UiT The Arctic University of Norway

Faculty of Biology, Fisheries and Economics

Homesick plants – a study on Plant-soil feedback in home and foreign soil following a latitudinal sampling gradient from Morocco to Svalbard

Supervisors: professors Kari Anne Bråthen and Laura Jaakola

Karoline Helene Aares

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Foreword

This experiment is part of the Microecol project, funded by the Spanish Research Agency (CGL2017-84515-R) granted to prof. Francisco I. Pugnaire. Field sampling in Morocco, Spain, France, Switzerland and Norway was led by respectively prof. Francisco I. Pugnaire, Christian Kindler, prof. Richard Michalet, post-doc. Christian Schöb and prof. Kari Anne Bråthen. The experiment was supervised by prof. Kari Anne Bråthen and conducted in collaboration with bachelor student Torunn Bockelie Rosendahl.

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Abstract

Plant-soil feedbacks receive increasing attention as impactors of plant performance and drivers of plant community composition. How plant-soil feedbacks act in introduction events regarding both native and foreign species is a topic requiring more research. In this aspect, two particular theories are of interest, Home-field advantage, and Enemy-release. The former predicts that plants perform best in their native range due to positive Plant-soil feedbacks with beneficial soil biota. The latter predicts that plants will have increased performance in novel habitats, as they escape from species-specific soil-borne pathogens. While both these phenomena might be at play in introduction events, the unanswered question remains on their relative importance for predicting net plant-soil feedbacks. “Are plant-soil feedbacks more positive in native or foreign soils?” This is an indoor experimental study using minimally treated soils of six alpine grassland sites in Europe and Northern Africa, and seeds from four of those sites. Seedlings were planted in native and foreign soil and growth was compared. Climate was also manipulated, simulating Arctic and Temperate alpine grassland climates regarding temperature and photoperiod. The results reveal that home-site advantage overshadows impacts by other drivers, in the sense that plants benefitting from home soil showed stronger growth trends than plants benefitting from foreign soil. Moreover, plants perform best in climates resembling their native climate. This study concludes that plant-soil feedbacks and climate may limit establishment of populations outside their native ranges, and that plant-soil feedbacks might be controlled more by positive interactions than what earlier studies have concluded.

Keywords: Plant-soil feedback, indoor growth experiment, plant performance, home soil, foreign soil, graminoid, forb, grasslands, home-site advantage

1 Introduction

While a lot of research has been directed at understanding aboveground plant interactions, there are large knowledge gaps on abiotic and biotic plants-soil interactions (Bever *et al.* 2010; Bardgett & Van Der Putten 2014; Van Der Putten *et al.* 2016). Increasing attention is being directed towards belowground ecosystems, and how they affect plant communities (Bever *et al.* 2010). In particular, plant-soil feedback (PSF) has been proposed as a predictor for plant growth (Van Der Putten *et al.* 2013; Pugnaire *et al.* 2019). PSF occurs when a plant alters its surrounding soil environment, which in turn implicates local plant performance (Bever *et al.* 2010). These feedbacks are positive when the soil environment changes to benefit plant performance, and negative when the changed soil environment limits plant performance (Van Der Putten *et al.* 2013).

PSF is further categorized based on whether the soil alteration impacts conspecifics or heterospecifics (Bever *et al.* 1997). Direct PSF occurs when a plant species alters the soil so that only conspecifics are affected (Van Der Putten *et al.* 2013); for example seeds may germinate differently in varying proximity to conspecific standing crops (Janzen 1970; Bever *et al.* 2010; McCarty-Neumann 2010). Indirect PSF occur when heterospecifics are impacted (Bever *et al.* 1997). For example, soil moisture and temperature fluctuations are stabilized by the alpine plant *Azorella monantha*, facilitating the growth of heterospecifics (Cavieres 2005). In plant introduction events, the relative importance of indirect versus direct PSF is essential in anticipating the performance for native and introduced plants, since foreign plants are susceptible only to indirect PSF (Levine *et al.* 2006; van der Voorde 2011; Lau & Suwa 2016). If the indirect PSF experienced by foreign plants are different from that experienced by native plants, this dynamic may have implications for foreign versus native plant fitness.

PSF occur via both abiotic and biotic pathways. Positive abiotic PSF can benefit introduced plants by making the ecosystem more inhabitable (Cavieres 2005). One example of positive abiotic PSF is when aboveground plant litter insulates soil, ultimately benefitting plants with a low tolerance for fluctuations in soil temperature (Cavieres *et al.* 2014). Contrarily, negative abiotic PSF occurs when plants deplete the soil of nutrients (Hayes 2014), resulting in decreased plant performance due to nutrient shortage (Png *et al.* 2019).

PSF occur via biotic pathways when plants alter soil communities, which in turn affect plant performance (Hayes 2014). Most documented biotic PSF are caused by alterations in soil mutualist, decomposer or pathogen communities (Bever *et al.* 2010; Van Der Putten *et al.* 2016).

Positive biotic PSF occur when plants promote the growth of their respective soil mutualists (Bever *et al.* 2010; Teste *et al.* 2017) and decomposers (Palozzi & Lindo 2018). Plant performance is improved through enhanced nutrient accessibility (Van Der Putten *et al.* 2016) or increased tolerance to abiotic stress and pathogens (Smith 2008; Sikes 2010). Promoted soil mutualists can further drive selection on plant establishment, promoting plant species that best utilise these mutualists (Bever *et al.* 2010). In some instances, this dynamic could enhance the growth of plant species that have occupied the soil for longer than the newcoming species (Lau & Suwa 2016). Plants promote the decomposers that are best suited for decomposing their respective litter types, so that these grow in abundance (Palozzi & Lindo 2018). A faster decomposition of plant litter speeds up nutrient cycling, ultimately facilitating nutrient access for nearby plants (Van Der Putten *et al.* 2016; Veen *et al.* 2019). Mutualist- and decomposer driven PSF both alter soil abiotic parameters through change of nutrient content, linking abiotic and biotic PSF.

Negative biotic PSF limits plant performance through build-up of soil pathogens (Mills & Bever 1998). Natural selection promotes the soil pathogens that are the most able to exploit host plants. Therefore, plant performance can decrease over time as pathogens accumulate, consequently limiting growth (Klironomos 2002). Notably, most documented instances of PSF are negative (Klironomos 2002; Bever 2003).

After a plant is introduced into a new habitat, it often benefits from the lack of species-specific soil pathogens. This phenomenon is regarded as the Enemy-Release Hypothesis (Van Der Putten *et al.* 2013; Lau & Suwa 2016; Dukes *et al.* 2019). Under certain conditions, pathogen release may substantially impact plant performance. In order for this to occur, the native soil community must fail to exploit the foreign plant (Inderjit 2010). In addition, the introduced plant must gain an advantage over individuals in the native plant community

before the soil pathogens adapt to it. In short, whether pathogen release induces advantages large enough to promote foreign over native plants is context dependent.

PSF is a sum of several plant-soil interactions occurring simultaneously (Van Der Putten *et al.* 2013). Native plant PSF can be relatively more positive than PSF experienced by foreign plants (Palozzi & Lindo 2018). In competition events, advantage from enemy release can lose importance due to foreign plants lacking positive PSF experienced only by native plants. Home-site advantage has been documented in various transplant studies, where plants have grown better in home soil than in foreign soil (Pregitzer *et al.* 2010; Bennington *et al.* 2012). Native plants sometimes perform better due to the presence of specialised decomposers. Improved decomposition generates available nutrients more rapidly in soils surrounding native plants, benefitting their growth over that of foreign plants (Veen *et al.* 2015; Palozzi & Lindo 2018; Veen *et al.* 2019). Moreover, home-site advantage has been documented when plants have been transplanted within their original distribution range (Bennington *et al.* 2012). Factors beyond litter-decomposer dynamics can lead to a plant thriving in home soil over foreign soil. For example, native soils usually contain a mutualist community promoted by native species, which could lead to home-site advantages (Bever *et al.* 2010).

Alpine grassland plant communities are dominated by perennial grasses and forbs (García-González 2008). The combination of low winter temperatures and grazing pressure inhibits the establishment of forests and thickets while annual snow cover further constrains the length of the growing season (Begon 2005). At the same time, these communities often display rapid nutrient cycling when compared to other biomes. This is in part due to fertilization by herbivores, and partly because of rapid growth rates during the growth period, followed by large litter input during senescence (Begon 2005). Although this ecotype exists worldwide, alpine grassland communities vary in both species composition and climate regime. Latitudinal variations provide differences in photoperiod and light intensity, driving divergent adaptations for native plants (Begon 2005). Soil community compositions are also controlled by factors such as snow cover and which plant species are present (Gavazov 2010).

As global climate changes at an unprecedented rate, both soil (Frey 2008; Cregger 2014) and plant communities (Parmesan & Yohe 2003; Alexander *et al.* 2018) are expected to change. Alpine grassland communities are uniquely vulnerable to foreign plant introductions (Alexander *et al.* 2015; Alexander *et al.* 2018). Increased temperatures affect soil communities and alter functional group compositions, such as the ratio of bacterial to fungi (Cregger 2014). Assuming such changes affect PSF, temperature increase has the potential to influence PSF (Van Der Putten *et al.* 2016; Pugnaire *et al.* 2019). At the same time, temperature increase is expected to change alpine plant communities through niche tracking, as alpine plants disperse upwards in altitude, following their climatic optimum and facing competition from foreign plants dispersing from lower altitudes (Parmesan & Yohe 2003; Urban *et al.* 2012; Alexander *et al.* 2015). This, coupled with anthropogenically aided introductions has resulted in establishment of plant species beyond their native ranges, despite unfamiliar temperature and photoperiods (Parmesan & Yohe 2003). However, climatic variables might still influence the outcome of plant introductions directly on plant species, and indirectly through interactions with PSF (Van Der Putten *et al.* 2016; Pugnaire *et al.* 2019).

The aim of this study is to comparatively evaluate the effect of PSF on the performance of alpine grassland plants in native and foreign soils. My approach is to do a reciprocal planting experiment, where seedlings are being planted in both native and foreign soils, and their growth is being compared. Following a latitudinal gradient from Morocco to Svalbard, I collected soil and seeds from six alpine grasslands. In this project, I aim to address the following questions: 1) Do plants perform best in soils of their native habitat, or do they perform better when introduced into soils where they have no ecological history? and 2) is growth improved in native climates, or do plants benefit from being grown in a foreign climate? I present six hypotheses regarding plant growth in response to growing in home or foreign soil and climates, where the first three regard to PSF, and the latter three concern the effect of climate: 1) plants grow better in their home soil than in foreign soil, 2) plants grow better in foreign soils than in home soils, 3) the effect of soil origin is context specific; variation in soil abiotic conditions cause some plants to grow better in home soil and others to grow better in foreign soil. 4) Plant growth is improved in home climate, regardless of soil

origin, 5) plant growth is improved in foreign climate, regardless of soil origin and, 6) climate and soil interact, so that climate effect depends on whether plants grow in home soils or foreign soils. The results from this study can give implications for a better understanding of PSF dynamics related to plant introductions, as well as to the importance of climatic variables regarding PSF and foreign plant species performance.

2 Material and Methods

2.1 Study sites

Soil and seeds were collected from six sites on following a latitudinal gradient from 32°N to 78°N. At each site alpine grasslands were targeted. Aiming for similar climate regimes caused altitudinal variation between sites, with the northernmost sites being closer to sea level and the southernmost sites laying almost 3000 meters above sea level (see Table1). The sites were, from south to north, Oukaïmeden, Atlas, Morocco, Borreguiles area, Sierra Nevada, Spain, Aragnouet, Pyrenees, France, Flüela pass, Davos, Switzerland, Varanger peninsula, Norway, and Adventdalen, Svalbard (see Figure 1). The sites in Atlas, Sierra Nevada, Pyrenees, and Alps are all characterized as alpine grasslands, while Varanger and Svalbard are Arctic tundra grasslands. These sites, while harbouring co-occurring species and in many ways providing similar habitats, do vary in climatic conditions as well as soil properties (see Table 1).

Figure 1: Study sites for soil and seed sampling

Table 1: Climatic, geological and spatial variation between study sites for soil and seed sampling. Yearly precipitation and average yearly temperatures from sites were recorded from respectively (en.climate-data.org 2020a), (Oliva 2011), (fr.climate-data.org 2020), (MeteoSwiss 2020), (en.climate-data.org 2020b), (Førland 2003; Hanssen-Bauer 2019). Photoperiod for all sites was obtained from (timeanddate.com 2020). Growth period in Svalbard was recorded from (Karlsen 2014), while growth period from other sites were recorded from (FAO-GAEZ 2012). Soil type was recorded from (FAO-UNESCO 1974b) and are categorized using the world reference base for soil resources.

