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Plant-Soil Feedback: Alpine Grassland Plants in Home and Away soil

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Table of Contents

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Abstract

For the grassland, plant soil feedback (PSF) has been the focus of much recent research to understand plant species dynamics. Experimental methods are very important in the plant soil feedback (PSF) analysis, and it has been observed that various PSF experimental approaches yield in different feedback values. More field type experiments are required to understand the role of PSFs in plant communities in natural sites. Here, I describe an experiment designed to test PSFs for grassland in field type conditions. In my research field-soil from six different sites (subsites/replicates) along the latitudinal gradient in alps and tundra region of Europe are considered to determine the impact of away and home soils in the growth of forbs and grass in the alpine grassland. These collected soils were directly used (without any conditioning or sterilization) for the response phase experiment to understand the PSF direction and strength.

Plant–soil feedback effects have been statistically (directly by Anova) analysed using the plant total biomass data subjected to two treatments ('Home' vs. 'Away' soil and 'Home' vs. 'Away' climate). We found that although effects varied between soil sites, PSF were more often positive for plants growing in their home soil than for plants growing in away soil. In our study, we also examined plant-soil feedback responses to two important climate factors together, photoperiod (15hrs and 24hrs) and temperature (+12 ºC and +15 ºC), representing climate of the Alps and/ or Tundra region respectively. We found that experimental home climate resulted in positive PSF, where plants showed greater growth in plant traits, such as biomass, root length, canopy height and root mass fraction. It was also observed that the direction of growth was also affected with the choice of soil origin (home vs. away) in conjunction with the home climate. These results in plant-soil feedbacks were not consistent across a simulated community of grass and forb (simulated by planting one grass and one forb species together in single pot). We also observed that plant origin is another factor along with soil origin and climate origin which may contribute to strength and direction of the PSF in grassland. These data should aid theory and predictions for conservation and restoration applications in alpine grassland by showing the relative importance of 'home' soil and 'home' climate for grass and forb.

Keywords: Grassland, Plant soil feedback, home soil, away soil, graminoid, forb

1.Introduction

Grasslands cover significant land of the earth (excluding Antarctica and Greenland) and they provide substantial ecosystem services as well. In recent years, there has been major changes in grassland globally because of multiple reasons such as land usage, climate change and invasive species (Schucknecht, Kramer et al. 2020, Bråthen, Pugnaire *et al*. 2021). Plant soil feedbacks (PSFs) are suggested to be of high importance for plant species performance and diversity in grasslands (Cortois, Schröder-Georgi et al. 2016, van der Putten, Bradford *et al*. 2016). PSFs can play an important role in altering plant species interactions and promoting species coexistence in grassland (Bever, Westover *et al*. 1997, Bever 2003). Understanding such interactions on field level is essential for the management and restoration of grassland ecosystems.

1.1 What is PSF?

PSF is a process where plants change biotic and abiotic properties of soil they grow in, and this affects the ability of plants to grow in that soil in the future (Bever, Dickie *et al*. 2010). Main factors which contribute to the PSF are such as accumulation of soil nutrients (Wardle, Bonner *et al*. 1999), symbiotic mutualists (Klironomos 2002, van der Putten, Bradford *et al*. 2016), nutrient immobilization or depletion (Berendse 1994), and accumulation of soil pathogens (van der Putten, Bradford *et al.* 2016). Last two decades focus of PSF research has been on finding out how the plant species differentially alter biotic and abiotic soil conditions that in turn affect growth of other conspecific and heterospecific individuals in the soil (Bever 1994, Wardle, Yeates *et al*. 2004, van der Putten, Bardgett *et al*. 2013). PSF is classified in two categories: i) positive PSF, and ii) negative PSF (Bever, Westover *et al.* 1997, Wardle, Yeates et al. 2004, Bezemer, Lawson et al. 2006, Cortois, Schröder-Georgi *et al*. 2016, van der Putten, Bradford et al. 2016). When a plant performs (grow, survive) better in soils conditioned by heterospecific and promotes community diversity, it is termed as negative PSF. A positive PSF means that a plant's growth is increased in conspecific-conditioned soil and promotes monotypic stands. The combined effects of plant-plant interactions and PSFs are likely to amplify negative interactions in high-resource environments and enhance positive biotic interactions in low-resource environments (Lekberg, Bever *et al.* 2018).

1.2 PSF approach: ‘Home’ vs ‘Away’ soil

Researchers have used many different methods to conduct PSF experiments, each of which was developed to address particular questions or hypothesis, and these methods come with wide

range of limitations as well (Kulmatiski, Beard *et al*. 2008, van der Putten, Bardgett *et al*. 2013, van der Putten, Bradford *et al*. 2016, De Long, Heinen *et al*. 2019). Some of the approaches used to study the PSFs effect for soil are: soil sterilization (comparing growth of on non-sterilized vs. sterilized soils), addition of soil inoculum to sterilized background soil (comparing growth of plants on soil with vs. without soil organisms) and two phase experiments (first soil conditioning by plant species and second comparing growth of plants on the conditioned soil) (van der Putten, Bradford *et al*. 2016). The two-phase approach, first conditioning phase and second response or feedback phase, remains one of the most common approach for PSF research (Bever, Westover *et al*. 1997, van der Putten, Bardgett *et al*. 2013). If the soil is conditioned in the first phase by the same plant which is used for the growth response in the second phase study, it is called "home" condition. On the other hand, if the soil is conditioned with a different plant (other than response phase plant species) during the conditioning phase then it is called "away" (or "foreign") condition (Klironomos 2002). Thus, in this PSF method plant growth on self-cultivated ('Home) soil can be compared to growth on soil cultivated by other species ('Away) (Bever 1994).

Most of these two phase PSF approach continues to rely on greenhouse experiments, which may be good for developing conceptual models of PSF around different plant community but there will be always a question mark how good PSFs measured in the greenhouse are correlated with PSFs measured in the field (Bever, Westover *et al*. 1997, Kulmatiski, Beard *et al.* 2008). There are high chances that abiotic and biotic settings of the soil is not same for the greenhouse and the field (Heinze *et al*., 2016; Schittko *et al*., 2016). To prepare the greenhouse soils, one usage small amount of live soil to sterilized and inoculated the greenhouse soil and this soil preparation process could be favourable in plant species growth (De Deyn *et al*., 2004; Howard *et al*., 2017). Another drawback of greenhouse experiment is frequent fertilization along regular watering which can develop arbuscular mycorrhizal fungi in the soil (Schmidt *et al*., 2011). These artificially created differences in the soil's property in greenhouse experiments, which may not be good enough to conclude in real field situation, have encouraged for two phase PSF research using the higher field conditions. Field-based studies that integrate naturally co-occurring systems of plants, microbes and their local soil are needed to further test the hypothesis that resource availability is an effective predictor of the direction and magnitude of PSFs. The main motivation behind my thesis research is to use more natural soil from the field directly. Soil sampled from different sites was used in the experiment without a conditioning

phase with local species. This helps in achieving more realistic result for the alpine grassland plant species growth in the response phase of "Home" vs. "Away" PSF experiment.

1.3 Importance of climate in PSF

Climate conditions are an important factor in the higher latitudes and altitudes of the alpine region because highland has shorter growing season and longer harsh winter (Billings and Mooney 1968). Both temperature (Wu, Dijkstra *et al*. 2011, van der Putten, Bradford *et al*. 2016) and photoperiod (Sinclair, Ray *et al*. 2003, Adams and Langton 2005) are found to affect plant performance severely. Plants and soil organisms respond differently to changes in temperature, either along latitudinal or elevational gradients, as well as due to climate change (Classen, Sundqvist *et al*. 2015). Shifts in soil community structure as a result of climate change can affect direction of PSF through interactive effects (Bennett and Klironomos 2019). Abiotic stressors, such as temperature, have been shown to strengthen the effects of both pathogens and mutualists on plant performance (Pineda, Dicke *et al.* 2013), which will alter the strength and direction of PSFs. For example, under cold conditions with slow recycling of nutrients, plants may be more dependent on symbiotic soil biota for acquisition of nutrients. Under warmer conditions, the activity of arbuscular mycorrhizal fungi (AMF) is expected to decrease (Mohan, Cowden *et al*. 2014).

1.4 Objective and Hypothesis of the thesis

The aim of the present study was to investigate PSF effect on the growth of grass and forbs in two-species communities along the latitude gradients of alpine grassland in 'home' and 'away' conditions of soil and climate. The roles of competition and facilitation changes along the latitude gradients in the grassland (Henttonen, Mäkinen *et al*. 2014), so that the role of PSF is expected to change accordingly . Due to change in the soil properties and climate along the latitude, soil biota community structure changes as well (Lu, He *et al.* 2018). This change in soil biota along the latitude of Alpine region in Europe may have significant impact on the plant growth. Therefore, understanding the PSF in responses of soil variation along the latitude and climate changes in the alpine grassland is of great importance.

I examined how PSF effects of home and away soil influence the performance of grass (*Phleum alpinum* and *Nardus stricta*) and forbs (*Cerastium alpinum* and *Parnassia palustris*) species from the two-alpine region (Alps (Switzerland) and Sierra Nevada (Spain)). For this study, I have planted one grass species and one forb species from the same origin together in a

pot for simulating two-species communities. While conducting the PSF study in grassland systems, it is important to consider the correct level of covariate such as life form (grass vs. forb vs. shrub vs. tree) and species origin (native vs. non-native vs. invasive). Previous studies have found that different plant functional group in grasslands respond differently to PSF (Kulmatiski, Beard *et al.* 2008). A majority of the studies on PSF taken place in grassland systems (i.e., grasses and forbs), found that PSFs were large and negative (Kulmatiski, Beard et al. 2008).

Field soil from six sites (four Alpine and two Tundra region) was collected from their natural habitat and environment. Soil conditioning or treatment was considered unnecessary because plant species were collected from the same site meaning their home soil was collected. All soil sites (Atlas, Sierra Nevada, Pyrenees, Alps, Varanger and Svalbard) are easily distinguished as it is above the tree line. No trees grow in this zone due to the harsh climatic conditions which is defined by short, cool summers with long, cold, and snowy winters. These grasslands are dominated by grass and forbs species only. In the feedback phase, all grass and forbs species were grown in home soil (one), as well as in away soils (three from Alpine and two from Tundra) in the control environment of greenhouse. All combination of plan-soil replicate was grown in two different climates conditions (varying in photoperiod and temperature), north climate (resembling to above arctic summer) and south climate (resembling to summer of high-altitude Alpine grassland).

During the feedback phase, we measured plants performance at end of the plant growth experiment to test whether 'home' vs 'away' PSF effects change the plant growth. In most of the studies three approaches have been adopted to quantify the PSF: 1) change in the individual plant growth after the soil conditioning (Veen, de Vries *et al.* 2014, Cortois, Schröder-Georgi *et al*. 2016, Zhang, Van der Putten *et al.* 2016); and 2) percentage increase in the grass or Forbes coverage over a period (De Long, Heinen *et al.* 2019, Kulmatiski 2019). In this work, second approach has been used to quantify the PSF i.e. change in the belowground plant traits (below ground biomass, root volume and root length) and aboveground plant traits (aboveground biomass, canopy heigh and in some cases total plant biomass) is used as the main plant growth parameter for the PSF effect study.

Thus, this thesis work focuses on the PSF effects, along the latitudinal alpine region, on grass and forb species for 'home' vs 'away' soil, and 'home' vs 'away' climate. For both soil and climate types, we addressed three questions. (i) What is the effect of soil origin on the plant

growth? (ii) What is the influence of climate on the growth of the plant? (iii) How well can soil and climate as an interaction factor explain the growth of the plant communities in different conditions? We tested five hypotheses: (1) Growth of plants in their home soil will be better than growth of plants in away soil irrespective of climate origin; (2) Plants grow better in home climate compared to away climate irrespective of soil origin; (3) Growth of plants are affected by combination of climate origin and soil origins; (4) Plants growth is best in home soil and in home climate combination; (5) Plant origin affect the growth performance in different soil sites. The comparison of 'home' vs. 'Away' soil assumes that soil organisms with a specific relationship to the plant are more abundant in 'home' than in 'Away' soil.

2. Materials and Methods

2.1 Study system:

This study took place at the phytotron at the UiT-Arctic University of Norway using plant seeds and soil collected from sites of Europe region from latitudinal gradient 32°N (Atlas, Morocco) to 78°N (Svalbard, Norway). Four sites in the alpine region (Atlas (31º05N, 7º90E), Sierra Nevada (37º08N, 3º39E), Pyrenees 42º61N, 1º47E), Alps (46º75N, 9º95E)) and two sites in tundra region (Varanger (70º42E, 29º42E) and Svalbard (78º10N, 16º04E)) were included as shown in Figure 1. All these sites fall in different climate zones: above arctic region (Varanger and Svalbard) have 24 hrs photoperiod in summer while Southern part of Alps (Atlas, Sierra Nevada, Pyrenees, and Alps) having photoperiod varying from 12 hr to 15 hrs (Table 1 for more detail comparisons). Not only photoperiod, but these different photoperiod sites also experience major difference in temperature and precipitation during the summer. For the above arctic region average summer temperature ranges from 3 ºC degree to 12 ºC degree and for the Southern Europe region temperature vary from 9 ºC degree to 18 ºC degree during the summer.

