habitat and treatment. M = mesic habitat. W = wet habitat. C = control treatment. I = icing treatment. Th = Thaw-freeze treatment. Salix = *S. polaris*. Gram = *A. borealis*, *P. arctica*, *D. fisheri* and *C. neglecta*. Bist = *B. vivipara*. Luz = *L. confusa*, Equi = *E. arvense*.

(Intercept)	*Above-ground biomass* Expected mean	95 % CI	n	*Below-ground biomass* Expected mean	95 % CI	n
Salix : M : C	1.18	0.76 – 1.96	10	8.71	6.15 – 11.72	10
Salix : M : I	1.21	0.84 – 1.65	13	7.88	5.73 – 10.38	13
Salix : M : Th	1.00	0.62 – 1.46	10	7.79	5.37 – 10.64	10
Salix : W : C	0.56	0.26 – 0.97	8	2.81	1.32 – 4.85	8
Salix : W : I	0.46	0.20 – 0.84	8	3.40	1.73 – 5.62	8
Salix : W : Th	0.44	0.13 – 0.93	5	4.96	2.43 – 8.38	5
Gram : M : C	0.91	0.64 – 1.21	20	2.95	1.91 – 4.20	20
Gram : M : I	0.99	0.74 – 1.27	26	3.47	2.47 – 4.65	26
Gram : M : Th	0.94	0.67 – 1.25	20	3.37	2.25 – 4.70	20
Gram : W : C	0.65	0.41 – 0.94	17	2.37	1.39 – 3.61	17
Gram : W : I	0.32	0.16 – 0.52	18	1.40	0.69 – 2.36	18
Gram : W : Th	0.69	0.38 – 1.08	10	3.67	2.08 – 5.70	10
Bist : M : C	0.28	0.10 – 0.56	10	1.36	0.48 – 2.69	10
Bist : M : I	0.26	0.10 – 0.48	13	1.18	0.46 – 2.26	13
Bist : M : Th	0.27	0.09 – 0.53	10	1.19	0.38 – 2.44	10
Bist : W : C	0.34	0.12 – 0.67	8	1.37	0.41 – 2.88	8
Bist : W : I	0.25	0.07 – 0.54	8	1.39	0.42 – 2.91	8
Bist : W : Th	0.07	0.00 – 0.33	5	0.57	0.01 – 2.02	5
Luz : M : C	0.40	0.18 – 0.71	10	2.48	1.22 – 4.20	10
Luz : M : I	0.42	0.21 – 0.71	12	2.47	1.30 – 4.01	12
Luz : M : Th	0.52	0.25 – 0.90	9	3.76	2.08 – 5.94	9
Luz : W : C	0.42	0.12 – 0.89	5	1.59	0.35 – 3.72	5
Luz : W : I	1.64	0.90 – 2.61	4	2.64	0.92 – 5.25	5
Luz : W : Th	0.57	0.08 – 1.51	2	1.69	0.06 – 5.55	2
Equi : M : C	0.12	0.00 – 0.42	5	2.24	0.69 – 4.69	5
Equi : M : I	0.16	0.02 – 0.43	7	3.12	1.45 – 5.44	7
Equi : M : Th	0.08	0.01 – 0.44	3	2.00	0.31 – 5.19	3
Equi : W : C	0.12	0.01 – 0.35	8	2.18	0.90 – 4.02	8
Equi : W : I	0.18	0.04 – 0.44	8	3.56	1.85 – 5.83	8
Equi : W : Th	0.02	0.06 – 0.29	3	0.57	0.01 – 2.03	5

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