Site	**Coordinates**	**Altitude (metres above sea level)**	**Yearly precipitation (mm)**	**Photoperiod mid-July (hours/24h)**	**Growth period length (days)**	**Soil type (FAO – unesco)**	**Average yearly temperature (ºC)**
Atlas	31°05N, 7°90E	2700	699	12	120-149	Rendizinas	7.8
Sierra Nevada	37°08N, 3°39E	2800	690	14.5	150-179	Calcic Cambisols	3.9
Pyrenees	42°61N, 1°47E	2100	1400-1500	15	210-239	Eutric Cambisols	9.6
Alps	46°75N, 9°95E	2300-3000	2100	15	90-119	Rankers Lithosols	0
Varanger	70°42N, 29°42E	18	549	24	90-119	Orthic podzols	1.5
Svalbard	78°10N, 16°04E	30	190	24	50-60	Leptic Cryosol	-3.8

Even though some species co-occur between sites, species abundances vary, as revealed by field transect analyses. The Atlas site was dominated by the forbs *Leontodon hispidus*, *Ranunculus sp*, and the sedge *Carex sp*. The Sierra Nevada site was dominated by the grass *Festuca regularis* and the forbs *Lotus glareosus and Gentiana sp*. The Pyrenees was a typical *Nardus stricta* grassland, with the dominating graminoids *Nardus stricta, Carex semprevivirens* and *Agrostis tenuis*. In the Alps, the dominating species were the grasses *Deschampsia cespitosa, Nardus stricta* and *Agrostis sp*. The Varanger Peninsula sites were dominated by the graminoids *Deschampsia cespitosa, Poa sp*., *Luzula multiflora* and *Luzula sudetica*. In Svalbard, the dominating species were the dwarf shrub *Salix polaris*, the grasses *Poa alpina* and *Poa arctica*, and the forb *Bistorta vivipara*.

2.2 Sampling

2.2.1 Soil collection design

Within each of the six sites, five or six subsites at least 100 meters apart were subjectively chosen for soil collection (see Table 2). Within each subsite, the species composition of the grassland community was analyzed along a set of five-meter-long transects, with distance between transects of at least two meters (see Table 2). Soil was collected along every transect, so that each transect contributed to one soil replicate. Number of replicates and transects per subsite varied among sites (see Table 2). In Atlas, Sierra Nevada, Pyrenees and the Alps, there were six replicates, whereas in Varanger and Svalbard there were three sampling replicates. For all sites to have equal number of replicates from all subsites, each replicate from Svalbard and Varanger was split into two sub-replicates.

Table 2: Soil collection design.

Site	Subsite	Transect/Replicate	Sub-replicate
Atlas Mountains	6	5	-
Sierra Nevada	5	6	-
Pyrenees	5	6	-
Alps	5	6	-
Varanger Peninsula	6	3	2
Svalbard	6	3	2

2.2.2 Soil collection

Soil was collected at each meter mark along the transects. Prior to soil collection, aboveground litter layer was removed on the elected collection spot. Soil was then sampled from the upper 10 centimeters of the soil profile and mixed in separate plastic bags for each replicate. From Atlas, Sierra Nevada, the Pyrenees and the Alps, approximately 3 dl of soil was collected from each replicate. From Varanger and Svalbard, approximately 6 dl of soil was collected from each replicate. All soil collection equipment was cleaned and sterilized

between each sample using 70% ethanol, 30% distilled water solutions together with paper and, if necessary, a sterilized toothbrush. Soils were then transported to the phytotron belonging to UiT The Arctic University of Norway and stored in 0.5°C prior to further processing.

2.2.3 Seed collection

From each site, seeds were collected from abundant graminoid and forb species that had ripe seeds in the sampling period. The seeds were collected directly from the plants and stored in plastic bags labelled with site and plant name. Seeds were then transported to the phytotron belonging to UiT The Arctic University of Norway, were they were stored in -18°C prior to further processing.

2.3 Soil and seed preparation prior to experiment

2.3.1 Soil preparation

Soil samples were transferred to paper bags and dried in a drying oven (60°C for Atlas soils, other soils on 30°C for 48 hours). After drying, soils were sieved through a 2 mm sieve and stored in paper bags in room temperature until further use.

2.3.2 Germination, planting and growth

For the planting experiment, a substrate was made for each soil replicate, containing 1 dl of soil and 1 dl of agra perlite. In order to plant the seedlings, pots of 10 cm diameter were filled with 0.5 dl of agra perlite in the bottom, followed by the substrate.

Seeds were placed for 1.5 month at 0.5 °C in pH-neutral sand which was watered by distilled water. Seeds originating from Varanger and Svalbard were put in 18°C under 24/24h light in a greenhouse for germination. Seeds originating from the other 4 sites were placed to germinate in growth chambers with 18°C and 15 hours of light and 9 hours of darkness per 24 hours. For some species, unsuccessful germination in sand led to the need of subsidizing seedling amount by planting additional seeds in petri dishes on moist filter paper. Germinated seedlings from the respective plant origins were planted in soil from all six sampling sites, five being regarded “foreign” and the soil sampled at same site as seeds being “home” (see

Figure 3). Plants were watered with distilled water for the first 3 weeks, followed by watering using tap water. After planting, the seedlings were wrapped in transparent plastic for 6 weeks, which was gradually removed.

2.3.3 Plant communities used

The aim was to use one forb species and one graminoid species from each site and plant these together in pots of soil from the different sites. In this way each individual pot would contain one "plant origin" of two plants representing each site, and soil from one specific site. In the end, which species were planted depended on germination success in the lab, (see Table 3 and Figure 2). This was because I encountered difficulties in obtaining enough seedlings of each species to replicate the plant-soil combinations as desired. From Atlas, the grass *Anthoxanthum odoratum* and the forb *Leontodon hispidus* were used. From the Pyrenees, only *Leontodon pyrenaicus* had sufficient amount of germinated individuals so that the experiment's replicate requirement could be met. Therefore, the Pyrenees plant origin contained just one species. From Varanger, the grass *Deschampsia cespitosa* and the forb *Rumex acetosa* were chosen. From Svalbard, only a sedge, *Luzula confusa*, had sufficient germination, so that Svalbard units also contained only one species. From Sierra Nevada and the Alps, I was unable to germinate enough plant individuals of any species to include these plant sites in the experiment.

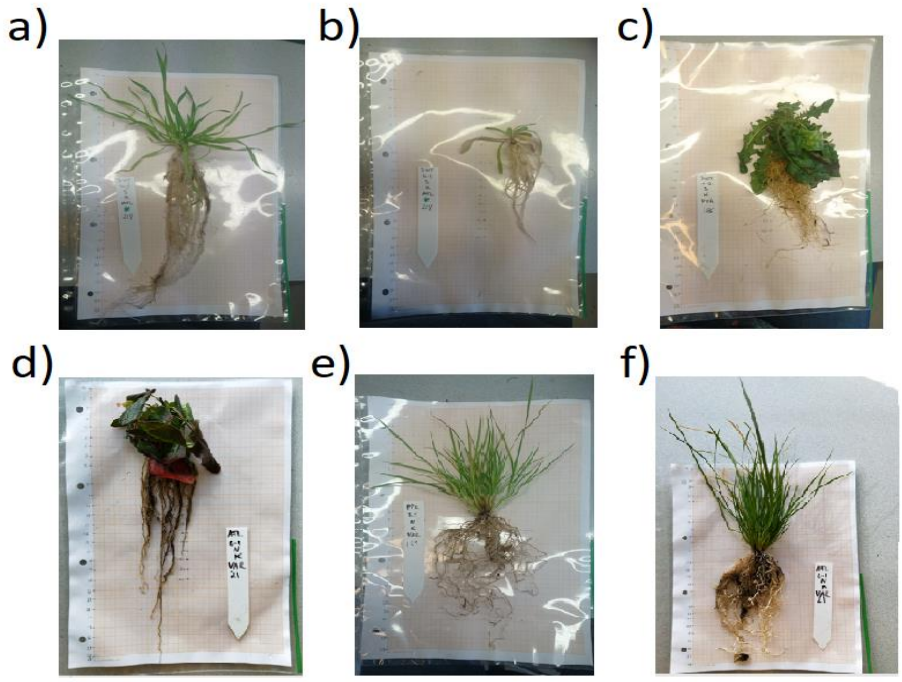

Figure 2: Examples of harvested plant species used in the experiment from a)-b) Atlas Mountains, c) Pyrinees. d)-e) Varanger Peninsula, f) Svalbard.

Table 3: Plant species from the different sites used in the experiment.

Origin	**Functional group**	**Species**
Atlas Mountains	Graminoid	*Anthoxanthum odoratum*
Atlas Mountains	Forb	*Leontodon hispidus*
Pyrenees	Forb	*Leontodon pyrenaicus*
Varanger Peninsula	Graminoid	*Deschampsia cespitosa*
Varanger Peninsula	Forb	*Rumex acetosa*
Svalbard	Graminoid	*Luzula confusa*

2.3.4 Study planting design

Plants were planted in soil from all six sampling sites and watered according to need. From this study design, the variable “soil origin” defined “home” soil as soil sampled in the same site as the seeds, and “foreign” soil as soil sampled from any of the other five sites (see Figure 3).

The experiment was replicated in two simulated climates, in order to control for effects produced by varying climate between sites (see Figure 3). This was done using growth chambers with adjustable temperature and light. In accordance with climate data for the growing season, I simulated the Pyrenees (South) and Varanger (North) climates regarding photoperiod and temperature. South was given 15 hours of sunlight/day and North was given 24 hours sunlight/day. South was given 15 degrees Celsius during light hours and 9 degrees Celsius during dark hours, whereas North was given 12 degrees Celsius for 12 hours and 9 degrees Celsius for 12 hours per day. The variable “climate regime” defined Atlas and Pyrenees plants to be growing in “home” climate if they were placed in the southern climate simulation, while Varanger and Svalbard plants were considered growing in “home” climate if placed in the northern climate simulation. Conversely, “foreign” climate for Atlas and Pyrenees plants was the northern climate simulation, while foreign climate for Varanger and Svalbard plants was the southern climate simulation.

		Climate			
Soil		Home		Foreign	
	Home	ATL	S	ATL	N
		ATL		ATL	
		PYR	S	PYR	N
		PYR		PYR	
		VAR	N	VAR	S
		VAR		VAR	
		SAF	N	SAF	S
		SAF		SAF	
	Foreign	ATL	S	ATL	N
		SNV, PYR, SWT, VAR, SAF		SNV, PYR, SWT, VAR, SAF	
		PYR	S	PYR	N
		ATL, SNV, SWT, VAR, SAF		ATL, SNW, SWT, VAR, SAF	
		VAR	N	VAR	S
		ATL, SNV, PYR, SWT, SAF		ATL, SNV, PYR, SWT, SAF	
		SAF	N	SAF	S
		ATL, SNV, PYR, SWT, VAR		ATL, SNV, PYR, SWT, VAR	

Soil site	Plant origin	Climate Simulation
ATL – Atlas Mountains	ATL – Atlas Mountains	S – South
SNV – Sierra Nevada	PYR – Pyrenees	N – North
PYR – Pyrenees	VAR – Varanger Peninsula	
SWT – Alps	SAF – Svalbard	
VAR – Varanger Peninsula		

Figure 3: Study planting design using soil of six origins and seedlings of four sites. Seedlings are planted in respectively all soil types, where “home” is soil originating in the same site as the seedlings, and “foreign” is soil originating from any of the other five sites. For each seedling-soil combination, there are two replicates, where one is placed in the “Southern” climate simulation, and one is placed in the “Northern” climate simulation. The Southern climate simulation has 15 hours of light and 9 hours of darkness per 24 hours, and temperatures is 15ºC in light periods, and 9ºC in dark period. The Northern climate simulation has 24 hours of light per 24 hours, where temperature is 12ºC for 12 hours, and 9ºC for 12 hours, per 24 hours. For Atlas and Pyrenees plants, home climate is set as the Southern climate simulation. For Varanger and Svalbard plants, home climate is set as the Northern climate simulation.

2.4 Soil nutrient data

Soil samples from each replicate were analysed for total C and N content was recorded using a LECO Truspec C/N analyser (St. Joseph, MI, USA) and organic C after removal of inorganic carbon with HCl 2N (Schumacher, 2002). Anion phosphate (PO_4^{3-}) and sulphate (SO_4^{2-}) concentrations in water extract (1:5 soil:water) were analysed by HPLC (Metrohm, HE, Switzerland). Soil nitrate (NO_3^-) and ammonia (NH_4^+) were extracted with potassium chloride (KCl 2M) and their contents were determined with an automatic continuous segmented flow analyser (model SAN++, Skalar Analytical B.V., Breda, The Netherlands). Other elements were determined after acid digestion with an inductively coupled plasma (ICP) emission spectrometer (ICAP 6500 DUO Thermo; Thermo Scientific, Wilmington, DE, USA). All soil nutrient data along with descriptions of methods for soil analyses were provided by a project partner at the CEBAS-CSIC ionomics lab (Murcia, Spain).