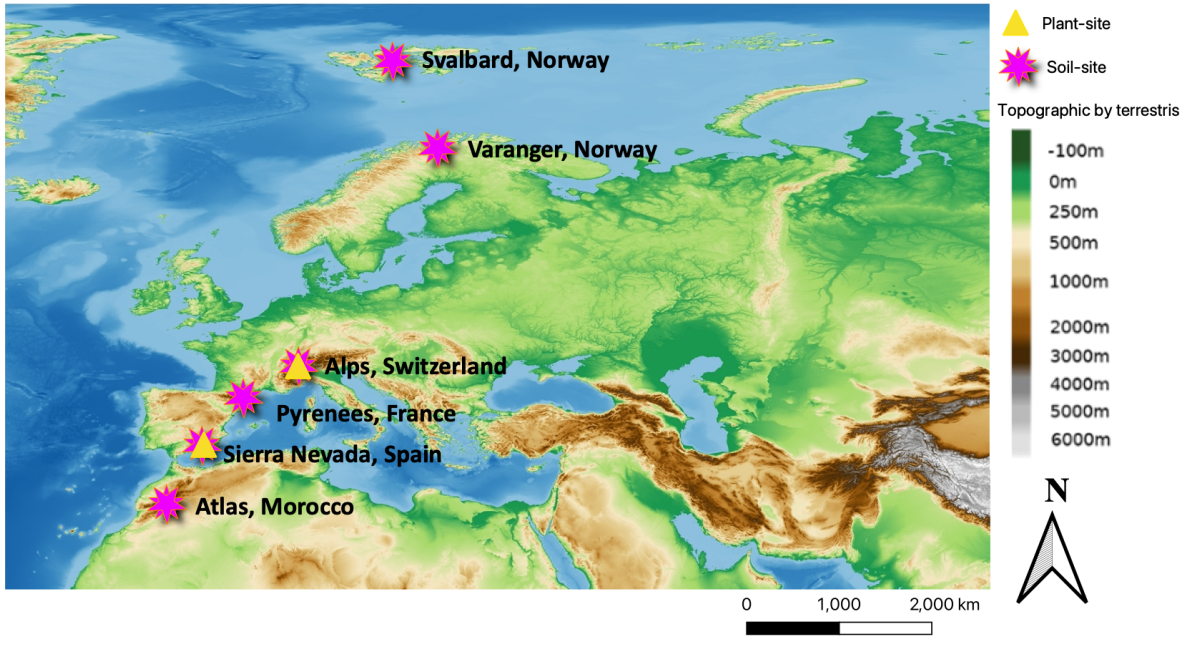


Figure 1: Six soil sampling study sites in Southern and Northern Europe and two seed sampling study sites in southern Europe. Map was created using the (QGIS-3.16.11) software and open street map used from http://ows.terrestris.de/osm/service.

Table 1: Climatic, geological and spatial variation between study sites for soil. Average July precipitation and average July temperatures from sites were recorded from respectively (en.climate-data.org 2020a). Photoperiod for all sites was obtained from (en.climate-data.org). Growth period in Svalbard was recorded from (Karlsen 2014), while growth period from other sites were recorded from (FAO-GAEZ 2012).

Site	Coordinates	July Average Temperature	Precipitation in July	Photoperiod in July	Growth Period
Atlas	31°05N, 7°90E	20.5 ºC	26 mm	12.36 hours	120-145 days
Sierra Nevada	37°08N, 3°39E	26.1 ºC	0 mm	12.5 -15 hours	150-179 days
Pyrenees	42°61N, 1°47E	22 ºC	41 mm	15 hours	210-239 days
Alps	46°75N, 9°95E	9.6 ºC	164 mm	8.4 -15 hours	90-119 days
Varanger	70°42N, 29°42E	12.7 ºC	89 mm	24 hours	90-119 days
Svalbard	78°10N, 16°04E	4.7 ºC	40 mm	24 hours	50-60 days

2.2 Collection of soil

From each soil site (Figure 2), five or six subsites were chosen for soil collection at least 100 meters apart. Within each subsite, a set of five metre long transects with distance between each transects was at least two meters. Soil was collected at every transects so that each transect contributed to one soil replicate. Number of replicates and sub replicates (transects) per subsite varied among different soil sites. Soil was collected from each meter mark along the transects. During soil collection aboveground litter was removed at the collection site. Soil was sampled from the upper 10 cm of the soil profile and mixed in separate plastic bag for each replicate. From Atlas, Sierra Nevada, Alps and Pyrenees approximately 3 dl of soil was collected from each replicate. From Varanger and Svalbard 6 dl soil was collected from each replicate (see Figure 2). All soil collection equipment was cleaned and sterilized between each sample with

70% ethanol and 30% distilled water solution together with paper. Soil were then transported to Phytotron at UiT The Arctic University of Norway and stored at 0.5 ºC to further processing. Soil collection was performed previous to this thesis and is also described in (Aares 2020).

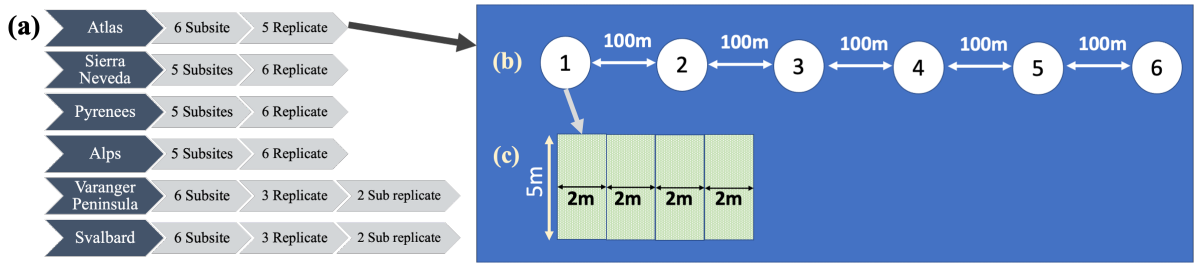


Figure 2: (a) Soil sites, subsites and replicates details; **(b)** A sampling transect of soil collection site in Atlas. 1-6 represent the subsites; **(c)** Transect/replicate for Atlas subsite -1 is shown in enlarged image. Similar pattern was followed for other five soil sites during the soil collection.

2.3 Collection of plants seeds

The focal plants of seeds in my study were collected from two alpine grassland, Sierra Nevada (Spain) and Alps (Switzerland), having a latitudinal gradient of 37ºN and 47ºN (Figure 1). My thesis is complementing that of Aares (2020), who did the same experimental setup on the four other plant origins (Atlas (ATL), Pyrenees (PYR), Varnager (VAR) and Svalbard (SVL)). From Alps (SWT) and Sierra Nevada (SNV) seeds were collected from abundant graminoid and forb species that had ripe seeds in the sampling period. The seeds were kept in plastic bags which was labelled using the site and plant name, and brought to biology building of UiT The Arctic University of Norway. They were stored in -18 ºC for further processing. Many plant species seed (see Table 2) from the two plant sites (as shown in figure 1) were collected for this PSF research work. Germination of all the collected seeds (see Table 2) were carried out for providing seedlings in sufficient numbers to replicate them in the plant growth experiment. Two plant species (one forbs and one grass) from each side which had sufficient seedlings in the end, were hence included in the plant growth experiment (Table 2). Graminoid (*Phleum alpinum* from Alps and *Nardus stricta* from Sierra Nevada) and forbs (*Cerastium alpinum* from Alps and *Parnassia palustris* from Sierra Nevada) were finally considered for the PSF experiment as they had enough seedlings. Details of germination and plant growth experiments are discussed below in section 2.4.

Table 2: List of plant species from two different sites used for germination and the final plant growth experiment

Origin site	Functional group	Species for Germination	Species considered for plant growth
Sierra Nevada	Forb	*Pedicularis aurea*	No
Sierra Nevada	Forb	*Parnassia palustris*	Yes
Sierra Nevada	Forb	*Euphracea spp*	No
Sierra Nevada	Graminoid	*Carex nigra*	No
Sierra Nevada	Graminoid	*Phleum bra..*	No
Sierra Nevada	Graminoid	*Nardus stricta*	Yes
Alps	Forb	*Ligusticum mutelliina*	No
Alps	Forb	*Cerastium alpinum*	Yes
Alps	Forb	*Potentilla aurea*	No
Alps	Graminoid	*Phleum alpinum*	Yes
Alps	Graminoid	*Nardus stricta*	No
Alps	Graminoid	*Deschampsia caespitosa*	No

2.4 Experimental Design:

Over an experimental period of 11 weeks, plants of two origin sites were grown for studying the effect of plant-soil feedback based on soil origin ('Home' vs 'Away') and climate ('Home' vs 'Away') according to a study design as shown in Figure 3. The experiment was carried out in two phases; 1) in the first phase germination of all the collected seedlings from two study sites and 2) in the second phase plant growth of the most germinated seeds, as discussed in previous section, were studied in 'Home' and 'Away' soil sites with simulated climate condition (North and South).

"Home soil" and "home climate" was defined with reference to plant origin. For example, Alps soil (SWT) is considered as 'Home' as soil sample in the same site as the plant origin SWT, and all other five soils is considered as 'Away'.

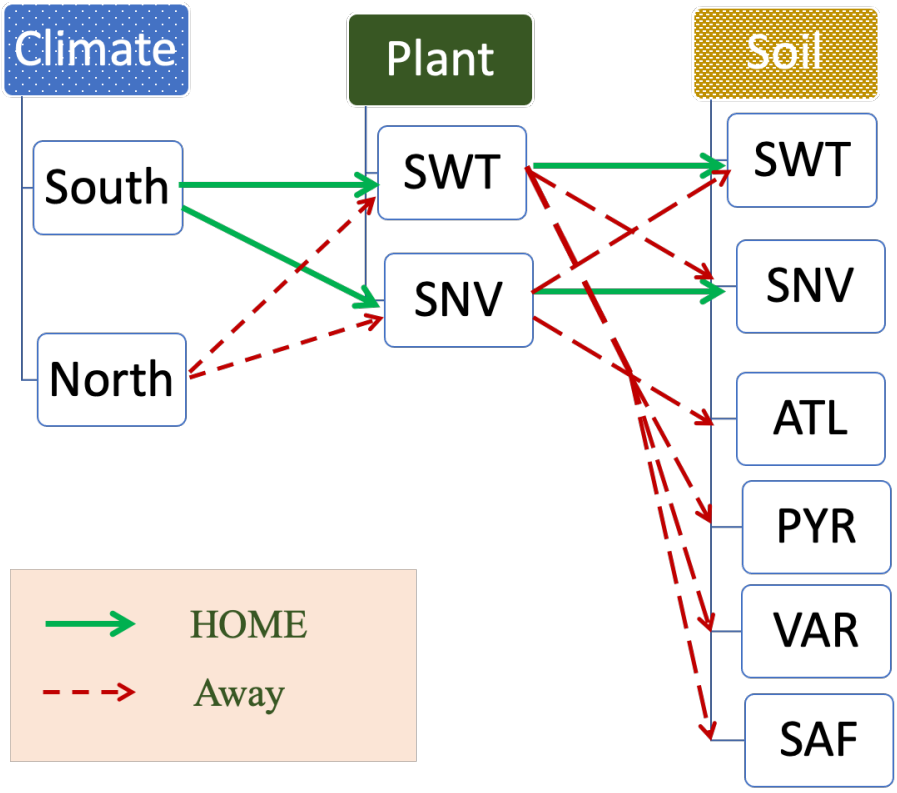


Figure 3: Study design for the two plants sites in six soil sites and two different climates. "Home" is referred to soil sites or climate, which match with the plant's origin, and "Away" is referred to the soil originating from any of the other five sites and the climate different from the plant origin site. For each plant-soil combination, one replicate is placed in the "Southern" climate simulation, and one replicate is placed in the "Northern" climate simulation. The southern climate simulation has 15 hours of light and 9 hours of darkness each day, and temperatures is set to 15 ºC in the light periods, and 9 ºC in dark time of the day. The northern climate simulation has all day light, where temperature is set to 12 ºC for half day, and 9 ºC for other half of the day.

Schematic steps of experimental and analysis for this PSF research work is shown in Fig 4 and each step is presented in detail below.