2.5 Harvest

After 11 weeks of growth, the plants were harvested. Prior to harvesting the plants, leaf number for forbs and shoot number for graminoids were recorded. These two parameters were joined together as one parameter, called leaf/shoot, describing leaf number of forbs and shoot number for graminoids. Then the plants were gently removed from their pot, and soil was rinsed away from the roots. Roots were disentangled and for pots containing more than one plant, these were separated. Canopy height was measured as the average of the three longest leaves from the crown to their tip (± 1 mm). Belowground traits measured were length of the three longest roots when stretched out and averaged in the same way as canopy height. This trait was called root length. Roots were then compressed by hand to measure root diameter on millimetre accuracy level. This was done at four different lengths: 0.5 cm away from crown, first quarter of total root length, half of total root length, and tip of longest root. These measurements were used to calculate a proxy to root volume as shown in Figure 4.

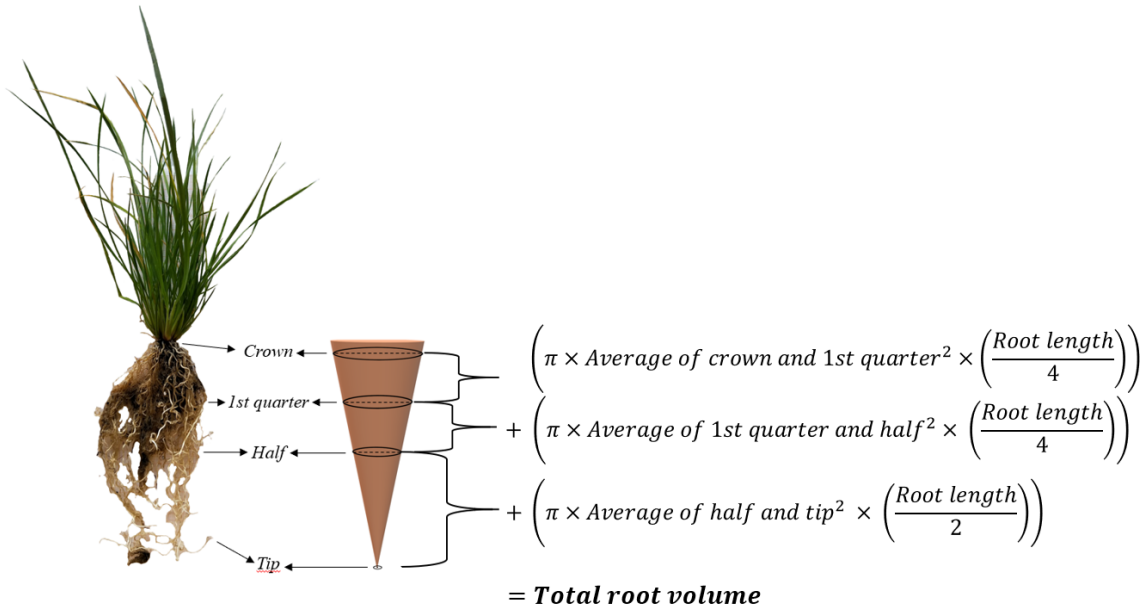

Figure 4: Proximate root volume calculations for belowground weight. The diameter of the crown and the diameter of the root at the 1st quarter down its full length was averaged and used for the calculation of volume of the upper ¼ of the total root length. Average of 1st quarter and half is the mean of the diameters measured on the first ¼ of total root length and in the middle of total root length. Average of half and tip is the mean of the diameters measured in the middle of total root length and at the tip of the longest root. Root length is the total length from crown to the tip of the longest root when the roots are physically stretched out.

After these measurements were taken, plants were cut at the crown and aboveground and belowground plant material was placed in separate paper bags that were dried at 60°C for 48 hours. Then, the aboveground and belowground plant material was separately weighed in order to get aboveground and belowground dry mass. This measurement was recorded in grams with three additional decimals. Total dry mass for each plant was calculated by summing aboveground and belowground dry mass for each plant.

2.6 Data analyses

2.6.1 Preparation of predictors for linear modelling

Statistical data analyses were conducted using software R. 3.6.3 (R Core Team, 2020). My approach to detecting effects from soil origin and climate regime was using linear mixed modelling with these factors as main predictors for traits related to plant performance. The

research question relates to general effects on plants. Therefore, measurements from pots containing two plants (Atlas and Varanger), were summed or averaged between plants of the same pot, so that each plant-soil combination would have one observation. Mass measurements, leaf/shoot numbers and approximate root volume were summed up between the graminoid and forb of the respective soil-plant combinations. Due to large differences in plant phenology between forbs and graminoids, canopy height and root length were first scaled using the scale function, and then averaged. The scale function calculates the mean and standard deviation of all the observations of the chosen parameter, and gives each parameter a score, defined by subtracting the mean and dividing by the standard deviation. In other words, it scores the observations by how far away from the mean they are (if they are average, relatively positive or relatively negative, and how positive or negative they are).

In order to produce both concise results that would be calculable in Si-units and accounting for various plant traits, I ran parallel linear mixed models with two different response variables; Total plant mass, and a calculated plant performance index, that included three aboveground and three belowground traits. Aboveground and belowground traits were studied together since they correlated well and there was no detected asymmetry between them. Traits used were; canopy height, shoot/leaf number, aboveground and belowground mass, root length and approximate root volume. In order to create the plant performance index, shoot/leaf number, aboveground and belowground weight and approximated root volume were scaled similarly as canopy height and root length. These scaled values were then summed up for each individual observation (plant-soil combination). For observations where 3 or more of the variables used in the calculation were missing, the plant performance index was recorded as Not Available (NA). In total, 29 observations were lost from the dataset, out of a total of 362 measurements. Out of these 29 NA's, 22 were in home soil, and 7 were in foreign soil. Climate simulation was North for 13 and South for 16 of the NA samples. Of NA samples, Climate regime was home for 19 samples, while 10 were in away climate.

Since both total plant mass and the plant performance index were strongly right skewed, I transformed them to a normal distribution in order to run linear models. This was done for the plant performance index by first adding 2.5 to all observations in order to make

all observations positive, and then normal distribution transforming them using cube root transformation. Total plant mass was directly transformed using cube root transformation.

2.6.2 Selection on fixed predictors for linear modelling

The main predictors, soil origin and climate regime were meant to answer the research question through displaying how plants performed in home versus foreign soil and climate. In order to control for possible confounding from other varying factors in the experiment, I added some additional predictors to the models. Since there were two plant species from Atlas and Varanger, and only one plant species from the Pyrenees and Svalbard in the experiment, possible variation due to this factor was tested by including "Number of plants in pot" as fixed predictor.

Since soils varied in nutrient contents, I included Soil nutrient data in the linear models. In order to select which soil parameters to use, I conducted a non-metric multidimensional scaling (NMDS) using the vegan package. I also used tools from the stats package. The output was used to check which soil parameters varied the most, and whether these were correlated. Three largely varying, and non-correlating parameters were chosen (soil nitrogen, soil calcium and soil potassium), see Figure 6.

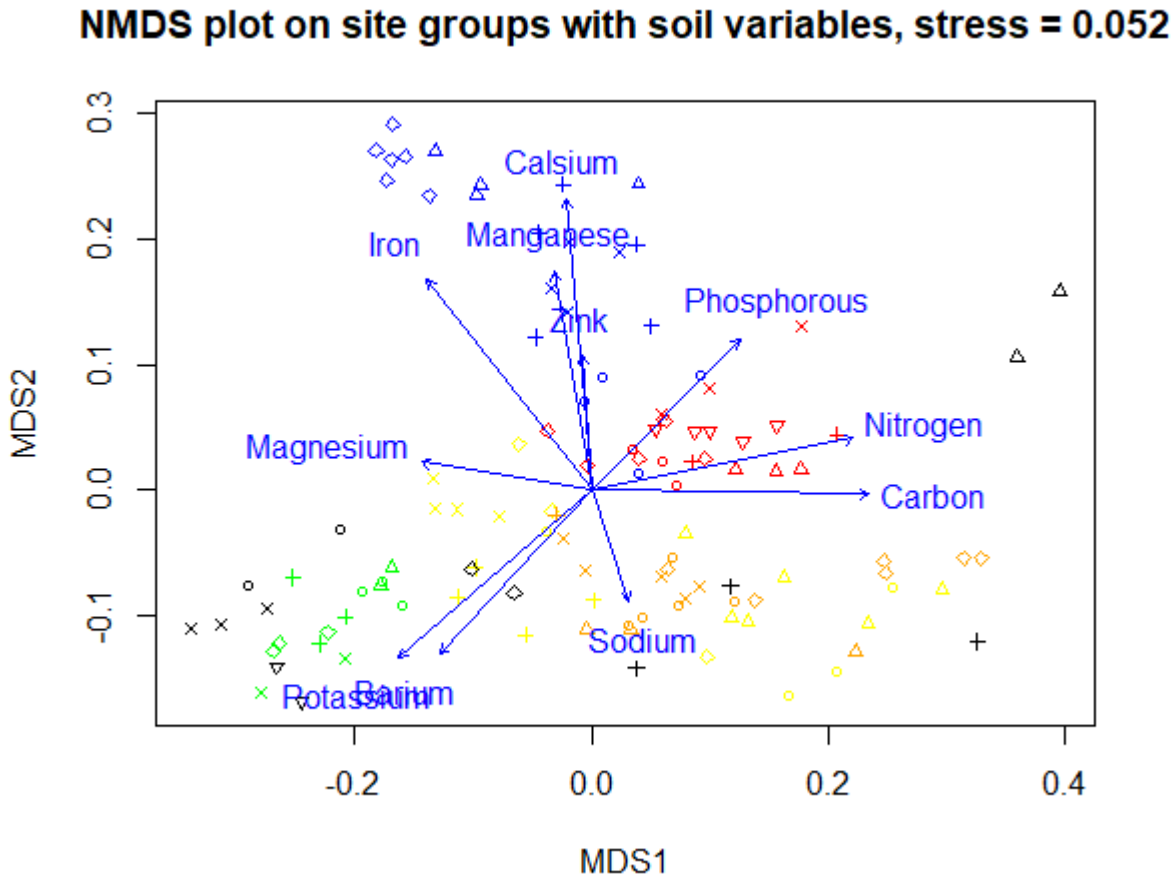

Figure 6: NMDS ordination plot for soil parameters. Length of arrows indicate how much the parameters vary between soil samples, and direction indicates correlations between parameters, meaning that parameters with similar directions are correlating. Soil samples are marked with varying colors and symbols (for more information regarding soil sample variation, see Appendix, figure VI)

2.6.3 Linear mixed modelling

Linear mixed models were built using the lmer function in the lme4 package with the package LmerTest running in the background. I used the function stepAIC in the cAIC4 package to determine if predictors should be put as additive or interacting in my models. In accordance with the output from this function, all predictors in my models were put as additive effects. The choice on which predictors to include in my models was based on relevance to the research questions. The hierarchical soil sampling design was included as random factors, since variation caused by soil site, subsite or replicate was out of interest to the research

questions. In general models including data from all plant origins, plant origin was also included as random factor, since these models were meant to detect general effects. I ran parallel models, using either cube root transformed plant performance index or cube root transformed total plant mass as response variables (Appendix code I and II). In addition to the main models including all observations, I also ran sub-models for each individual plant origin (Appendix, code III-X). This was done in order to detect possible asynchronies in effect size or direction between different plant origins. Estimates from the model output of models using total plant mass as response variable were back transformed by exponentiation with 3 as exponent, and then converted to milligrams by multiplying with 1000.

3 Results

3.1 Plant growth in different soil and simulated climates

There were large variations on plant growth in different soils (see Figures 7 and Appendix, Figure I and II). Notably, there were similar trends for total plant mass and plant performance index. Plants displayed a relatively large growth in Atlas soils, followed by Pyrenees soils and Alps soils. Plant growth in Sierra Nevada soils was intermediate, whereas growth was smaller in Varanger soils and minimal in Svalbard soils. Between plant origins, there was also large variation in growth (see Figure 8 and Appendix, Figure I and II). Atlas and Varanger plants scored highest in both plant mass and plant performance index, whereas Pyrenees plants had lower plant performance index and total plant mass. Svalbard plants had the smallest growth of all plants included in the experiment.

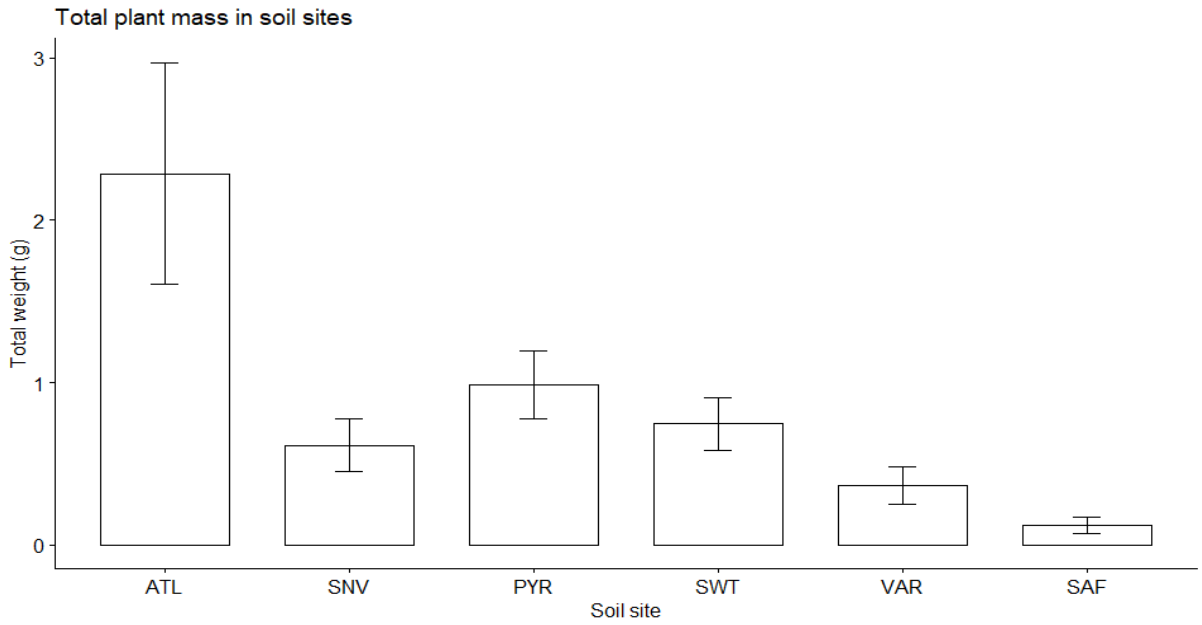

Figure 7: Total plant mass (grams) in soils of different soil site origins (not cube root transformed). Soil origin names are abbreviated so that ATL, SNV, PYR, SWT, VAR and SAF respectively represent Atlas, Sierra Nevada, Pyrenees, Alps, Varanger Peninsula and Svalbard. The whiskers show the confidence intervals for each category.

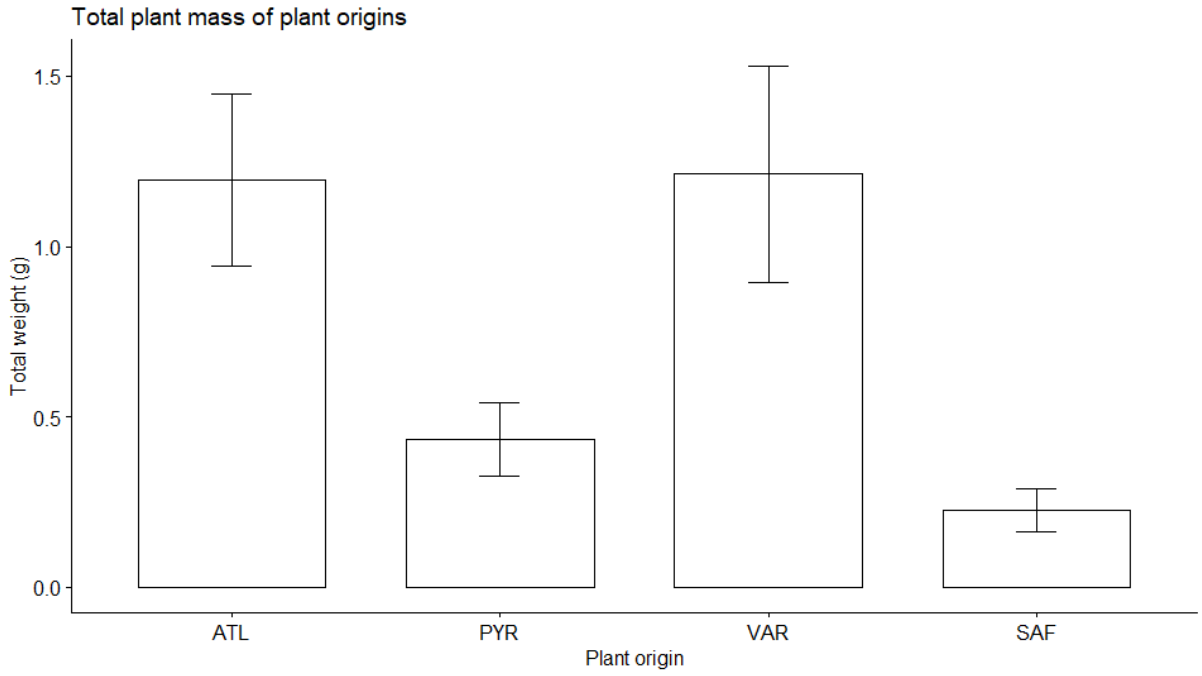

Figure 8: Total plant mass (grams) for different plant origins (not cube root transformed). Plant origin names are abbreviated so that ATL, PYR, VAR and SAF respectively represent Atlas, Pyrenees, Varanger Peninsula and Svalbard. The whiskers show the confidence intervals for each category. Notably, Atlas and Varanger plant origins contain two plant species, whereas Pyrenees and Svalbard plant origins contain one plant species.

There were generally slight differences in plant growth between the simulated climates (see Figure 9 and Appendix, Figure III). Total plant mass was slightly larger for Atlas plants in the "north" simulated climate than in the "south" simulated climate. Pyrenees plants produced more total plant mass in the south simulated climate than in the north simulated climate. Varanger and Svalbard plants had higher total plant mass in the north simulated climate than in the south simulated climate. Plant performance index (prior to cube root transformation) for Atlas and Pyrenees plants was weakly higher in the south simulated climate, while Varanger plants had weakly higher plant performance index in the north simulated climate. Svalbard plants had a substantially higher plant performance index in the north climate simulation than in the south climate simulation.

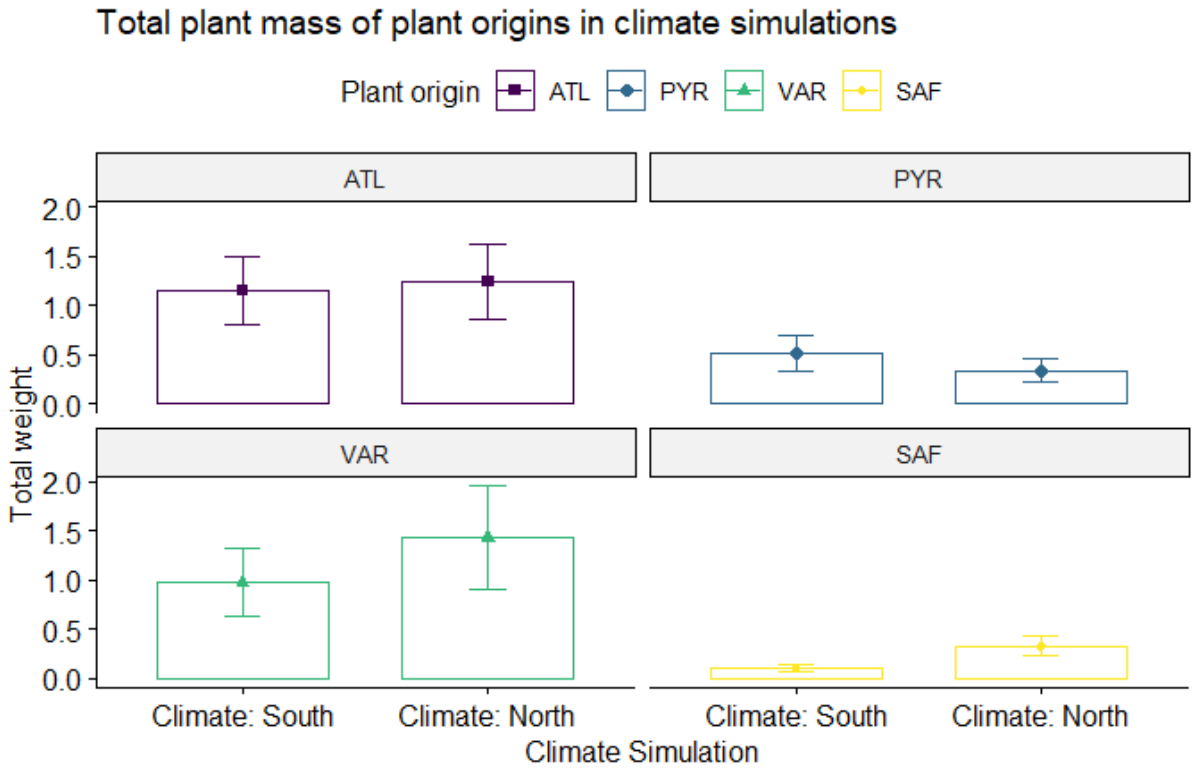

Figure 9: Total plant mass (not cube root transformed) of plant origins growing in different climate simulations (measured in grams). Plant origin names are abbreviated so that ATL, PYR, VAR and SAF respectively represent Atlas, Pyrenees, Varanger Peninsula and Svalbard. Total plant mass is facetted by plant origin, so that each of the four sub-plots display total plant mass for each individual plant origin separately. The whiskers show the confidence intervals for each category, and the symbol (square for Atlas, Diamond for Pyrenees, Triangle for Varanger and circle for Svalbard) marks the average value.

3.2 Plant growth as a response of soil and climate origin, number of plants in pot and soil nutrient content

3.2.1 Net effects for all plants

3.2.1.1 Growth in home versus foreign soil

The main models including all plant origins revealed that plants in sum grew better in home soils than in foreign soils (see Figure 10, Table 4 and Appendix, Table I for details). Both plant performance index and total plant mass displayed a significant increase in home soil over foreign soil.

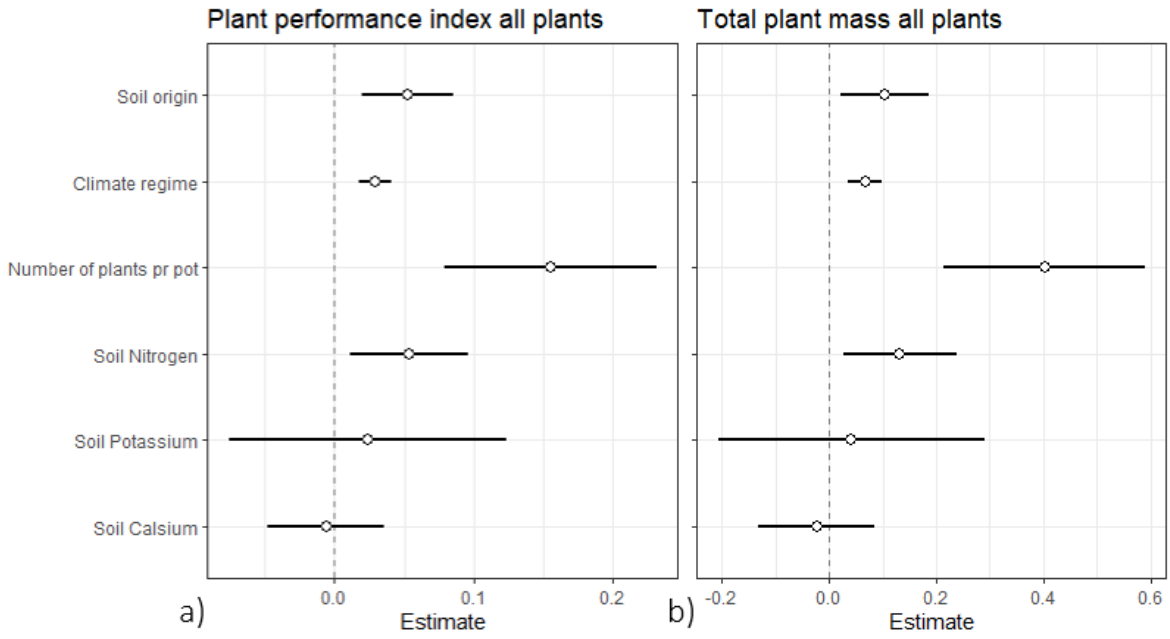

Figure 10: Estimate plots for main model outputs with cube root transformed plant performance index a) and cube root transformed total plant mass b) as response variables. The intercept of the models (what variables within each predictor is being compared with) is whatever observation for each predictor that comes first in the alphabet, or the smallest number for numerical variables. Therefore, the Soil origin and Climate regime estimates being positive means that Home benefits plant growth over Foreign (F comes before H in the alphabet). Consequently, positive estimates for Number of plants in pot mean that pots containing two plants score higher than pots containing one plant. The same goes for the soil nutrients, nitrogen, potassium and calcium. Length of the lines for each estimate show the confidence intervals for each estimate. Notably, ranges of the x-axes are differently scaled between a) and b).

Table 4: Back transformed linear model estimates for models predicting total plant mass for respectively the main model and the sub-models studying plant origins separately (Atlas, Pyrenees, Varanger and Svalbard). Marginally significant estimates (p≤0.10) are marked with one star (*), significant estimates (p≤0.05) are marked with two stars (**). Estimates for fixed predictors display difference between intercept and one unit "increase" being either the next categorical variable (alphabetically ordered) or one numerical unit, for numerical variables (for example, the main model estimates, a 1.125 mg higher total plant mass for plants grown in home relative to foreign soil). . Estimates are displayed in milligrams (mg). Notably, sub-models could not predict effect of number of plants in pot since all pots would have the same amount of plants.