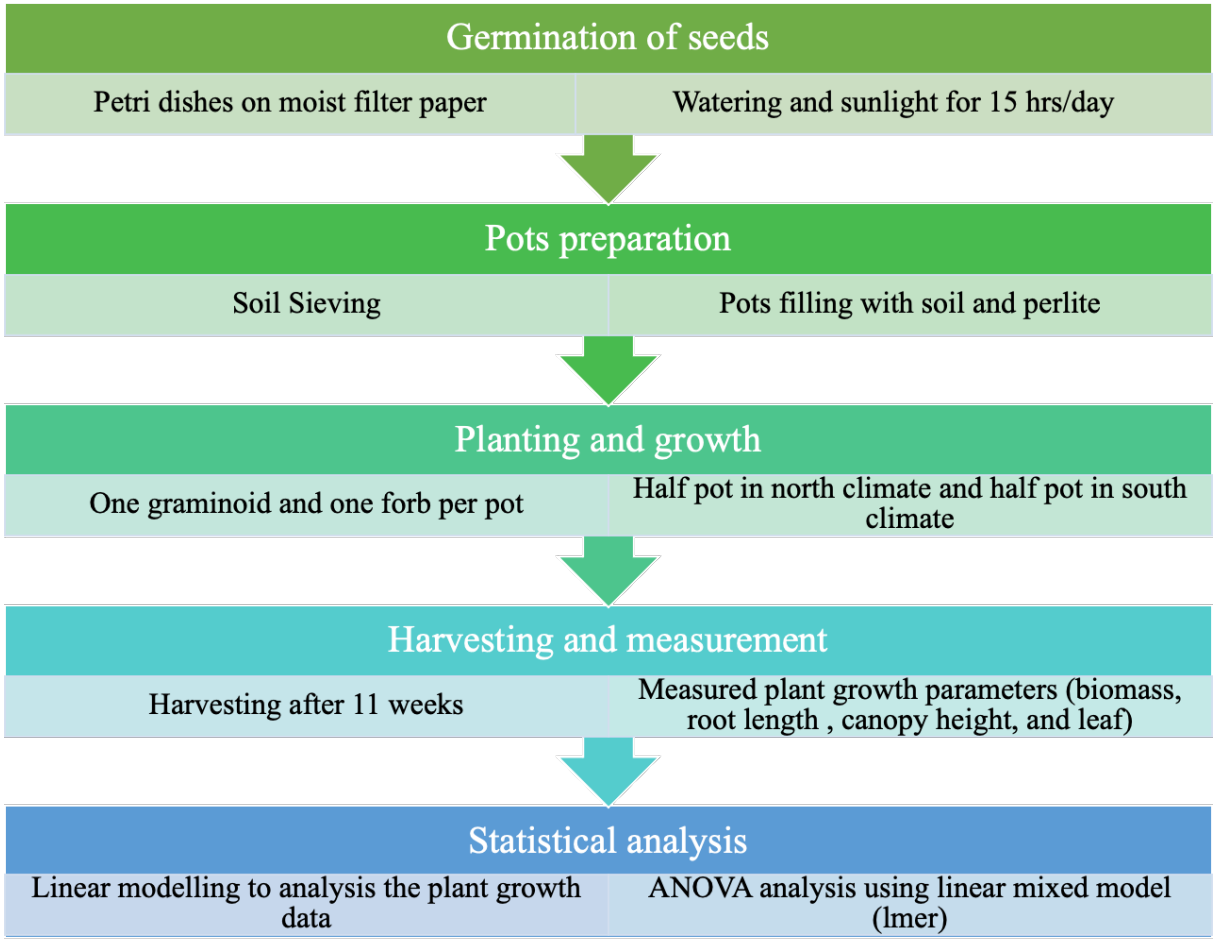


Figure 4: Schematic diagram of plant–soil feedback (PSF) growth experiment and analysis in 'home' vs 'away' soil and climate. First stage was seed germination followed by plants growth of the targeted species' seedling until all seedlings have died or matured, and finally analysis of the traits related to the plant performance.

2.4.1 Seeds germination

Germination processes for different plant species seeds (Table 2) were carried out in petri dishes on moist filter paper. Seeds were placed to germinate in growth chambers with 18°C temperature all the time, and simulated light for 15 hours every day. Since germination of seeds on petri dishes was not successful enough for plant growth study on different soil replicate, seeds were also germinated on sand in a plastic box. For germination on sand, seeds were placed for 1.5 month at 0.5 °C in pH-neutral sand and watered by distilled water when it required.

Some seeds of the selected plant species were not germinated in enough numbers to be used as replicate in plant-soil combinations. The focus was to use one forb species and one graminoid species from each of the two plant origin sites (Alps and Sierra Nevada) and plant them in

couple in soil pots prepared from six sites. In this way each individual pot would contain one "plant origin" of two plants representing each site, and soil from one specific site. From Sierra Nevada the grass *Nardus stricta* and forb *Parnassia palustris* were used and similarly from the Alps grass *Phleum alpinum* and forb *Cerastium alpinum* were used.

2.4.2 Soil preparation

All six soil sites were dried in an oven for 48 hours using paper bags. Drying temperature for Atlas soil was 60 ºC and all other soil were dried at 30 ºC. After complete drying, soils were sieved using the 2 mm sieve and stored in a new paper bag with proper labelling at room temperature. After that perlite mixture was sieved gently using the same size, 2 mm, sieve and stored in a separate paper bag. Sieved soil and perlite were mixed, and total volume of 2 dl/pot were stored in the original paper bag with updating the label (adding "Soil volume correct"). Cleaned and dried all 167 pots followed by spraying a solution of 70% ethanol, and 30% distilled water. All pots were assigned with a unique ID number and it was also prepared the painting tape attach labels with ID matching the ID of the stick-in-soil label to the side of the pot. All the dried pots were placed on trays and tray was covered with transparent plastic. In total there were 167 pots which were distributed on 12 trolley (16 pots per trolley), and we put 86 pots in Southern climate and 81 pot in Northern climate room. All trays were labelled according to climate replicate (North/South).

2.4.3 Planting and growth

Germinated seedlings were cleaned using distilled water and canopy height of both grass and forb was measured. Two germinated seedlings, one graminoid and one forb, per pot were planted from the respective plant origins. Germinated seedlings from the respective plant origins were planted in all six sampling soil sites. There were five 'Away' soil sampling site and one 'Home' site which was matching to plant origin (as shown in Figure 3).

Pots of 10 cm diameter were used for plant growth experiments. They were filled with 1 dl of agra perlite in the bottom and 1 dl of soil on the top of the perlite. All plants pots were covered by transparent plastic, while maintaining safe distance from the growing plants, to avoid the transpiration.

Pots were divided equally into two simulated climates regime, to control the effects produced by varying climate between 'Home' and 'Away' sites. In accordance with climate data for the growing season, Alps (South) and Svalbard (North) climates were simulated by adjusting the

photoperiod and temperature accordingly (Figure 3). The variable “climate regime” defined Alps (SWT) and Sierra Nevada (SNV) plants to be growing in “Home” climate if they were placed in the southern climate simulation, while both plants to be growing in “Away” climate if they were placed in the northern climate regime.

After planting, the pots were covered in transparent plastic for 6 weeks so that plants did not lose transpiration. First five weeks, distilled water were used to water all the plants, followed by watering using tap water. Plastic was removed step by step in six weeks. Pots were weeded on regular interval to avoid the growth of unwanted seedling of other species. Special treatment for one week was given to the plants growing in the northern climate with a ‘warm spell’ in southern climate because the plants in pot containing two individuals of each are growing to be reduced to one.

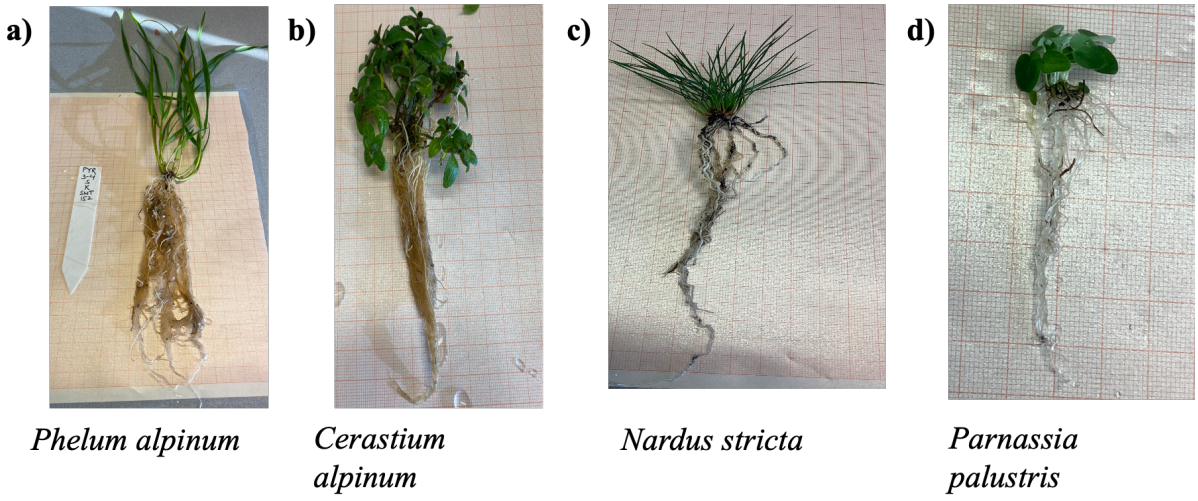


Figure 5: Pictures of a plant individuals after harvesting, representing each species included in the study design a) & b) Alps (SWT) graminoid b) Alps (SWT) forb c) Sierra Nevada (SNV) graminoid d) Sierra Nevada (SNV) forb.

2.4.4 Plants harvesting and plant traits measurement

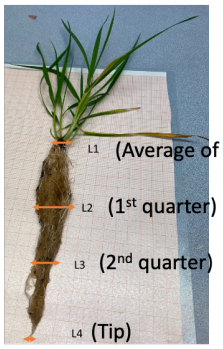
After 11 weeks of growth, most of the plants in all pots showed good growth in Alps and SNV plants species as shown in Figure 5. Prior to harvesting, all dead leaves were removed and placed in paper bag with id of pots. After those plants were gently removed from their pot, and soil was rinsed away from the roots. Roots were disentangled due to pots containing more than one plant, and these were separated. Different plants traits aboveground and belowground biomass, root length, root volume, canopy height, leaf and/or shoot number were determined.

Detail procedure for the different trait measurements is mentioned in the Table 3. For each plant, the number of dead, mature, and senescing leaves were recorded. Then, leaf number for forbs and shoot number for graminoids were recorded, and Leaf by shoot ration was calculated by dividing leaf number of forbs and shoot number for graminoids.

Table 3: Plant traits measurement procedures

Measurement	Procedure
Aboveground and belowground dry mass	Oven dried at 60 ºC for 48 hours and then measured separately in grams of aboveground for forb and graminoid and belowground forb and graminoid dry mass. All measurements were done to three decimal points.
Total biomass	Adding the belowground biomass and aboveground biomass.
Canopy height	Measured the three longest leaves from crown to leaf tip (± 1 mm) on graph paper and averaged them to determine the canopy height.
Leaf number forb	Counted the total number of leaves and shoot number of forbs.
Shoot number graminoid	Counted total number of shoots of grass.
Root length	Carefully stretching the roots on the graph paper and measured the length of three longest roots from crown to tip and recorded their average.
Root diameter	Roots compressed by hand and measured in mm at four different root lengths, first 0.5 cm away from the crown, then first quarter of total root length, next to half of total root length and finally at tip of longest root.
Root volume	Measured the diameter from crown to root tip into four different parts and calculated using mathematical formula by assuming root is divided in three cone shape as shown in Figure 6.(Ostonen, Püttsepp et al. 2007)

(a)



(b)

$$\text{Root Volume} = \left(\pi \times (Average\ of\ crown\ and\ 1^{st}\ quater)^2 \times \left(\frac{Root\ of\ length}{4}\right)\right) + \left(\pi \times (Average\ of\ 1^{st}\ quater\ and\ 2^{nd}\ quater)^2 \times \left(\frac{Root\ of\ length}{4}\right)\right) + \left(\pi \times (Average\ of\ 2^{nd}\ quater\ and\ tip)^2 \times \left(\frac{Root\ of\ length}{2}\right)\right)$$

Figure 6: Proximate root volume calculations for belowground weight by assuming it is made of three cone shapes. (a) Diameter measured for different part of the root along its length: L1, L2, L3 and L4 are diameter 0.5cm away from the crown, at the 1st quarter, at the 2nd quarter or half and at the tips respectively. (b) Mathematical equation for calculation of the root volume by assuming it is sum of three cones along the root length as shown by orange line as separator in the figure a. Root length measurement method is mentioned in Table 3.

2.5 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 Statistical analysis

All Statistical data analyses were conducted using software R. 3.6.3 (R Core Team, 2020).

All data were first checked for homogeneity of variance and normal distribution of errors. It is difficult to perform linear mixed model analysis with skewed data and there is high chance of boundary condition failure, which results in warning during the regression. In case the data for a given variable was skewed then square-root and log10 conversion was performed for the sake of transforming them to a normal distribution, to meet the assumption of the statistical test.

Principal component analysis (PCA) a multivariate analysis method has been performed on the soil datasets consisting of (number of rows = 156) from 6 soil sites to investigate the distribution of soil nutrients in the soil profile (Lomeling, Otwari et al. 2015). PCA is a technique which

reduces the dimensionality of multivariate data by removing Interco relations among variables. PCA helped in identifying the important soil nutrient properties in all six sites which will be considered for further statistical analysis.

The plant performance dataset consists of leaf, stem, and root dry mass and/or length data for the four plant species grown in different soils and climate combination. Data were analysed by comparing all soil sites and comparing home soil vs. away soil origin. Analyses were performed for each climate origin (home or away climate) separately. Prior to analyses, data of traits related to plant performance (canopy height, shoot/leaf number, aboveground and belowground mass, root length and approximate root volume) from the two plants (one forb and one graminoid) from the same pot with the same soil replicate and same climate treatment were averaged. Traits related to plant performance of forb and graminoid in the same pot was averaged because they represented two individuals per pot-community. Before conducting analysis, data were checked for homogeneity of variance and normality was confirmed by inspection of the histogram plots for all response variable (plant performance parameters).