Fixed Predictors	Main model (mg)	Atlas (mg)	Pyrenees (mg)	Varanger (mg)	Svalbard (mg)
Intercept	0.004	812.166**	30.080	695.506**	62.571**
Soil origin (Home versus Foreign)	1.125 **	65.451	60.698*	-20.346	-27.818**
Climate regime (Home versus foreign)	0.301**	0.001	0.033	0.006	5.832**
Number of plants per pot (1 versus 2)	64.965**	-	-	-	-
Soil Nitrogen (g/100g)	2.230**	3.443	46.268**	1.443	0.614*
Soil Potassium (g/100g)	0.069	-4.173	0.003	5.735	0.001
Soil Calsium (g/100g)	-0.014	-0.074	-0.006	0.778	-0.002

3.2.1.2 Growth in home versus foreign climate

The main models including all plant origins revealed a statistically significant benefit of growing in home climate over foreign climate, although weaker than that detected for soil origin effects (see Figure 10, Table 4 and Appendix Table I for details).

3.2.1.3 Effects of other variables

Number of plants per pot

Both the model with plant performance index and total plant mass as response variables predicted a strong positive effect from increasing number of plants per pot (see Figure 9, Table 4 and Appendix, Table I for details). In other words, it was be predicted that plant performance and total plant mass increased substantially for Atlas and Varanger plants compared to Pyrenees and Svalbard plants.

Soil nutrients

The effect of Soil nitrogen on the plant performance index and total plant mass was weak and positive, similar in effect size to effect of soil origin (see Figure 10, Table 4 and Appendix, Table I for details). Neither soil potassium nor soil calcium displayed any statistically significant effects as a response to plant performance index or total plant mass (see Figure 9, Table 4 and Appendix, Table I for details).

3.2.2 Individual plant origin effects

3.2.2.1 Growth in home versus foreign soil

The sub-models studying separate plant origins revealed contrasting effects of growing in home versus foreign soil (see Figure 11, Table 4 and Appendix, Tables II and III for details). Effects were not significant from neither plant performance index not total plant mass on Atlas plants, although estimates trended towards a positive response in home soil. Pyrenees plants had a marginally significant, but relatively strong increase in plant performance index and total weight in home soil over foreign soil. There was very large variation within estimates for Varanger plants for either response variables, causing no statistically significant effect from soil origin. Estimates for Svalbard plants displayed a slightly decreased growth in home soil relative to foreign soil.

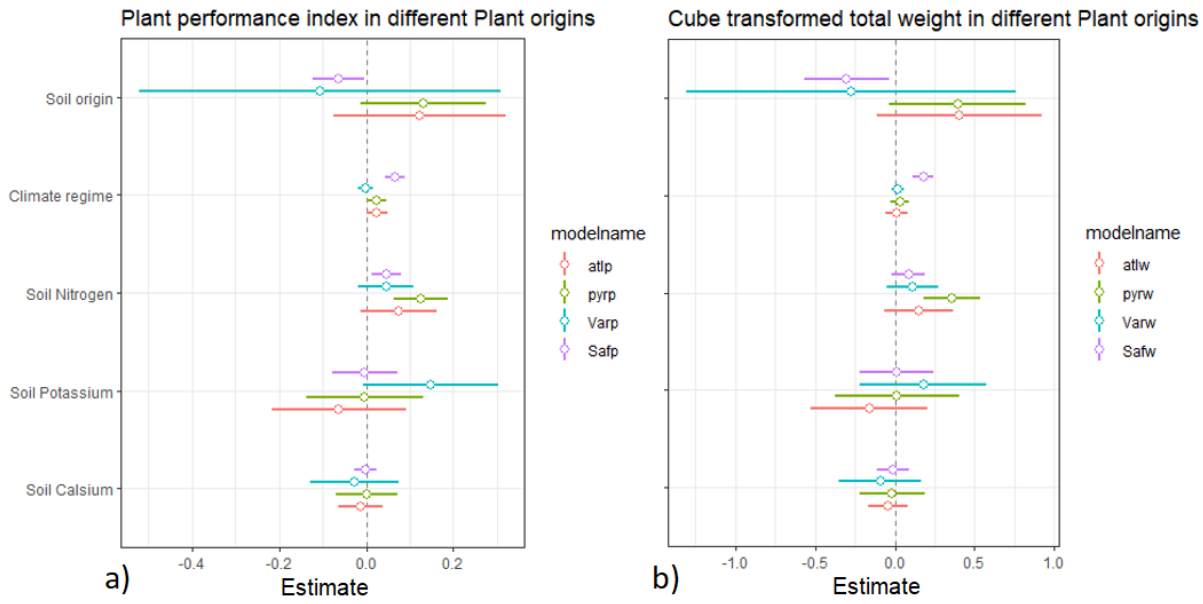

Figure 11: Estimate plots for separate plant origin model outputs with plant performance index a) and total plant mass b) as response variables. Different colors represent different models, so that red means Atlas, green means the Pyrenees, blue means Varanger and purple means Svalbard. The intercept of the models (what variables within each predictor is being compared with) is whatever observation for each predictor that comes first in the alphabet, or the smallest number for numerical variables. Therefore, the Soil origin and Climate regime estimates being positive means that Home benefits plant growth over Foreign (F comes before H in the alphabet). Consequently, positive estimates for the soil nutrient contents, nitrogen, potassium and calcium, mean that plants grown in soils of higher nutrient inputs score higher. Length of the lines for each estimate show the confidence intervals for each estimate. Notably, the ranges of the x-axes are differently scaled between a) and b).

3.2.2.2 Growth in home versus foreign climate

Simulated home climate had a positive effect on most plant origins (see Figure 11, Table 4 and Appendix, Tables II and III for details). Atlas plants displayed the largest increase in plant performance index in home climate over foreign climate. Moreover, all other plant origins had significant increases in plant performance index in home climates, except for Varanger plants which showed a neutral response. Svalbard was the only plant origin that had significantly higher total plant mass in home climate than in foreign climate.

3.2.2.3 Effects of confounding variables

Soil nutrients

Soil nitrogen content had a significant positive effect on growth for most plant origins (see Figure 11, Table 4 and Appendix, Tables II and III for details). For Atlas plants, this effect was marginally significant on plant performance index, but not significant on total plant mass. Pyrenees plants experienced a stronger positive effect from increased soil nitrogen content, both on plant performance index and total plant mass. The sub-models for Varanger plants did however not give statistically significant estimates for soil nitrogen. Svalbard plants benefitted from increased soil nitrogen content, although estimates were weaker than those of other plant origins.

Soil potassium content had no significant effect on neither of the plant origins except for Varanger plants. Varanger plants had a marginally significant estimate for plant performance index, but no significant estimates for plant mass (see Figure 11, Table 4 and Appendix, Tables II and III). For soil calcium, none of the plant origins displayed significant or marginally significant responses (see Figure 11, Table 4 and Appendix, Tables II and III).

4 Discussion

4.1 Main findings

Individual plant origins (Atlas, Pyrenees, Varanger and Svalbard) to some extent showed varying growth trends in home and foreign soil. Pyrenees plant growth trends suggest a weak benefit of home soil over foreign soil, whereas Svalbard plants grew slightly less in home soils than in foreign soils. My analysis did not detect significantly different growth trends in home and foreign soil for Atlas and Varanger plants. However, Atlas plants had a tendency towards larger growth in home soil than foreign soil. These findings give some support to my 3rd hypothesis, that effect of soil origin on growth is context-specific in the sense that home soil is relatively beneficial to the growth of some plants, while other plants grow better in foreign soil. However, effects for plants benefitting from home soil were much stronger than

those of plants benefitting from foreign soil. Therefore, the net effect across plants is positive. Also, the enlarged sample size of a complete analysis gave more significant results than individual plant origin analyses. Therefore, overall results support my 1st hypothesis, stating that plant growth is generally increased in home soil compared to foreign soil.

Effect from climate was weaker than effects from soil, but plants showed more similar growth trends in respect to climatic parameters. Plants generally benefitted from growing in light and temperature conditions resembling their home climate. This effect was detected for all individual plants but Varanger plants. No substantial interaction between climate and soil origin effects on plant growth was detected. In sum, my 4th hypothesis is strengthened, stating that plant growth is improved in home climate, regardless of soil origin.

4.2 Plant growth in home versus foreign soil and climate

4.2.1 Plant growth in home versus foreign soil

Effect of home versus foreign soil on plant growth trended towards a home-site advantage, but varied based on plant origin. While Pyrenees plants grew better in home soils, Svalbard plants grew better in foreign soil. For Svalbard plants, the observed growth trend may be a product of soil context specificity rather than generalizable Plant-soil feedback (PSF). Svalbard soils had a clay-like, compact structure that absorbed less water and dried out faster than the other soil types in the experiment. In addition, the Svalbard soil contains relatively low amounts of important soil nutrients such as nitrogen and phosphorous (see Appendix, Figure IV and V). Other plants also displayed less growth in Svalbard soil (see Figure 7), indicating that poor soil quality might have overshadowed PSF, leading to Svalbard plants performing better in foreign soil types.

Despite some foreign soil types having higher nutrient contents, Pyrenees plants performed better in home soil. This indicates that Pyrenees plant growth patterns are likely caused by home-site advantage. Other studies have documented *Leontodon* spp. to have positive (in ’t Zandt *et al.* 2019) or negative (Semchenko *et al.* 2018) PSF in home soil versus foreign soil. This indicates that net PSF can vary between cases. In my case, home-site advantage proved more beneficial for growth of Pyrenees plants than the higher nutrient contents in for instance Atlas soil (see Appendix, Figure VI and V), which importantly

promoted the larger growth for all other plant origins in the experiment (see Figure 7 and Appendix, Figures I and II). Such a phenomenon could be caused by a strong home-field advantage from decomposers (Palozzi & Lindo 2018) or more mutualist associations in native soil, aiding nutrient uptake (Bever *et al.* 2010), pathogen protection and abiotic stress tolerance (Smith 2008; Sikes 2010). This outcome is in line with the findings of Palozzi *et al.*, (2018), where home-site advantage benefitted plants despite foreign soil being more nutrient rich.

In the case of Varanger and to some extent Atlas plants, no conclusion can be made. Responses for Varanger plants varied greatly, some individuals grew better in home soil while others grew better in foreign soil. It is therefore likely that growth of the plants sampled from Varanger are dependent on other factors than home versus foreign soil. It is also possible that large variations within soil parameters in the Varanger soil has led to an unprecise response for individuals grown in home soil (see Appendix, Figure VI), although this effect being the sole reason is unlikely judging from the small variation within Varanger plants grown in home soil (see Appendix, Figure I and II). It is also possible that the growth of plants from Varanger and Atlas could be affected by differential responses of graminoids and forbs, as detected by other studies (Cortois 2016; Bardgett 2017; Bennett *et al.* 2017). Effects between functional groups were not in the scope of this experiment and further research is required to detect if they could cause patterns observed here. In the case for Atlas plants, sampled soil limitation lead to a smaller sample size for Atlas soil, so that the sample size for Atlas plants growing in home soil is smaller than that of all the other plants (10 Atlas plants grew in home soil, contrasting respectively 16, 17 and 16 for Pyrenees, Varanger and Svalbard plants). It is therefore likely that a larger sample size would have given more precise results for Atlas plants.

Increased plant growth in home over foreign soils is in accordance with previous findings supporting Home-site advantage (Pregitzer *et al.* 2010; Palozzi & Lindo 2018). In accordance with the framework of Van Der Putten *et al.*, (2016), either soil mutualists, soil decomposers, or both together may be more beneficial to native plants than foreign plants. In accordance with home-field advantage theory (Palozzi & Lindo 2018), the presence of conspecific litter and decomposers promoted by conspecific plants in the field likely

facilitates high performance in home soils. Furthermore, when plant-mutualist associations are different for native versus foreign plants, then the effect of soil mutualists in home versus foreign soil may be substantial (Bever *et al.* 2010; Teste *et al.* 2017; Dukes *et al.* 2019). Indeed, plant-mycorrhizal associations turn out to be more specific than previously documented (McGonigle 1990; Fitter 2005). Soil mutualist communities could therefore promote native plants over foreign plants whenever foreign plants and native plants associate with different mutualist species (Anacker *et al.* 2014). Nutrient acquisition strategies vary across the plant species included in this project. While most of the plants have arbuscular mycorrhizal associations (Crush 1973; Schulze 2005; Bassin 2017; Kariman *et al.* 2018), the forb from Varanger as well as the graminoid from Svalbard plants are non-mycorrhizal (Smith 1996; Muthukumar 2004). Whether these variations have affected PSF differences in foreign and home soil is beyond the scope of this study, but possibly inspires for further research.