I started modelling with assuming "soil sites, climate replicate, and soil nutrient" as fixed effects in our model and plant origin as random variables. To test whether plant growth effects on both soil sites and climate replicate, it was fitted using LMER function of LMMs (normal error distribution, identity link function) with "canopy height," "root length," "root volume," "plant biomass" and "soil nutrient as response variables. The function pamer.fnc in the package LMER Convenience Functions (Tremblay and Ransijn 2012) was used to perform ANOVA for the best linear mixed effects models.

To determine the effect of soil origin ('Home' vs 'Away') and the climate origin ('Home' vs 'Away') on plant growth parameters, linear mixed modelling was performed using LMER function. For each plant measurement type, the following linear mixed effects models were fitted: (1) additive model containing the fixed predictor terms: soil origin, climate origin and important soil nutrient (nitrogen, phosphorous, and organic carbon), and random effect of soil sites and subsites; and (2) interaction model that consider interaction between soil origin and climate origin as a fixed predictor and a random effect of soil sites and subsites. Different response variables, such as total biomass, root length, canopy height and root volume were analysed in the above models to understand the PSF effect. For clarity, the data and R code are provided as supplementary data (Data S1).

3. Results

3.1 Soil Nutrient PCA

PCA results, in Figure 7, showed significant relationships between some soil nutrients with PC1 and PC2 axes. Also, among different soil factors, the distribution of soil-sites was most strongly controlled with some soil characteristics such as phosphorous, organic carbon, and total nitrogen. Result of principal component analysis showed, the first two principal components together accounted for 59.9% of the total variance in data set. Therefore, 33.6 and 23.3% variance were accounted by the first and second principal components, respectively.

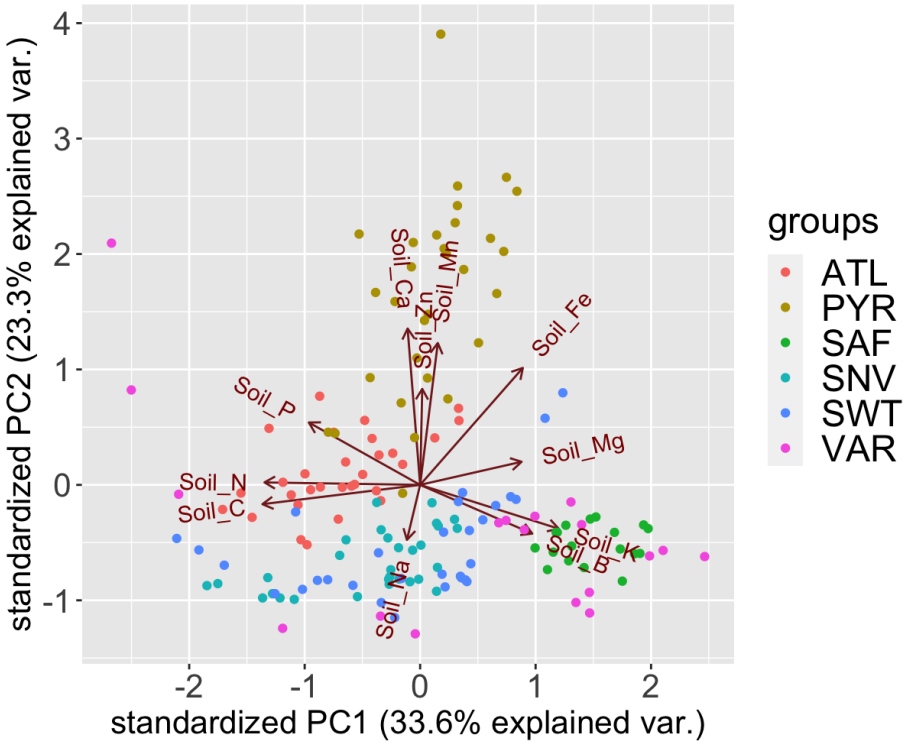


Figure 7: PCA analysis for soil nutrients. Length of arrows indicate how much the parameters vary between soil samples, and direction indicates correlations between parameters, meaning that parameters with similar directions are correlating. Soil samples are marked with varying colours.

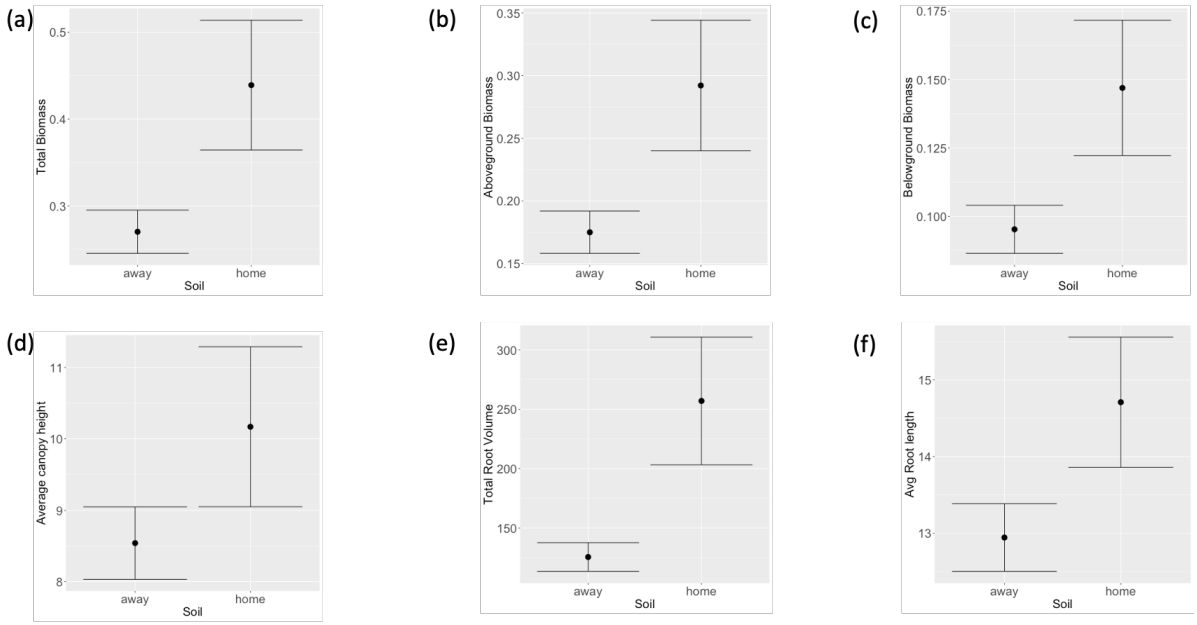


Figure 8: The graph of dependence of the different plant traits on the soil origin (home or away): (a) total biomass (g dry weight) ±SE, (b) aboveground biomass (g dry weight) ±SE, (c) belowground biomass (g dry weight) ±SE, (d) canopy height ±SE, (e) root volume ±SE and (f) root length ±SE of grass and forb when grown in all six-soil sites as shown in Fig.1. In all plots, the middle dot on the vertical line indicates the mean value of data for given plant traits. The top horizontal line indicates the value of standard error above the Mean Value. The bottom horizontal line indicates the value standard error below the Mean Value. For all plants one site is home and other five soil sites are away.

3.2 Normalization of Plants traits performance data

Plant traits (total biomass, root length and canopy height) value per pot is plotted as histogram in Fig. S1a, d, g. It is clear from the histogram that plant traits data are mostly skewed and need transformation to normalize them for further statistical analysis. Log10 and square root (sqrt) conversion of data is considered in this study to normalize the data and is plotted in Fig. S1 b, c, e, f, h, i. Biomass and canopy height become more normalized after log conversion, and root length look normalized in the square root conversion.

3.3 Plant growth comparison in different Soil origin (‘Home’ vs ‘Away’)

Standard deviation error bars with mean for different plant traits (total biomass, aboveground and below ground biomass, root length, canopy height and root value) performance data with respect to soil origins are plotted in Figure 8. Standard deviation error bars for all plant traits do not overlap for ‘Home’ and ‘Away’ soil origin (Fig. 8), it's a clue that the difference in plant growth may be significant based on soil origin. Total plant biomass was higher in ‘Home’ soils

than in ‘Away’ soils from sites (Fig. 8a) and this was true for all plant species (In Appendix Fig. S2). Plant species allocated more biomass aboveground in soils from home sites than from away soil sites, indicated by a significantly higher above ground biomass (mean approx. 0.29g dry weight) compared to below ground biomass (mean approx. 0.14 g dry weight) for all plant species (Fig. 8b & 8c).

Further we analysed the plant growth parameter on the soil site basis as well. It is clear from Fig.S3 (in Appendix) that plants from Sierra Nevada (SNV) show relatively better growth in plants traits in home soil (which is SNV). In case of Alps plant (SWT) species best growth of plants traits (such as biomass, and canopy height) are not in home soil as shown in appendix Fig. S3. In general, growth of Sierra Nevada plant species is less compared to Alps plants species. Both plant origins from SWT and SNV (not depending on origin sites) shows worst performance in the Svalbard (SAF) and Varanger (VAR) soils. Box plot for total biomass (in appendix Fig. S4) data shows the distribution of numerical data and skewness.

3.4 Plant growth comparison in different climate origin (‘Home’ vs ‘Away’)

Standard deviation error bars for different plant traits (total biomass, aboveground and below ground biomass, root length, canopy height and root value) performance data with respect to climate origins are plotted in Figure 9. Again, in case of ‘Home’ and ‘Away’ climate standard deviation error bars for all plant traits do not overlap. Similar corelation of plants traits is found in case of soil origin (Fig. 8). Even though the aboveground (mean approx. 0.25 g dry weight) and belowground (mean approx. 0.13 g dry weight) biomass difference is relatively low in case of home vs away climate, but the trend shows the home climate has positive impact on the plant’s biomass growth. It was found that canopy height (Fig. 8d & Fig. 9d), root volume (Fig. 8e & Fig. 9e) and root length (Fig. 8f & Fig. 9f) show more positive growth in the home soil as well as in home climate.

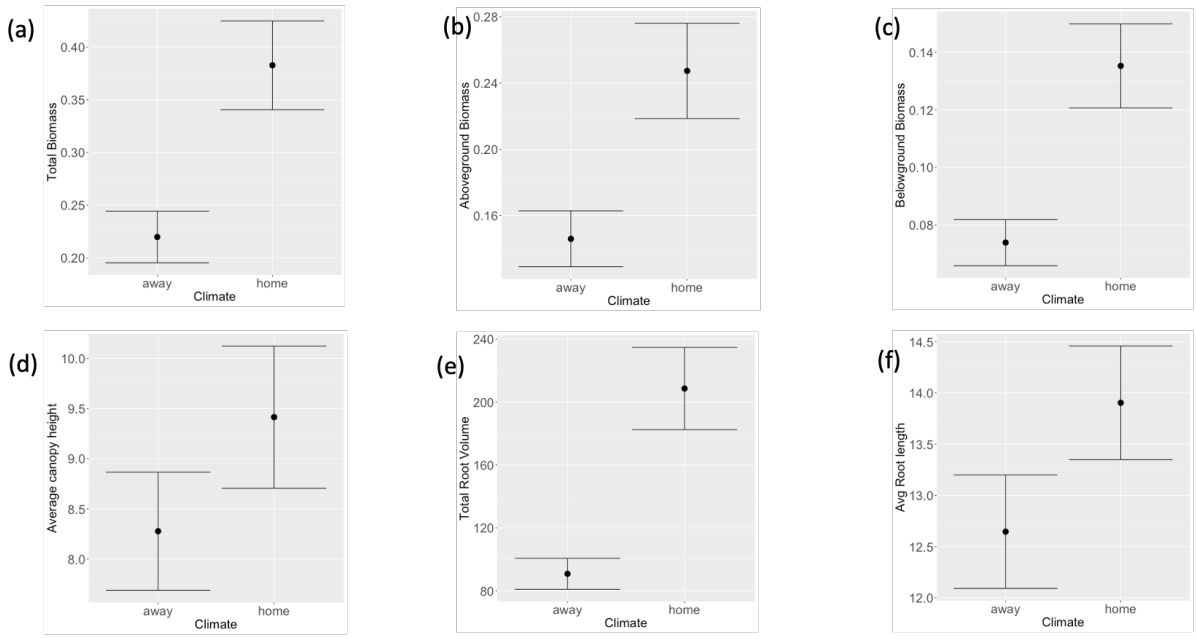


Figure 9: The graph of dependence of the different plant traits on the climate origin ('Home' and 'Away'): (a) total biomass (g dry weight) ±SE, (b) aboveground biomass (g dry weight) ±SE, (c) belowground biomass (g dry weight) ±SE, (d) canopy height (cm) ±SE, (e) root volume (mm^3) ±SE and (f) root length (cm) ±SE of grass and forbs when grown in all six-soil sites as shown in Fig.1. For both plants South climate is home and North climate is away. In all plots, the middle dot on the vertical line indicates the mean value of data for given plant traits. The top horizontal line indicates the value of standard error above the Mean Value. The bottom horizontal line indicates the value standard error below the Mean Value. For all plants one site is home and other five soil sites are away.