Enemy-release is not indicated to have a generalizable impact on plant growth in my case, since plants in sum grew less in foreign soil. This finding refutes predominant conclusions within literature which state that PSF is predominantly negative, foremost driven by species-specific soil-borne pathogens and that being put in a novel habitat enhances growth due to the absence of these (Callaway *et al.* 2011; Van Der Putten *et al.* 2016; Pugnaire *et al.* 2019). On the contrary, results from this study indicate that the growth of alpine grassland plants is more sensitive to positive PSF than negative PSF, and that these are enhanced in a plant's native habitats. In accordance with theory of Inderjit *et al.*, (2010), it is also possible that native and foreign plants are equally affected by negative PSF so that enemy-release becomes absent. My findings may differ from the results of other studies due to differences in methodology. While many PSF studies use soil inoculums to represent differing soil biota, this experiment involved a comparison of relatively intact foreign and native soils, in agreement with suggestions of Brinkman *et al.*, (2010). An experimental design which uses intact soils may generate more accurate results regarding relative effect of positive and negative PSF. In fact, there is an increased awareness on how methodological approaches to PSF research produce differing results regarding feedback direction (Brinkman *et al.* 2010; Rinella & Reinhart 2018; Forero *et al.* 2019; Teste 2019; Peacher 2020), and

strength (Kulmatiski & Kardol 2008). For example, my approach is documented to render weaker effects than soil inoculum studies (Kulmatiski & Kardol 2008). The results from my approach indicate that plants could be more controlled by positive PSF than previously described in literature.

4.2.2 Plant growth in home versus foreign climate

All plants performed best in climatic conditions resembling their native habitat, except Varanger plants. Varanger plant growth varied too greatly for conclusions to be formed on effect of differing simulated climates. Since Atlas and Pyrenees and Svalbard plants have different climates in their native habitats, a generally increased growth in "home" climate indicates differing climate optimums for the plants in the experiment. While plant growth is often enhanced by both longer photoperiod (Sinclair 2003; Adams 2005) and increased temperature (Wu 2011; Van Der Putten *et al.* 2016), natural selection may have evolutionarily tailored plants to perform best under typical conditions of their native climates. Woody plants that originate from areas without midnight sun have been shown in some cases to perform better under moderately prolonged photoperiod, but radically prolonging photoperiod risks decreased growth (Castro *et al.* 2003; Way 2015; Tedla 2019). If grassland species react to adjusted photoperiod in a similar manner, then the Atlas and Pyrenees in this study may not have benefitted from the continuous light in northern simulated climate. At the same time, the performance of these plants may have been limited by cooler temperatures, resulting in decreased growth in foreign climate. At the same time, growth of the Svalbard plants may have been limited by shorter light hours in southern climate, a setback which might have overpowered a concurrent benefit from increased temperature. Such environmental adaptations to photoperiod and temperature could explain why plants in this experiment grew best in light and temperature conditions resembling their native climates.

The increased performance in home climate indicates that large climate heterogeneity between native and foreign habitats can limit performance of foreign plants. If this limited performance leads to decreased reproduction, this could further lead to limitations in establishment of stable populations outside the native range. However, literature on this effect for grassland species is scarce, suggesting that it is understudied.

4.3 Controlling for confounding from other variables

4.3.1 Number of plants per pot

Number of plants per pot had a strong positive effect on plant performance. Total plant production was more than doubled in pots containing two plants relative to pots containing one plant (see Figure 8). This could indicate that plants facilitated each other during the experiment, or it could be caused by species variation in growth rate, as pots containing two plants and pots containing one plant had different species. While plant-plant interactions have been documented to interact with PSF (Lekberg *et al.* 2018), no such interactions were detected in this study. This might be due to time limitations, as my experiment only lasted 11 weeks. The strong positive effect of number of plants in pot inspires further research on possible facilitation between neighbouring plants.

4.3.2 Soil nutrients

Soil nutrient content is a known predictor for plant performance (Evert 2013). Plants grow best in nutrient rich soils (Evert 2013). Therefore, a positive relationship between soil nutrient content and plant performance was expected. Soil nitrogen weakly benefitted plant growth, but no effect was documented from other soil nutrients included in analyses. Furthermore, soil nitrogen did not interact with effects from home and foreign soil. This indicates that PSF occur despite of differing soil nitrogen content. In my experiment, home-site advantage was documented for some plants despite of their home soils being more nutrient poor than foreign soils, in agreement with the findings of Pregitzer *et al.*, (2010). Such conclusions must however take into account the importance of scale, since substantially increased nutrient contents are documented to "turn off" PSF (in 't Zandt *et al.* 2019). Therefore, my results would arguably represent field conditions unaffected by substantial fertilization.

5 Conclusion

Summarizing my results, native-foreign plant-soil dynamics play a significant role in plant performance, possibly negatively impacting the ability of plant populations to sustain expansion beyond their native range. The observed trends indicate that native-foreign PSF are context specific, depending on the characteristics of individual species, environmental conditions and soil parameters. However, plants experiencing home-site advantage showed stronger effects, overshadowing impacts for plants with different growth trends. Ultimately, plant origin can, in some instances, predict the ecological impact of native and foreign plants, with all other fitness-determining factors being even. This understanding can help to better inform plant community and ecosystem management, particularly for alpine and tundra grassland species. Furthermore, it may provide useful insight for combatting the encroachment of non-native invasive plants species, one of the main processes driving biodiversity loss. This study serves as another stepping stone towards clarifying the role of PSF experienced by introduced and native plants.

The findings in this study inspire research on the importance of methodology for experimental PSF outcomes. They also underline the importance of research focusing on the role of functional groups and positive plant-plant interactions in introduction events. My findings ultimately show a new perspective on plant-soil feedback, from viewing plant-soil feedback in home soils as negative and pathogen-controlled, to positive and driven my mutualistic plant-soil interactions.

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Appendix

6.1 Codes for R-studio

Code I: Linear model predicting plant performance index, including all plant origins:

lmer(normalised_plant_performance_index~Soil_origin + Climate_regime + Number_of_plants_in_pot + Soil_N + Soil_K + Soil_Ca + (1|Plant_origin) + (1|Soil_site /Subsite/Replicate/Sub_replicate), data=completenew, na.action = na.omit)

Code II: Linear model predicting total plant mass, including all plant origins:

lmer(normTotal_weight~Soil_origin + Climate_regime + Number_of_plants_in_pot + Soil_N + Soil_K + Soil_Ca + (1|Plant_origin) + (1|Soil_origin/Subsite/Replicate/Sub_replicate), data=completenew, na.action = na.omit)

Code III: Linear model predicting plant performance index for Atlas originating plants:

lmer(normalised_plant_performance_index~Soil_origin + Climate_regime + Soil_N + Soil_K + Soil_Ca + (1|Soil_site/Subsite/Replicate/Sub_replicate), data=completenew, na.action = na.omit, subset = Plant_origin==c("ATL"))

Code IV: Linear model predicting total plant mass for Atlas originating plants:

lmer(normTotal_weight~Soil_origin + Climate_regime + Soil_N + Soil_K + Soil_Ca + (1|Soil_site/Subsite/Replicate/Sub_replicate), data=completenew, na.action = na.omit, subset = Plant_origin==c("ATL"))

Code V: Linear model predicting plant performance index for Pyrenees originating plants:

lmer(normalised_plant_performance_index~Soil_origin + Climate_regime + Soil_N + Soil_K + Soil_Ca + (1|Soil_site/Subsite/Replicate/Sub_replicate), data=completenew, na.action = na.omit, subset = Plant_origin==c("PYR"))

Code VI: Linear model predicting total plant mass for Pyrenees originating plants:

lmer(normTotal_weight~Soil_origin + Climate_regime + Soil_N + Soil_K + Soil_Ca + (1|Soil_site/Subsite/Replicate/Sub_replicate), data=completenew, na.action = na.omit, subset = Plant_origin==c("PYR"))

Code VII: Linear model predicting plant performance index for Varanger originating plants:

lmer(normalised_plant_performance_index~Soil_origin + Climate_regime + Soil_N + Soil_K + Soil_Ca + (1|Soil_site/Subsite/Replicate/Sub_replicate), data=completenew, na.action = na.omit, subset = Plant_origin==c("VAR"))

Code VIII: Linear model predicting total plant mass for Varanger originating plants:

lmer(normTotal_weight~Soil_origin + Climate_regime + Soil_N + Soil_K + Soil_Ca + (1|Soil_site/Subsite/Replicate/Sub_replicate), data=completenew, na.action = na.omit, subset = Plant_origin==c("VAR"))

Code IX: Linear model predicting plant performance index for Svalbard originating plants:

lmer(normalised_plant_performance_index~Soil_origin + Climate_regime + Soil_N + Soil_K + Soil_Ca + (1|Soil_site/Subsite/Replicate/Sub_replicate), data=completenew, na.action = na.omit, subset = Plant_origin==c("SAF"))

Code X: Linear model predicting total plant mass for Svalbard originating plants:

lmer(normTotal_weight~Soil_origin + Climate_regime + Soil_N + Soil_K + Soil_Ca + (1|Soil_site/Subsite/Replicate/Sub_replicate), data=completenew, na.action = na.omit, subset = Plant_origin==c("SAF"))

6.2 Figures

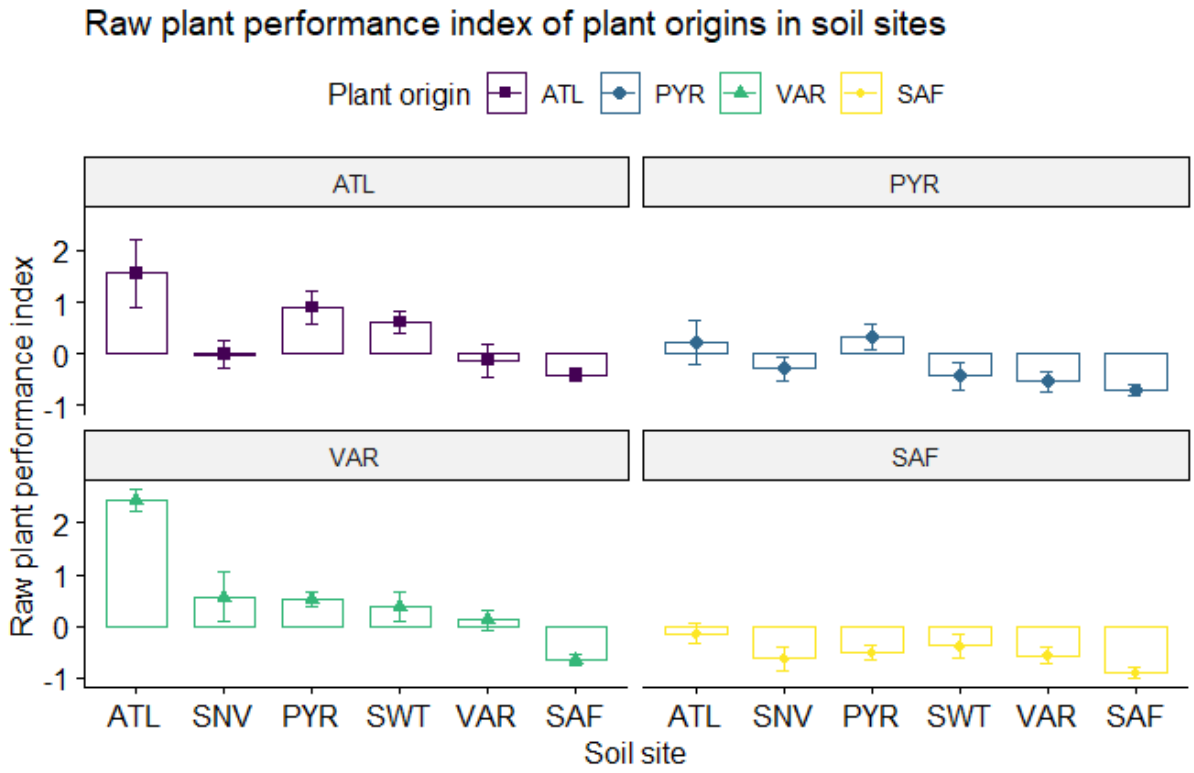

Figure I: Raw plant performance index (not cube root transformed) of plant origins in soils of different soil site origins. Plant origin and Soil origin names are abbreviated so that ATL, SNV, PYR, SWT, VAR and SAF respectively represent Atlas, Sierra Nevada, Pyrenees, Alps, Varanger Peninsula and Svalbard. Plant performance is facetted by plant origin, so that each of the four sub-plots display raw plant performance index for each individual plant origin separately. The whiskers show the confidence intervals for each category, and the symbol (square for Atlas, Diamond for Pyrenees, Triangle for Varanger and circle for Svalbard) marks the average value.