3.5 Effect of soil origin and climate origin combination on the plant growth

Next, we plotted the plant traits performance mean and one (1) standard deviation in the combination of soil origin and climate origin (Figure 10). Here, we grouped the data in different permutation of soil origin and climate origin as shown in figure 10e. In Fig. 10a and Fig. 10c, plants grown in home soil and in home climate had a significantly greater biomass (mean value of 0.55g per pot) and root volume (400 cm^3/ pot) than those grown in away soil and in away climate. In case of canopy height of plants (Fig 10b), there is positive impact (mean value of 11.5 cm/ pot) as well in home soil and in home climate, but home soil and away climate combination also shows good growth (9.5cm/ pot) of canopy height. For root length (Fig. 10 d) home soil and away climate show better growth (14.9 cm/pot) relative to in home soil and in home climate (mean root length 14.5cm/ pot). Overall plant traits show positive growth in home soil along with in home climate. On the other hand, worst performance for the plant trait can be observed in combination of 'Away' soil and 'Away' climate (Table 4).

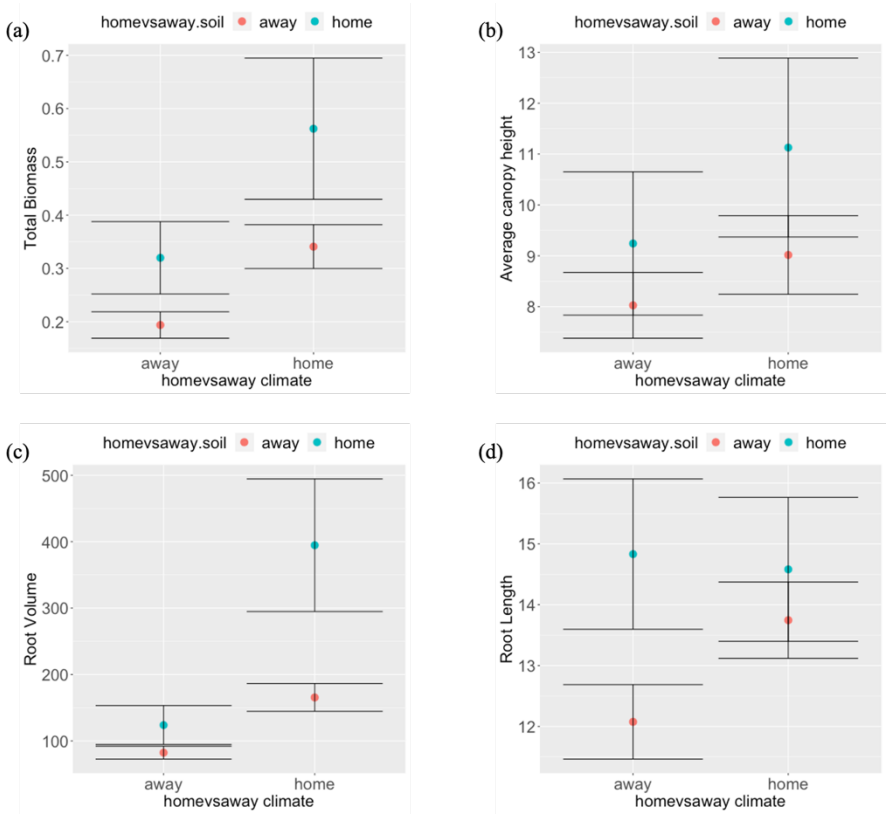


Figure 10: Interaction effect of the soil origins ('Home' and 'Away') and climate origins ('Home' and 'Away') on the plant traits growth performance: **(a)** total biomass (g dry weight) ±SE, **(b)** canopy height (cm) ±SE, **(c)** root volume (mm^3) ±SE, and **(d)** root length (cm) ±SE. On the X axis, climate origins are plotted, and soil origins are represented by the orange (Away) and green (Home) colour. In all plots, the middle dot on the vertical line indicates the mean value of data for given plant traits. The top horizontal line indicates the value of standard error above the Mean Value. The bottom horizontal line indicates the value standard error below the Mean Value.

Table 4: Plant traits performance matrix in different combination of climate and soil origin.

	Home Climate	**Away Climate**
Home Soil	High growth in plant traits	Average growth
Away Soil	Average growth	Low growth in Plant traits

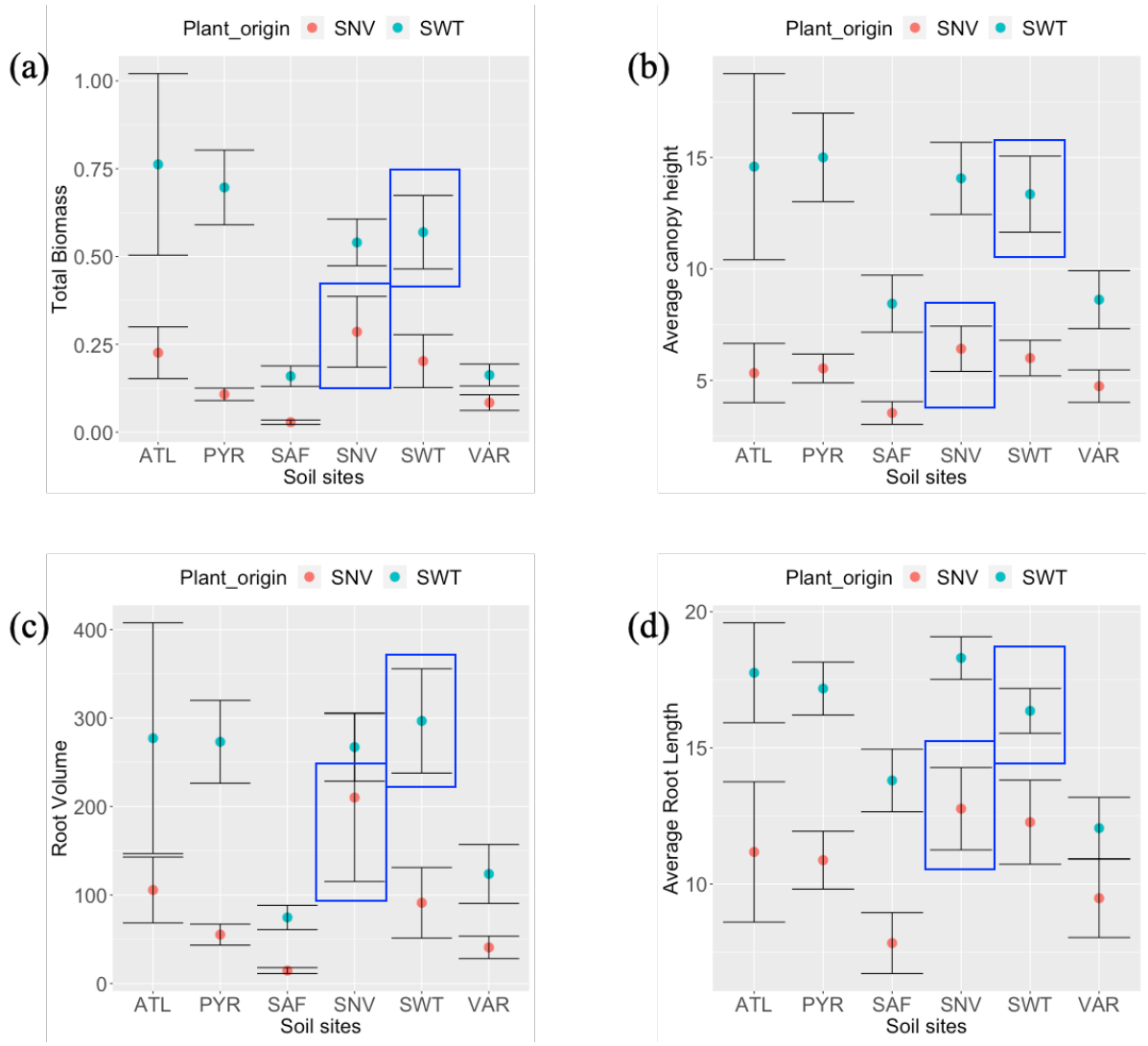


Figure 11. Plot of plants traits of different plant species on different soil sites: **a)** Total Biomass (g dry mass per pot, **b)** canopy height (cm per pot), **c)** root volume (cm^3 per pot) and **d)** root length (cm per pot). For SNV plant home soil is SNV only and all other soil sites are considered as away soil. 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 origin names are abbreviated so that SNV, and SWT respectively represent Sierra Nevada, and Alps. Data for home soil sites for the plant origin is highlighted in blue box. In all plots, the middle dot on the vertical line indicates the mean value of data for given plant traits. The top horizontal line indicates the value of standard error above the Mean Value. The bottom horizontal line indicates the value standard error below the Mean Value.

3.6 Plant growth performance depend on plant origin in different soil sites

Plant trait performance mean and one (1) standard deviation for two plant origins is plotted against the soil sites in Fig. 11. In general, all plants traits show higher growth in the Alps (SWT) plants compare to the Sierra Nevada (SNV) plants. It is also oblivious from the mean value of plant traits that SNV plants grow better in SNV soil sites compare to the other soil site. One doesn't see home soil benefit with the Alps plant (SWT) because most the plant traits mean is higher for other soil sites compare to SWT soil sites. If we compare the growth of Alps plant and Sierra Nevada plants in Pyrenees soil sites (PYR) and Svalbard soil site (SAF), growth trend is not similar. Alps plant growth is much better in PYR soil compared to SAF soil. On the other hand, Sierra Nevada plants have low growth in both soil sites (PYR and SAF).

3.7 Plant growth responses

First, we tried to understand the interaction of different plant traits (biomass, root length, canopy height and root mass fraction (RMF) (Pérez-Harguindeguy, Díaz et al. 2016) with soil sites, climate replicate and soil nutrients. The soil nutrient variables differed between the soil sites as noticed in the Fig. 7 (in appendix Fig. S5). Here for the LMM analysis I have considered four most significant nutrients (nitrogen, phosphorous, calcium, and carbon) decided by PCA plot, as fixed variable.

3.7.1 Plant traits performance on the soil sites

According to the linear mixed modelling (LMER) soil sites were significantly (P values <.001) and positively correlated with all plant traits parameters measured where plant origin is considered as a random variable (Table 5).

3.7.2 Plant traits performance on the climate replicate

Climate replicate (North and South) has mixed correlation with different plant traits parameters. Biomass is significantly correlated with the climate replicate ($P < 0.001$) and root length is marginal significant related ($P = 0.01$) (Table 5). Other two plant growth parameters, canopy height ($P = 0.1585$) and RMF (0.2779) are insignificantly dependent on the climate replicates.

3.7.3 Plant traits performance on different soil nutrients

Soil nitrogen shows significant correlation with the biomass ($P = 0.0004$) but the correlation turns insignificant for the other plant growth parameters (such as root length and canopy height)

(Table 5). In case of phosphorous canopy height shows significant correlation (P = 0.0035) but biomass (0.0148) and root length (0.0619) show marginal significant dependency.

Table 5: Linear mixed model ANOVA parameters (F Value and P_{lower}) for models predicting total plant mass on log_{10} scale, square root of root length, canopy height on log_{10} scale and square root of RMF. In this model soil sites, climate replicates along with main soil nutrient as a fixed variable, and plant origin (Sierra Nevada and Alps) as random variable. Marginally significant estimates ($p \leq 0.10$) are marked with one star (*), significant estimates ($p \leq 0.05$) are marked with two stars (**). Detail ANOVA data in appendix 9.

	Biomass (Log)		**Root Length (SQRT)**		**Canopy Height (Log)**		**RMF (SQRT)**	
Predictors ↓	F Value	P Lower	F Value	P Lower	F Value	P Lower	F Value	P Lower
Soil sites	37.4670	0.0000**	13.6290	0.0000**	19.6145	0.0000**	11.6804	0.0000**
Climate Replicate	29.7782	0.0000**	6.7817	0.0101**	2.0089	0.1585	1.1862	0.2779
Soil Nitrogen	13.846	0.0004**	0.4305	0.5128	0.2821	0.5961	2.9813	0.0863*
Soil Carbon	0.0008	0.9770	0.1044	0.7471	0.5824	0.4466	3.4639	0.0647
Soil Phosphorous	6.0826	0.0148**	3.5386	0.0619*	8.8285	0.0035**	0.0150	0.9025
Soil Calcium	0.7785	0.3790	0.0441	0.8339	0.5244	0.4701	0.0394	0.9105
Soil sites * Climate replicate	0.9442	0.4543	0.3280	0.8955	0.9892	0.4264	0.8108	0.5437

on the soil phosphorous. Carbon shows marginal significant correlation with RMF only and insignificant with all other plant growth parameters. Calcium shows insignificant relationship with all plant traits parameter and thus it will be not considered for further study.

Interaction term Soil sites and climate replicate

The interaction term soil site * climate replicate (in Table 5) does not seem to be significant predictor for the plant growth parameters because P value is always >0.1 and F is always less than one. So, this term will be removed from further analysis.

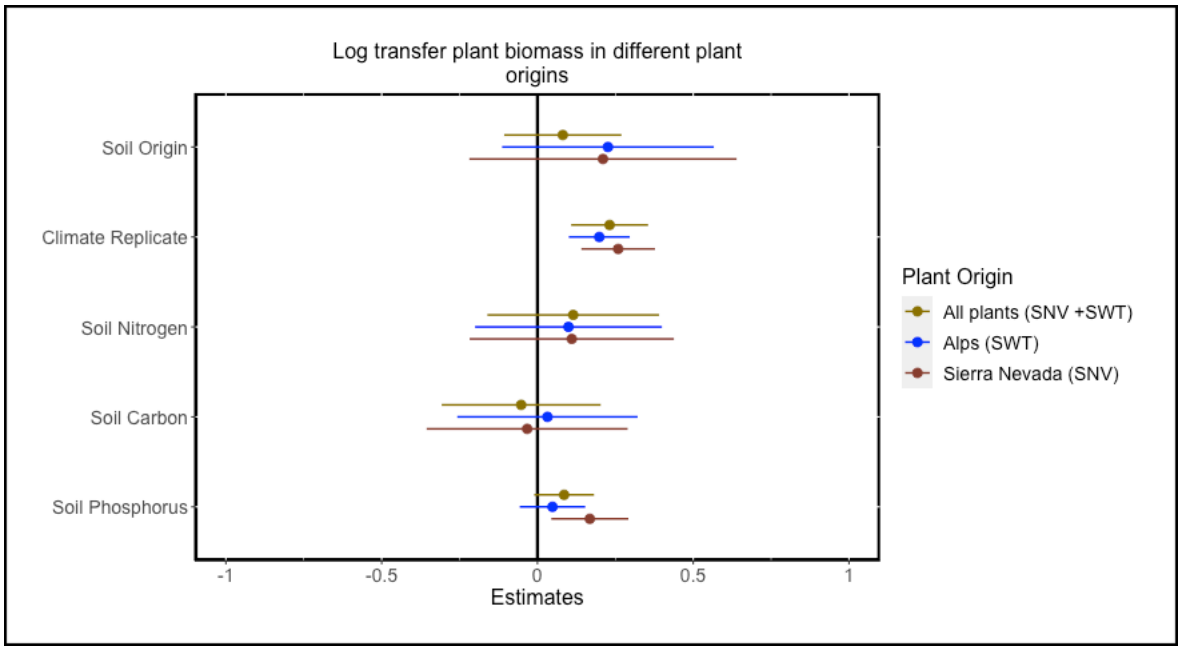


Figure 12: Estimate plots for Log10 transformed plant total biomass as response variables for different plants seed collection sites (Plants from both plant site, Alps, and Sierra Nevada). The intercept of the models (what variables within each predictor is being compared with) is whatever observation 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 'Away' (A comes before H in the alphabet). In case of soil carbon nutrient red lines indicates negative estimates, this mean plant biomass will decrease with the soil carbon. 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.

3.7.4 Plants growth in home versus away soil

The main model including all plant origins suggests that the soil origin is a not significant predictor ($p = 0.2493$) of biomass (see Table 6, Figure 12 and **Appendix, Table I** for details). This is also obvious from the fact that the estimate of soil origin in Figure 11 crosses the zero mark. But when we consider only the individual plant origins (SNV and SWT) in the model, then correlation of home vs away soil shows marginal significance ($P = 0.0717$) for Sierra Nevada (SNV) plants (see Figure 12, Table 6 and **Appendix, Table 1** for details).

3.7.5 Plants growth in home versus away climate

On the other hand, climate is significant predictor for biomass calculation in the main model with P_{values} is less than 0.001 (see Table 6, Figure 12 and **Appendix, Table I** for details). This is also obvious from the fact that the estimate of climate replicate in Figure 12 does not cross the zero mark and it is always in positive region. Similar relationship of climate is observed for

Table 6: Linear mixed model estimates and ANOVA parameters (F Value and P_{lower}) for models predicting total plant mass (in milligram) on Log scale for respectively the main model (include all plants from Sierra Nevada and Alps both) and the sub-models studying plant origins separately (Sierra Nevada and Alps). Marginally significant estimates ($p \leq 0.10$) are marked with one star (*), significant estimates ($p \leq 0.05$) 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, an antilog (0.08) (1.202 mg) higher total plant mass for plants grown in home relative to away soil). Estimates are displayed as Log10 of total biomass. Detail ANOVA data in appendix 9.

	Sierra Nevada (SNV)			**Alps (SWT)**			**Main Model (SNV+SWT)**		
Predictors ⬇	Estimate	F Value	P_{lower}	Estimate	F Value	P_{lower}	Estimate	F Value	P_{lower}
Soil origin (Home vs Away)	0.21	3.4135	0.0717*	0.23	1.0360	0.3142	0.08	1.3397	0.2493
Climate Replicate (Home vs away)	0.26	21.6052	0.0000**	0.20	17.6443	0.0001**	0.23	14.7515	0.0002**
Soil Nitrogen	0.24	13.2687	0.0007**	0.22	8.7548	0.0049**	0.26	6.2037	0.0140**
Soil Carbon	-0.00	0.1520	0.6986	0.00	0.0089	0.9253	-0.01	0.5002	0.4807
Soil Phosphorous	5.83	7.3345	0.0097**	1.67	0.8363	0.3653	2.96	3.0899	0.0812*

the individual plant origin (SNV and SWT) biomass calculation as well (see Figure 12, Table 6 and **Appendix, Table 1** for details).

3.7.6 Effects of Soil Nutrients

Among all soil nutrients, nitrogen shows significant predictor of main model (P = 0.0002) and phosphorous shows marginal significant predictor (P= 0.0812) (see Figure 12, Table 6 and **Appendix, Table 1** for details). Other soil nutrient such as carbon, and calcium are not significant predictors. For individual plant models, Nitrogen is significant predictor (P<0.001) for both plants but phosphorous is significant predictor in case of SNV (P = 0.0097) and insignificant predictor for the SWT plants (P = 0.3653).

4. Discussion

This study presents an experimental approach which involve natural field soil to analyse the PSF effect on the growth of grass and forbs in alpine region across a latitudinal gradient in Alps and Tundra. The results only partially supported the first hypothesis, there was positive growth in plant trait with respect to the soil origin ('Home' vs 'away'), but ANOVA parameters (F Value and P_{lower}) shows marginal significant correlation between the plant growth and soil origin. In all the plant species, plant growth was better in the home climate and there was clear trend in the magnitude of the correlation between the plant growth and the climate origin ('Home' vs 'away'), thus supporting our second hypothesis. The third and fourth hypothesis was also supported by the results which shows that plant growth is better explained in the combination of soil origin and climate origin together. Strong plant growth trend is observed for the 'home' soil and 'home' climate, and on the other hand growth was less in 'away' soil and 'away' climate combination. In support of the last hypothesis, there was clear plant origin impact in the magnitude of the correlation between the plant growth variation and the soil sites.

4.1 Plant growth in home versus away Soil

Enhanced growth in home soil compared to away soil overshadowed neutral and negative effects so that the net effect for all plants was positive. This suggest that positive plant-soil feedback is more common in home soils than in away soils. The results of current research, which focus on field type experiment, are consistent with previous findings that have demonstrated that home soil and/or home climate favour plant growth (Pernilla Brinkman, Van der Putten *et al*. 2010, van der Putten, Bardgett *et al.* 2013, Kulmatiski 2019). However, they are contradicting the consensus on negative PSF being more common than positive PSF (Klironomos 2002, Bever 2003, Kulmatiski and Kardol 2008). It is possible that negative PSF are over-represented in the literature, due to methodological issues in PSF research (Kulmatiski and Kardol 2008, Brinkman, Van Der Putten *et al*. 2010). Large uncertainties lie in the applicability of indoor experiment results to PSF in the field (Forero, Grenzer *et al*. 2019). Stress has been given on the experimental approach in case of plant soil feedback research (Kulmatiski, Beard *et al*. 2008, Pernilla Brinkman, Van der Putten *et a*l. 2010, Gundale, Wardle et al. 2019). Although appropriate study approach depends on research question (Brinkman, Van Der Putten *et al.* 2010), a number of studies are abandoning the traditional conditioning

phase study design with soil sterilization and reintroduction of soil inoculums, and are instead using intact field soils (Gustafson and Casper 2004, Bezemer, Lawson *et al.* 2006, Heinze, Sitte *et al.* 2016, Fry, Johnson *et al*. 2018).

Home advantage can be explained by the fact that abundance of soil organisms with a specific relationship to the plant in 'home' soil compare to away soil (Kulmatiski, Beard *et al*. 2008). There is a positive impact of home soil in the plant growth when comparing the home versus away soil, but there is obvious difference in extent of benefit of home soil because of plant origin. For Alps plants, the observed growth differences for plant performance parameters between home soil and away soil is less. This may be an effect of soil context specificity rather than generalizable Plant-soil feedback (PSF). There is home site advantage for the Sierra Nevada plants, and this can be SNV soils are deeper and greater structure and fewer rock fragments and are enriched with clay(Sánchez-Marañón, Delgado *et al*. 1996). These characteristics enhance the soil's ability to store nutrients and water. Home-site advantage proved more beneficial for growth of Sierra Nevada plant due to higher nutrient contents soil, for instance Atlas soil. Such a phenomenon of strong home soil advantage could be caused by more mutualist associations in home soil, aiding nutrient uptake (Bever, Dickie *et al*. 2010, Teste, Kardol *et al*. 2017), pathogen protection and abiotic stress tolerance (Sikes 2010, Aldorfová and Münzbergová 2019) or plant-mycorrhizal association (Sikes 2010, Mohan, Cowden *et al.* 2014).

Growth of all plant species is lowest in the Svalbard soil site because Svalbard soils inherent properties such as clay-like, compact structure that absorbed less water and dried out faster than the other soil types in the experiment (Sakata Bekku, Nakatsubo *et al.* 2018). In my study, biomass of plants grown in home soil was significantly different from biomass of plants grown in away soil. It could indicate that the feedback effects were species-specific, or that they were present more in 'Home as compared to the 'Away' soil (Kulmatiski, Beard *et al.* 2008).

4.2 Plant growth in home versus away climate

Plant growth should be benefited by the longer photoperiod as well as increased temperature (Adams and Langton 2005, Wu, Dijkstra *et al*. 2011, van der Putten, Bradford *et al*. 2016). Alps and Sierra Nevada plant species performed best in the home climatic, i.e. south climate, conditions even the photoperiod was shorter compare to away north climate with 24 hrs of photoperiod. The plants got adapted with their natural environment and grow better in the home climate (Duell, Zaiger *et al.* 2019). If grassland species react to adjusted photoperiod only, then

all plants in this study may 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 of north, resulting in decreased growth in away climate. Such environmental adaptations to photoperiod and temperature could explain why plants in this experiment grew best in light and temperature conditions resembling to the home climate.

These findings suggest that climatic heterogeneity could limit plant growth when plants are moved from one place to another. Interestingly, more than half of the species in this experiment occur in both arctic tundra grasslands and temperate alpine grasslands (Tackenberg 2019), and are present in both tundra grasslands and temperate grasslands included in this study. Thus, our findings suggest that individuals of one species respond differently to climatic stimuli if found in different climatic regimes.

4.3 Soil nutrients

Plants grow best in nutrient rich soils and thus, soil nutrient is a well define predictor for plant performance. However, research has found that PSF disappear when nutrient levels are strongly increased (in 't Zandt, van den Brink *et al*. 2019). This did not happen in our experiment. Soil nitrogen is strongly correlated to the growth of all plants and phosphorous has strong impact on the Sierra Nevada plants, but no effect was documented from other soil nutrients included in the analyses. Pyrenees soil contain quite high phosphorous and moderate nitrogen compared to the Alps soil. Maximum growth of total biomass is observed for the Alps origin plants in the Pyrenees soil. Not only biomass other plants traits (canopy height, and root length) show relatively better development in Pyrenees soil compared to the home soil which is Alps soil (SWT). For the Sierra Nevada soil origin, carbon content is quite high, but we do not see any correlation of plant traits growth of Sierra Nevada with carbon. This gives the feeling that other biotic and abiotic factors are helping more in the plant growths.

4.4 Growth of forb and grass communities in grasslands

To date, there appears to be a stronger focus on plant soil feedback in grassland ecological studies (Kardol, Bezemer *et al.* 2009, Harrison and Bardgett 2010, Rinella and Reinhart 2018, De Long, Heinen *et al*. 2019). However, and interestingly, greenhouse based experimental approaches are commonly included into PSF-based ecological studies, such as soil sterilization and conditioning, but fewer field studies (Kulmatiski, Beard *et al*. 2008). In this research work, I used the field soils from different latitudinal gradient of European alpine reason for the growth of grass and forb. It is quite interesting to see that different species of grass and forbs have

positive growth in home soil and home climate. There is better growth of Alps grass and forb species in different soil sites compare to home soils. It is also possible that the growth of plants from Alps could be affected by differential responses of graminoids and forbs, as detected by other studies (Cortois 2016; Bardgett 2017; Bennett *et al*. 2017). A more detail study is required to understand the effect of functional group in different soil sites.