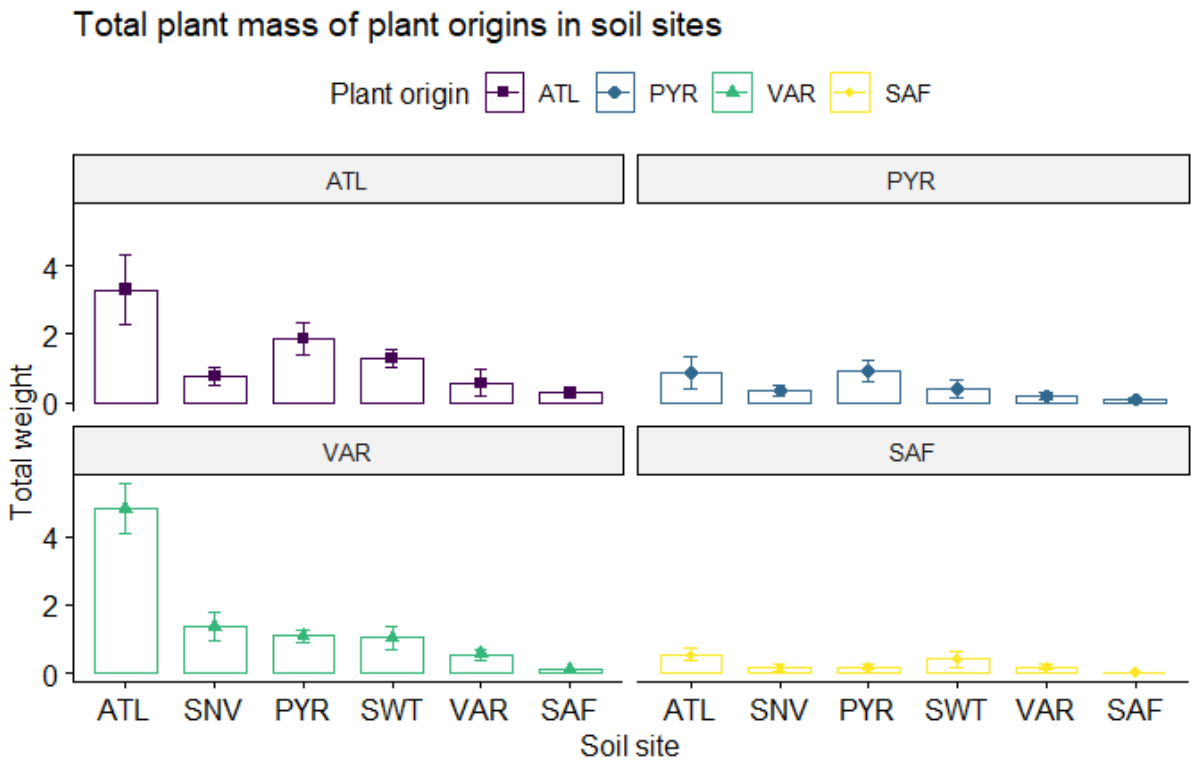

Figure II: Raw total plant mass (not cube root transformed) of plant origins in soils of different soil site origins (measured in grams). Plant origin and Soil origin names are abbreviated so that ATL, SNV, PYR, SWT, VAR and SAF respectively represent Atlas, Sierra Nevada, Pyrenees, Alps, Varanger Peninsula and Svalbard. Total plant mass is facetted by plant origin, so that each of the four sub-plots display total plant mass for each individual plant origin separately. The whiskers show the confidence intervals for each category, and the symbol (square for Atlas, Diamond for Pyrenees, Triangle for Varanger and circle for Svalbard) marks the average value.

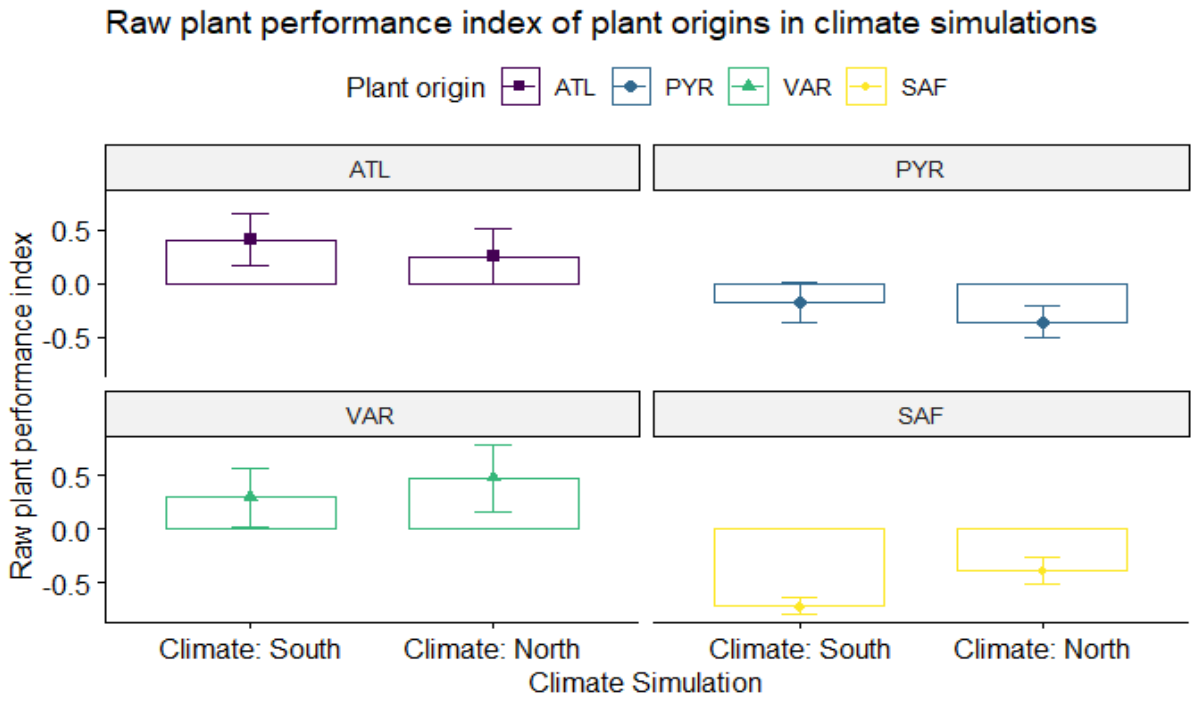

Figure III: Raw plant performance index (not cube root transformed) of plant origins growing in different climate simulations. Plant origin names are abbreviated so that ATL, PYR, VAR and SAF respectively represent Atlas, Pyrenees, Varanger Peninsula and Svalbard. The whiskers show the confidence intervals for each category, and the symbol (square for Atlas, Diamond for Pyrenees, Triangle for Varanger and circle for Svalbard) marks the average value.

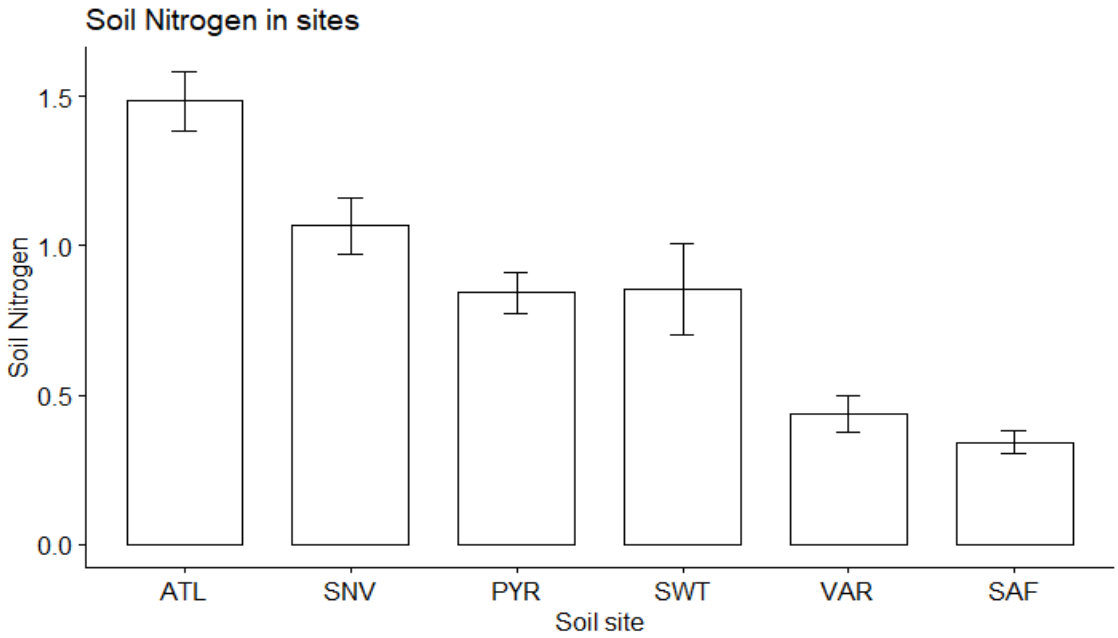

Figure IV: Soil nitrogen content (g/100g) in different soil sites included in the experiment. Soil origin names are abbreviated so that ATL, SNV, PYR, SWT, VAR and SAF respectively represent Atlas, Sierra Nevada, Pyrenees, Alps, Varanger Peninsula and Svalbard. This data was provided from my project partner at the CEBAS-CSIC ionomics lab (Murcia, Spain), and was extracted using the methods in chapter 2.4. The whiskers show the 95% confidence intervals for each category.

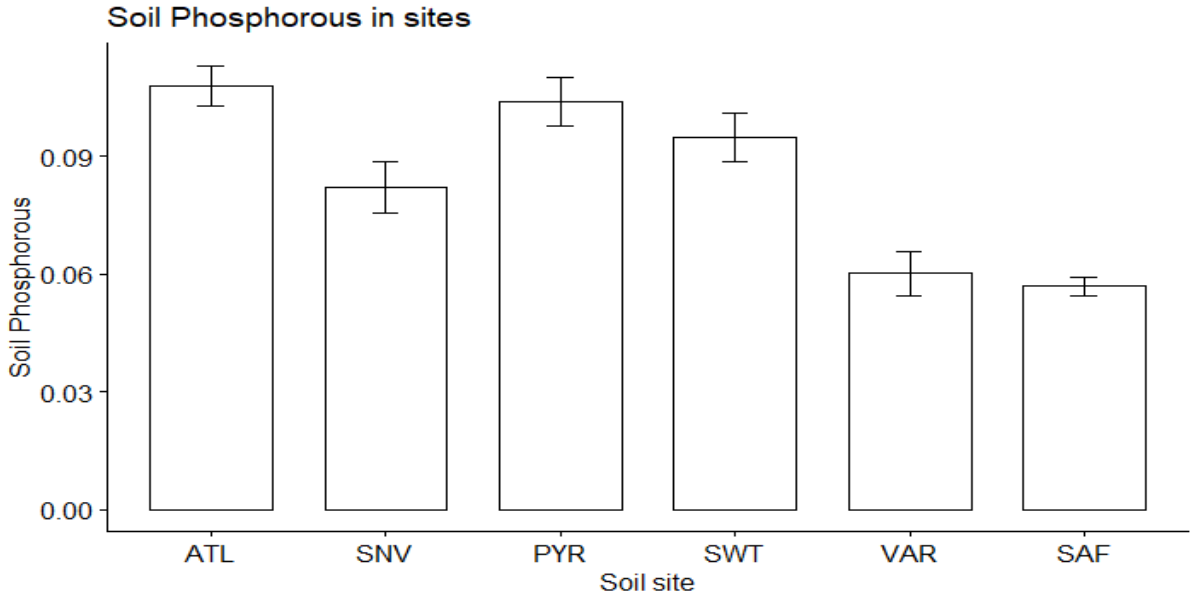

Figure V: Soil phosphorous content (g/100g) in different soil sites included in the experiment. Soil origin names are abbreviated so that ATL, SNV, PYR, SWT, VAR and SAF respectively represent Atlas, Sierra Nevada, Pyrenees, Alps, Varanger Peninsula and Svalbard. This data was provided from my project partner at the CEBAS-CSIC ionomics lab (Murcia, Spain), and was extracted using the methods in chapter 2.4. The whiskers show the 95% confidence intervals for each category.