4.5 Suggestions for future research

1. Palozzi & Lindo (2018) reported that the better performance in the home soil can be facilitated by the presence of conspecific litter and decomposers promoted by conspecific plants in the field. While our plants were not grown long enough to produce substantial amounts of litter for the soil decomposer community, feedbacks from litter produced in the conditioning phase might have benefitted the plants grown in their home soils. So it is worthy to try similar PSF experiment in the field environment for longer time where litter can be one of the predictor.
2. Change in the climatic affects soil microbes and soil microbe-plant interactions directly and indirectly (Classen, Sundqvist *et al*. 2015), but this aspect of the PSF is not part my research work. This can be exciting questions and areas for future research, what changes in these interactions due to temperature and photoperiod together, as it considered in my current work, may have on the co-existence among neighbours, and control grass and forbs populations in grassland.
3. Another important topic which required further research attention is nutrient acquisition strategies for the different plant species, grass or forbs, in the field experimental condition of soil origins and climate origins.
4. Plant-soil feedbacks have become a general mechanism of plant coexistence and abundance. Our PSF experiments have been performed with field soil in a pot with only two-plant community in a place. It is important to test whether or not increasing the number of plants (forbs or grass) or densifying the neighbour with other plant species going to affect the PSF values at similar magnitude or PSF will be significantly different and positively correlated with field measured PSFs, we compared PSF values from five different studies that measured PSF values in both greenhouse and field conditions.
5. I also observed that plant origin has role to play in deciding the strength of PSF in these experiments. But plant origin was not considered in detail here. Future work is required to understand the importance of plant origin in PSF direction and strength determination.

5 Conclusions

My experiment using field soil demonstrate that such an experimental design can successfully allow us to examine how plant soil feedback effects the plant species, forb and grass, in the grassland in the natural setting. The design described here could be applied across different grassland to understand about how different soil sites affect the development of plant communities and there-after plant community composition and performance.

All plants traits (biomass, root length, canopy height, root volume and root mass factor) showed better growth performance in the home soil compared to the away soil. Individual plant origins (SNV and SWT) showed varying growth trends in home and in away soil for different plant traits. However, effects for plants growth parameters benefitting from home soil were much stronger than those of plants traits benefitting from away soil. Therefore, the net effect across plants growth is positive in home soil.

Plants traits showed similar growth trends in respect to climate parameter, home and away. All the plant traits generally advanced from increasing in light and temperature conditions resembling their home climate. This effect was detected for both individual plants origin.

My results also highlight the importance of considering both home soil and home climate for the growth grass and forbs in the grassland.

My results further show clearly that these plant–soil feedback effects depend on plant origin of the species. Different soil sites might have not the same impact on two plant origins (SNV and SWT) because of different soil biota requirement of the plant species. Thus, it is important to consider plant origin as a predictor to analyse the plant growth performance of grass (or forb) species in soil sites.

It can be concluded safely that a number of experimental factors such as soil origin, climate and plant origin might affect plant soil feedbacks in the response phase in the field environment. In future for better understanding of ecosystem, more field type experiment is required to evaluate the importance of biotic and abiotic interactions over long periods between alpine grassland plant species and soil origin.

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Appendix

Appendix-1: R analysis

1. Soil PCA calculation and plotting:

```
soiltbl1.pca = prcomp(soiltbl1[,-(1:3)], center = TRUE,scale. = TRUE)

ggbiplot(soiltbl1.pca, groups = as.factor(soiltbl1$soil), varname.size = 4, varname.adjust =
1.5) + theme(legend.position = "right", axis.text = element_text(size = 16), axis.title =
element_text(size = 16), legend.text = element_text(size = 18), legend.title =
element_text(size = 18))
```

2. Linear mixed model for total biomass (in Log), root length (in square root), canopy height (in Log), and rmf (in square root) with predictor as Soil sites, Climate replicate and soil nutrient. Plant origin is considered as random variable

```
b0.plant.mass <- lmer(logmass ~ soil * Climate_replicate +  Soil_N + Soil_C + Soil_P +
Soil_Ca +  (1|Plant_origin), data=data_merge1, REML=F)

b0.plant.rootlength <- lmer(sqrtrootlength ~ soil * Climate_replicate +  Soil_N + Soil_C +
Soil_P + Soil_Ca +  (1|Plant_origin), data=data_merge1, REML=F)

b0.plant.canopy <- lmer(logcanopy ~ soil * Climate_replicate +  Soil_N + Soil_C + Soil_P +
Soil_Ca +  (1|Plant_origin), data=data_merge1, REML=F)

b0.plant.rmf <- lmer(sqrtrootrmf ~ soil * Climate_replicate +  Soil_N + Soil_C + Soil_P +
Soil_Ca +  (1|Plant_origin), data=data_merge1, REML=F)
```

3. Linear mixed model for total biomass (in Log) for plant origins, with predictor as Soil origin, Climate origin and soil nutrient. Soil sites/subsites is considered as random variable.

```
b0.plant.all <- lmer(logmass ~ homevsaway.soil + homevsaway.climate +

                Soil_N + Soil_C + Soil_P +  (1|soil/Subsite), data=data_merge1, REML=F)

b0.plant.swt <- lmer(logmass ~ homevsaway.soil + homevsaway.climate +

                  Soil_N + Soil_C + Soil_P +  (1|soil/Subsite), data=data_scale,
                REML=F,subset = Plant_origin==c("SWT"))

b0.plant.snv <- lmer(logmass ~ homevsaway.soil + homevsaway.climate +

                Soil_N + Soil_C + Soil_P +  (1|soil/Subsite), data=data_scale,
                REML=F,subset = Plant_origin==c("SNV"))
```

4. ANOVA function

```
pamer.fnc(b0.plant.swt)

pamer.fnc(b0.plant.snv)

pamer.fnc(b0.plant.all)
```

5. Print regression models of LMER analysis

```
tab_model(b0.plant.all, b0.plant.swt, b0.plant.snv, transform = NULL, dv.labels = c("Main
          Model", "Alps (SWT)", "Sierra Nevada (SNV)"), pred.labels = c("Intercept",
          "Soil Origin", "Climate", "Soil Nitrogen", "Soil Carbon", "Soil phosporus"), title
          = "Linear Mixed Model summary for Plant origin as random variable", string.ci =
          "95% CIs", string.p = "p-values")
```

Appendix-2: Histogram plot of plant traits data

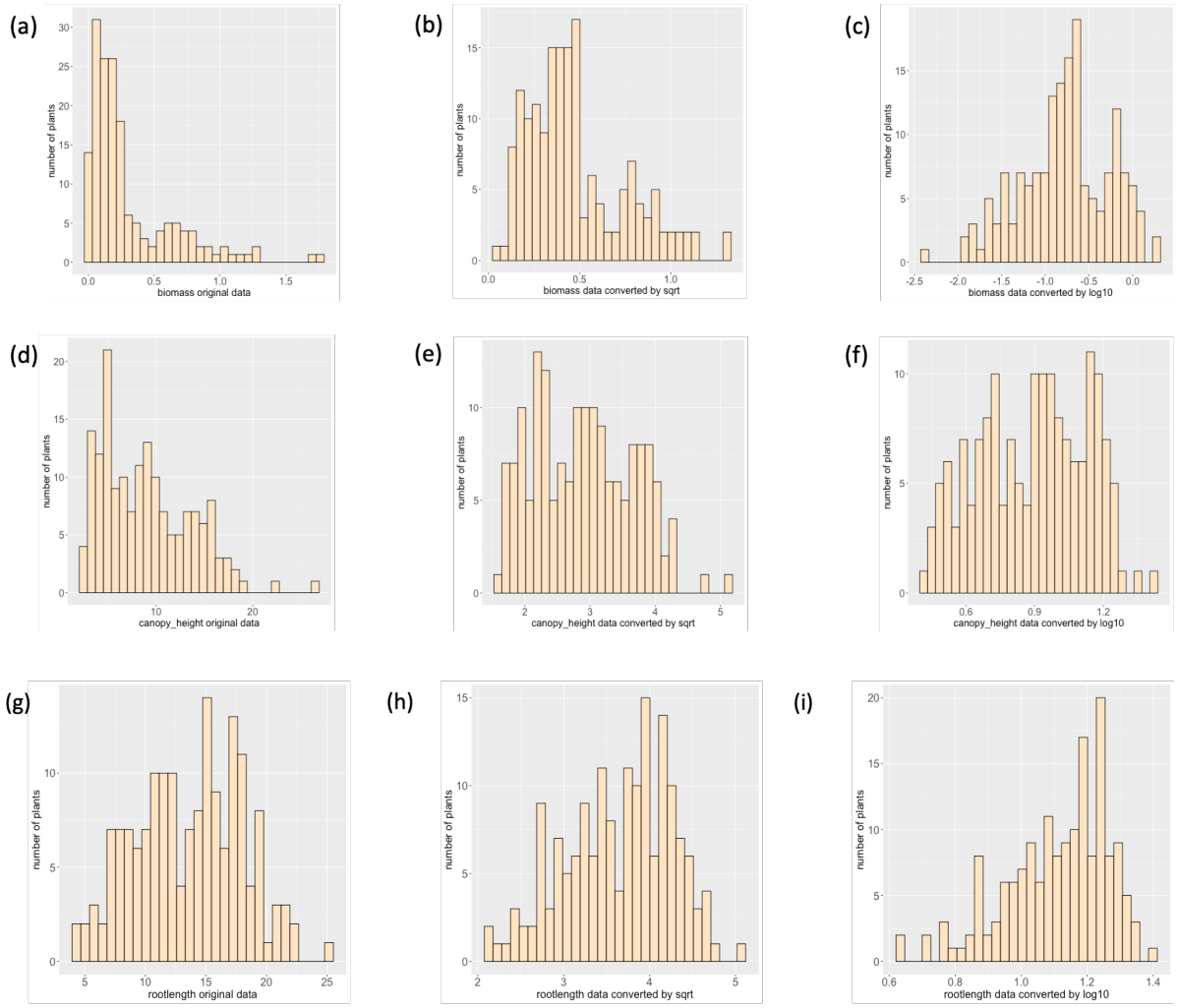

Figure S1: Average value of plant traits per plot is plotted here and for normalization of data square root and log10 conversion was performed. **a)** is total biomass value, **b)** and **c)** are square root and log10 of the total biomass respectively. **d)** is canopy height value, **e)** and **f)** are square root and log10 of the canopy height respectively. **g)** is root length value, **h)** and **i)** are square root and log10 of the canopy height respectively.

Appendix-3: Mean plot for plant origin and soil origin together for plant traits

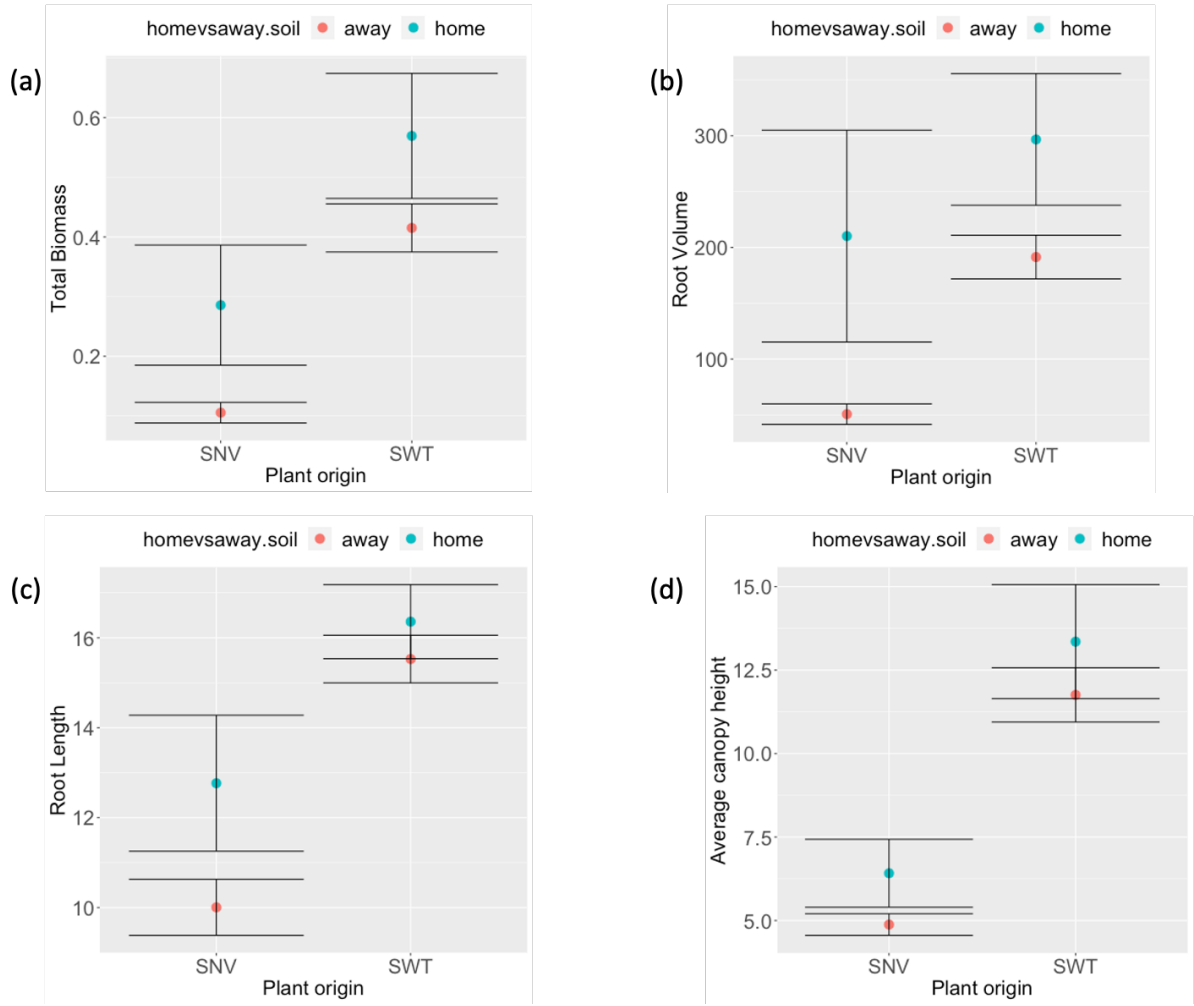

Figure S2. Different plant traits parameters compared for home soil vs away soil for both plants origin (SNV and SWT) separately: **(a)** total biomass (g dry weight) ±SE, **(b)** root volume (mm^3) ±SE, **(c)** root length (cm) ±SE, and **(d)** canopy height (cm) ±SE. Home soil shows better performance for all parameters compare to away. Plant origin names are abbreviated so that SNV, and SWT respectively represent Sierra Nevada, and Alps.