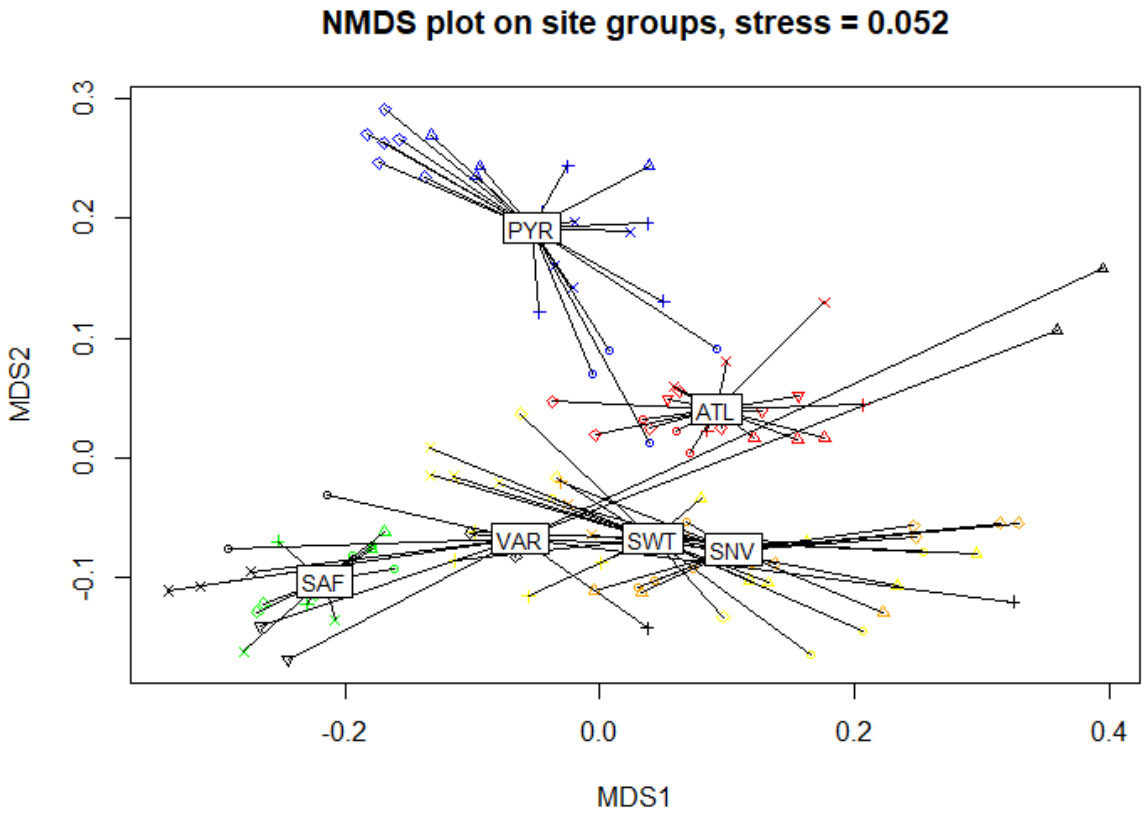

Figure VI: NMDS ordintation plot for variation between and within soil sampling sites regarding nutrient contents. Soil nutrient data was provided from my project partner at the CEBAS-CSIC ionomics lab (Murcia, Spain), and was extracted using the methods in chapter 2.4. The NMDS was conducted similarly to the NMDS in Figure 6, but with focus on site variations regarding nutrients, rather than nutrient variations regarding sites. Soil sampling site names are abbreviated so that ATL, SNV, PYR, SWT, VAR and SAF respectively represent Atlas, Sierra Nevada, Pyrenees, Alps, Varanger Peninsula and Svalbard. Observations within sites are marked with similar colors, while subsites are categorized by symbols (upwards versus downwards facing triangles, crosses, diamonds, circles and X-es).

6.3 Tables

Table I: Linear model output for main models predicting plant performance index (left) and total weight (right) using soil origin, climate origin, number of plants in pot, soil nitrogen, soil potassium and soil calcium as fixed predictors. As random factors are the hierarchical soil sampling design as well as plant origin. N stands for number of observations in the different random factor categories. P-values under 0.05 confidence interval significance level are marked in broad font.

Cube transformed Plant performance index and total weight main models

	Plant performance index			**Total weight**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	1.039	0.876 – 1.202	**<0.001**	0.016	-0.398 – 0.430	0.939
Soil_originSoil : Home	0.052	0.020 – 0.085	**0.002**	0.104	0.022 – 0.186	**0.013**
Climate_regimeClimate : Home	0.029	0.017 – 0.040	**<0.001**	0.067	0.035 – 0.099	**<0.001**
Number_of_plants_in_pot	0.155	0.080 – 0.231	**<0.001**	0.402	0.216 – 0.588	**<0.001**
Soil_N	0.054	0.012 – 0.095	**0.012**	0.132	0.027 – 0.237	**0.014**
Soil_K	0.024	-0.075 – 0.123	0.637	0.041	-0.206 – 0.289	0.743
Soil_Ca	-0.006	-0.048 – 0.036	0.775	-0.024	-0.131 – 0.084	0.667
Random Effects						
σ^2	0.00			0.02		
τ_{00}	0.00 $_{\text{Sub\_replicate:(Replicate:(Subsite:Soil\_site))}}$			0.02 $_{\text{Sub\_replicate:(Replicate:(Subsite:Soil\_site))}}$		
	0.00 $_{\text{Replicate:(Subsite:Soil\_site)}}$			0.00 $_{\text{Replicate:(Subsite:Soil\_site)}}$		
	0.00 $_{\text{Subsite:Soil\_site}}$			0.01 $_{\text{Subsite:Soil\_site}}$		
	0.01 $_{\text{Soil\_site}}$			0.05 $_{\text{Soil\_site}}$		
	0.00 $_{\text{Plant\_origin}}$			0.01 $_{\text{Plant\_origin}}$		
ICC	0.81			0.81		
N	4 $_{\text{Plant\_origin}}$			4 $_{\text{Plant\_origin}}$		
	3 $_{\text{Sub\_replicate}}$			3 $_{\text{Sub\_replicate}}$		
	6 $_{\text{Replicate}}$			6 $_{\text{Replicate}}$		
	6 $_{\text{Subsite}}$			6 $_{\text{Subsite}}$		
	6 $_{\text{Soil\_site}}$			6 $_{\text{Soil\_site}}$		
Observations	333			321		
Marginal R^2 / Conditional R^2	0.310 / 0.871			0.289 / 0.867		

Table II: Linear model output for main models predicting plant performance index separately for the plant origins (From left to right, Atlas, Pyrenees, Varanger and Svalbard). Fixed predictors are soil origin, climate origin, soil nitrogen, soil potassium and soil calcium. As random factors are the hierarchical soil sampling design. N stands for number of observations in the different random factor categories. P-values under 0.05 confidence interval significance level are marked in broad font.

Cube transformed Plant performance index in individual models for each plant origin

	Atlas			**Pyrenees**			**Varanger**			**Svalbard**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	1.377	1.216 – 1.537	**<0.001**	1.177	1.047 – 1.307	**<0.001**	1.343	1.124 – 1.562	**<0.001**	1.183	1.107 – 1.259	**<0.001**
Soil_originSoil : Home	0.123	-0.073 – 0.319	0.220	0.131	-0.012 – 0.275	0.073	-0.105	-0.518 – 0.308	0.618	-0.064	-0.123 – -0.005	**0.034**
Climate_regimeClimate : Home	0.024	0.000 – 0.048	**0.046**	0.023	0.000 – 0.045	**0.047**	-0.000	-0.017 – 0.017	0.961	0.067	0.045 – 0.090	**<0.001**
Soil_N	0.075	-0.012 – 0.161	0.090	0.125	0.063 – 0.186	**<0.001**	0.045	-0.018 – 0.108	0.158	0.047	0.013 – 0.081	**0.007**
Soil_K	-0.063	-0.216 – 0.089	0.417	-0.004	-0.137 – 0.130	0.956	0.148	-0.006 – 0.303	0.060	-0.004	-0.078 – 0.071	0.925
Soil_Ca	-0.013	-0.063 – 0.037	0.602	0.002	-0.068 – 0.071	0.962	-0.026	-0.127 – 0.075	0.612	-0.002	-0.027 – 0.024	0.906
Random Effects												
σ^2	0.00			0.00			0.00			0.00		
τ_{00}	0.00 $_{\text{Sub\_replicate:(Replicate:(Subsite:Soil\_site))}}$			0.00 $_{\text{Sub\_replicate:(Replicate:(Subsite:Soil\_site))}}$			0.00 $_{\text{Sub\_replicate:(Replicate:(Subsite:Soil\_site))}}$			0.00 $_{\text{Sub\_replicate:(Replicate:(Subsite:Soil\_site))}}$		
	0.00 $_{\text{Replicate:(Subsite:Soil\_site)}}$			0.00 $_{\text{Replicate:(Subsite:Soil\_site)}}$			0.00 $_{\text{Replicate:(Subsite:Soil\_site)}}$			0.00 $_{\text{Replicate:(Subsite:Soil\_site)}}$		
	0.00 $_{\text{Subsite:Soil\_site}}$			0.00 $_{\text{Subsite:Soil\_site}}$			0.00 $_{\text{Subsite:Soil\_site}}$			0.00 $_{\text{Subsite:Soil\_site}}$		
	0.01 $_{\text{Soil\_site}}$			0.00 $_{\text{Soil\_site}}$			0.04 $_{\text{Soil\_site}}$			0.00 $_{\text{Soil\_site}}$		
ICC	0.78									0.20		
N	2 $_{\text{Sub\_replicate}}$			2 $_{\text{Sub\_replicate}}$			2 $_{\text{Sub\_replicate}}$			2 $_{\text{Sub\_replicate}}$		
	4 $_{\text{Replicate}}$			4 $_{\text{Replicate}}$			4 $_{\text{Replicate}}$			4 $_{\text{Replicate}}$		
	6 $_{\text{Subsite}}$			6 $_{\text{Subsite}}$			6 $_{\text{Subsite}}$			6 $_{\text{Subsite}}$		
	6 $_{\text{Soil\_site}}$			6 $_{\text{Soil\_site}}$			6 $_{\text{Soil\_site}}$			6 $_{\text{Soil\_site}}$		
Observations	87			89			75			82		
Marginal R^2 / Conditional R^2	0.264 / 0.838			0.684 / NA			0.604 / NA			0.471 / 0.579		

Table III: Linear model output for main models predicting total plant mass separately for the plant origins (From left to right, Atlas, Pyrenees, Varanger and Svalbard). Fixed predictors are soil origin, climate origin, soil nitrogen, soil potassium and soil calcium. As random factors are the hierarchical soil sampling design. N stands for number of observations in the different random factor categories. P-values under 0.05 confidence interval significance level are marked in broad font.

Cube transformed Total weight in individual models for each plant origin

	Atlas			**Pyrenees**			**Varanger**			**Svalbard**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	0.933	0.541 – 1.324	**<0.001**	0.311	-0.067 – 0.690	0.107	0.886	0.335 – 1.437	**0.002**	0.397	0.156 – 0.638	**0.001**
Soil_originSoil : Home	0.403	-0.108 – 0.915	0.122	0.393	-0.033 – 0.818	0.070	-0.273	-1.303 – 0.757	0.604	-0.303	-0.567 – -0.040	**0.024**
Climate_regimeClimate : Home	0.010	-0.056 – 0.077	0.763	0.032	-0.025 – 0.088	0.269	0.018	-0.020 – 0.057	0.348	0.180	0.114 – 0.246	**<0.001**
Soil_N	0.151	-0.061 – 0.363	0.164	0.359	0.183 – 0.535	**<0.001**	0.113	-0.047 – 0.272	0.165	0.085	-0.016 – 0.187	0.100
Soil_K	-0.161	-0.524 – 0.202	0.386	0.014	-0.375 – 0.403	0.945	0.179	-0.217 – 0.575	0.377	0.011	-0.218 – 0.240	0.924
Soil_Ca	-0.042	-0.165 – 0.081	0.502	-0.018	-0.222 – 0.186	0.866	-0.092	-0.352 – 0.167	0.485	-0.013	-0.115 – 0.090	0.809
Random Effects												
σ^2	0.02			0.02			0.01			0.02		
τ_{00}	0.00 $_{\text{Sub\_replicate:(Replicate:(Subsite:Soil\_site))}}$			0.03 $_{\text{Sub\_replicate:(Replicate:(Subsite:Soil\_site))}}$			0.01 $_{\text{Sub\_replicate:(Replicate:(Subsite:Soil\_site))}}$			0.00 $_{\text{Sub\_replicate:(Replicate:(Subsite:Soil\_site))}}$		
	0.00 $_{\text{Replicate:(Subsite:Soil\_site)}}$			0.00 $_{\text{Replicate:(Subsite:Soil\_site)}}$			0.00 $_{\text{Replicate:(Subsite:Soil\_site)}}$			0.00 $_{\text{Replicate:(Subsite:Soil\_site)}}$		
	0.02 $_{\text{Subsite:Soil\_site}}$			0.00 $_{\text{Subsite:Soil\_site}}$			0.02 $_{\text{Subsite:Soil\_site}}$			0.00 $_{\text{Subsite:Soil\_site}}$		
	0.04 $_{\text{Soil\_site}}$			0.00 $_{\text{Soil\_site}}$			0.22 $_{\text{Soil\_site}}$			0.01 $_{\text{Soil\_site}}$		
ICC	0.75			0.65						0.38		
N	2 $_{\text{Sub\_replicate}}$			2 $_{\text{Sub\_replicate}}$			3 $_{\text{Sub\_replicate}}$			2 $_{\text{Sub\_replicate}}$		
	4 $_{\text{Replicate}}$			4 $_{\text{Replicate}}$			4 $_{\text{Replicate}}$			4 $_{\text{Replicate}}$		
	6 $_{\text{Subsite}}$			6 $_{\text{Subsite}}$			6 $_{\text{Subsite}}$			6 $_{\text{Subsite}}$		
	6 $_{\text{Soil\_site}}$			6 $_{\text{Soil\_site}}$			6 $_{\text{Soil\_site}}$			6 $_{\text{Soil\_site}}$		
Observations	82			86			72			81		
Marginal R^2 / Conditional R^2	0.294 / 0.823			0.479 / 0.817			0.707 / NA			0.422 / 0.643