Appendix-4: Plant origin and climate origin together for plant traits

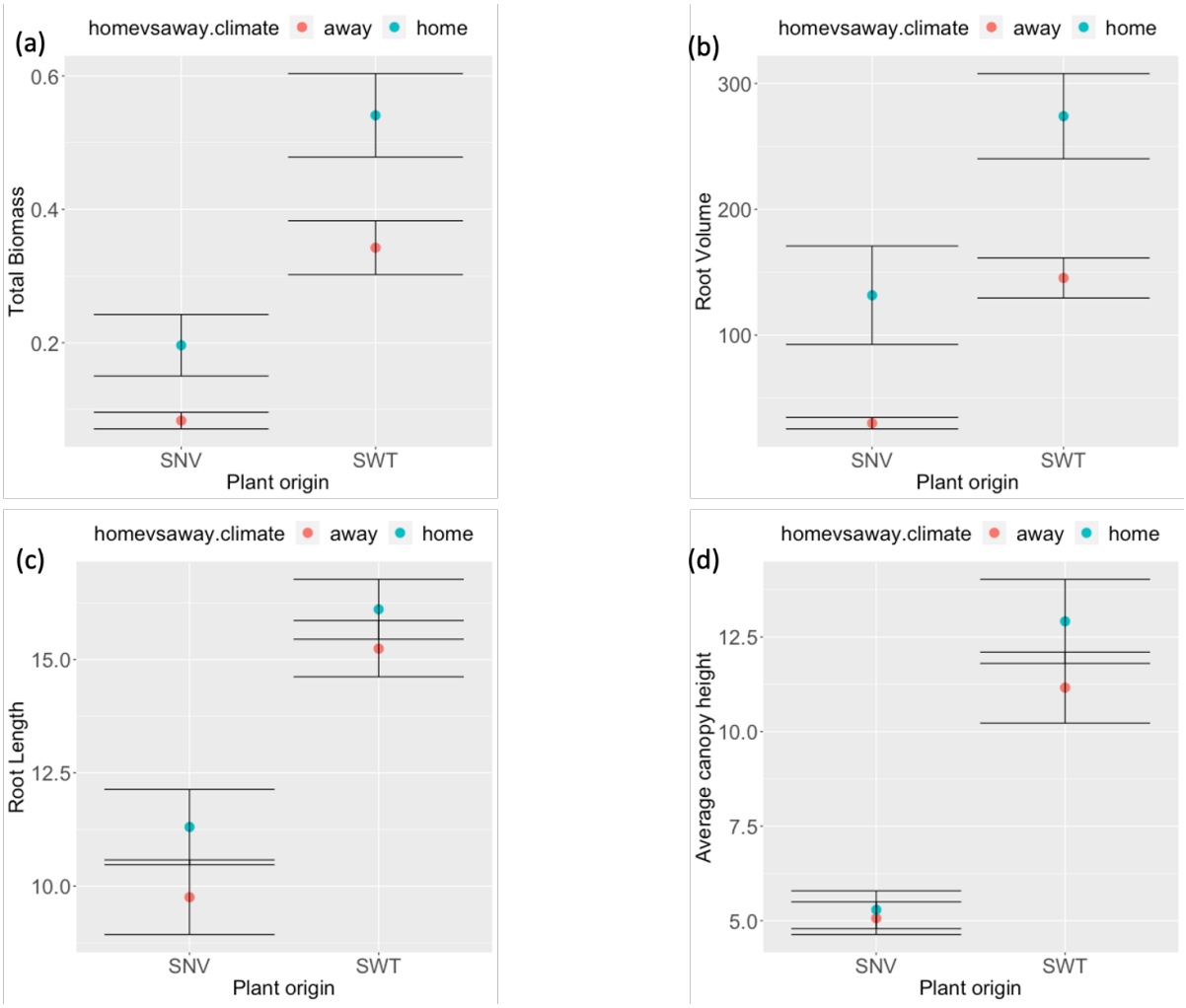

Figure S3. Different plant traits parameters compared for home climate and away climate for both plants origin (SNV and SWT) separately: **(a)** dry total biomass (g dry weight) ±SE, **(b)** root volume (mm^3) ±SE, **(c)** root length (cm) ±SE, and **(d)** canopy height (cm) ±SE. Home climate shows better performance for all parameters compare to away for all plant traits. Plant origin names are abbreviated so that SNV, and SWT respectively represent Sierra Nevada, and Alps.

Appendix-5: Box plot for plant origin and soil origin together for plant traits

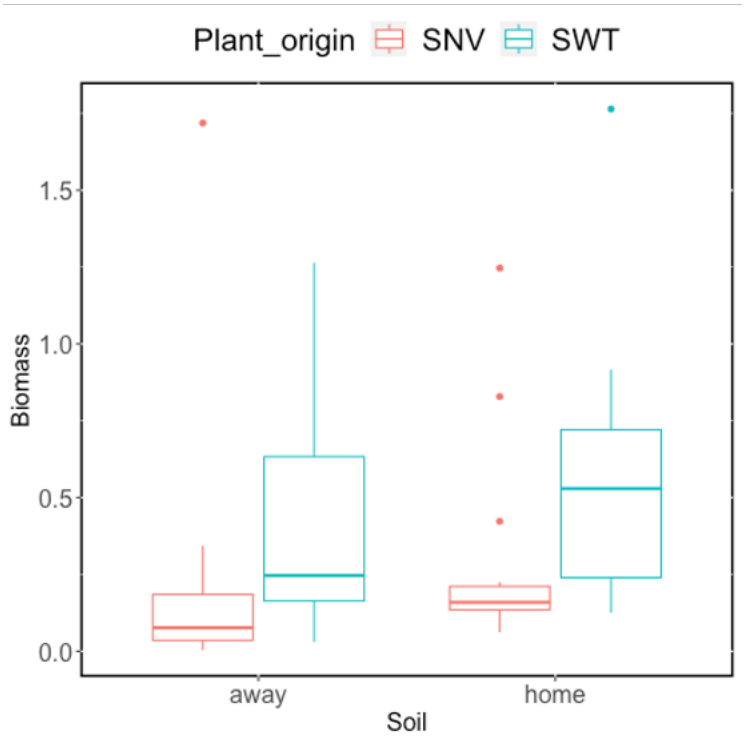

Figure S4. Boxplot of total biomass in 'Home' and 'Away' soil.

Appendix-6: Mean plot for soil nutrients against soil sites

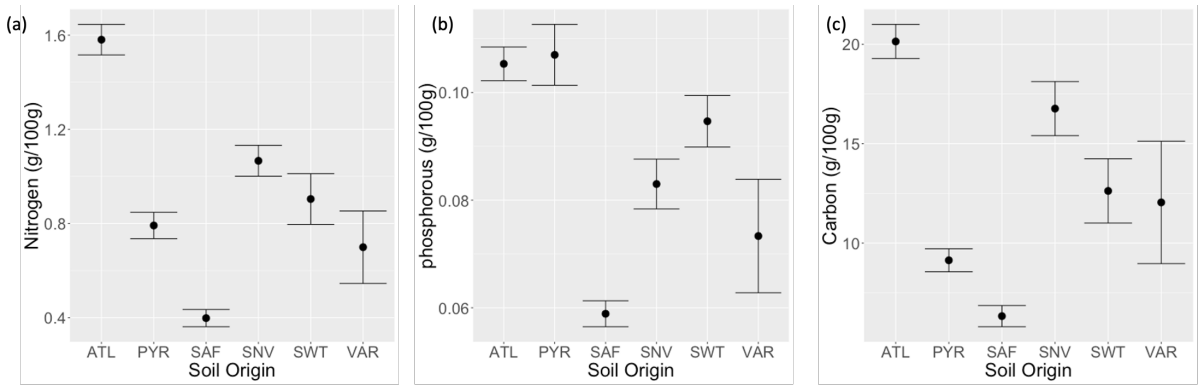

Figure S5: Soil nutrients content (g/100g) in different soil sites included in the experiment: **a)** nitrogen, **b)** phosphorous and **c)** carbon. Soil origin names are abbreviated so that ATL, SNV, PYR, SWT, VAR and SAF respectively represent Atlas, Sierra Nevada, Pyrenees, Alps, Varanger Peninsula and Svalbard. This data was provided from my project partner at the CEBAS-CSIC ionomics lab (Murcia, Spain).

Appendix-7: Summary for linear mixed model for different plant origin

Linear Mixed Model summary for Plant origin as random variable

	Main Model			Alps (SWT)			Sierra Nevada (SNV)		
Predictors	*Estimates*	*95% CIs*	*p-values*	*Estimates*	*95% CIs*	*p-values*	*Estimates*	*95% CIs*	*p-values*
Intercept	-1.24	-1.52 – -0.96	**<0.001**	-0.97	-1.28 – -0.67	**<0.001**	-1.81	-2.13 – -1.49	**<0.001**
Soil Origin	0.08	-0.11 – 0.27	0.394	0.23	-0.11 – 0.57	0.189	0.21	-0.22 – 0.64	0.332
Climate	0.23	0.11 – 0.36	**<0.001**	0.20	0.10 – 0.30	**<0.001**	0.26	0.14 – 0.38	**<0.001**
Soil Nitrogen	0.26	-0.36 – 0.87	0.412	0.22	-0.44 – 0.89	0.510	0.24	-0.48 – 0.97	0.505
Soil Carbon	-0.01	-0.04 – 0.03	0.687	0.00	-0.04 – 0.05	0.826	-0.00	-0.05 – 0.04	0.839
Soil phosporus	2.96	-0.37 – 6.29	0.081	1.67	-1.97 – 5.32	0.363	5.83	1.54 – 10.12	**0.008**
Random Effects									
σ^2	0.16			0.05			0.07		
τ_{00}	$0.00_{\text{Subsite:soil}}$			$0.02_{\text{Subsite:soil}}$			$0.02_{\text{Subsite:soil}}$		
	0.03_{soil}			0.02_{soil}			0.02_{soil}		
ICC	0.15			0.42			0.38		
N	6_{Subsite}			6_{Subsite}			6_{Subsite}		
	6_{soil}			6_{soil}			6_{soil}		
Observations	167			85			82		
Marginal R^2 / Conditional R^2	0.167 / 0.293			0.310 / 0.602			0.476 / 0.674		

Appendix-8: Summary for linear mixed model for different Soil

Linear Mixed Model summary for Soil site and Climate replicate interaction for total Biomass (log)

	All Plants Biomass		
Predictors	*Estimates*	*95% CIs*	*p-values*
Intercept	-1.67	-2.48 – -0.85	**<0.001**
Soil (PYR)	0.64	0.01 – 1.28	**0.045**
Soil (SAF)	0.14	-0.53 – 0.82	0.677
Soil (SNV)	0.60	-0.04 – 1.25	0.064
Soil (SWT)	0.61	-0.03 – 1.26	0.061
Soil (VAR)	0.31	-0.37 – 0.98	0.370
Climate	0.77	0.17 – 1.37	**0.012**
Soil Nitrogen	0.19	-0.29 – 0.67	0.442
Soil Carbon	0.00	-0.03 – 0.03	0.921
Soil phosporus	2.62	0.25 – 4.99	**0.031**
Soil calcium	-0.06	-0.21 – 0.08	0.384
Soil (PYR)*climate	-0.54	-1.17 – 0.09	0.090
Soil (SAF)*climate	-0.64	-1.26 – -0.01	**0.046**
Soil (SNV)*climate	-0.55	-1.18 – 0.07	0.083
Soil (SWT)*climate	-0.54	-1.17 – 0.08	0.089
Soil (VAR)*climate	-0.47	-1.10 – 0.16	0.142
Random Effects			
σ^2	0.08		
$\tau_{00\ Plant\_origin}$	0.08		
ICC	0.52		
$N_{\ Plant\_origin}$	2		
Observations	167		
Marginal R^2 / Conditional R^2	0.414 / 0.717		

Appendix-9: Analysis of variance (ANOVA) table for linear mixed model

Table S1: Analysis of variance (ANOVA) table for the linear mixed effects model with soil sites as random variable and interaction term of soil sites and climate replicates

Biomass (log)

	npar	Sum Sq	Mean Sq	F value	upper.den.df	upper.p.val	lower.den.df	lower.p.val	expl.dev.(%)
soil	5	13.1808	2.6362	13.629	151	0	149	0	21.0856
Climate_replicate	1	1.3117	1.3117	6.7817	151	0.0101	149	0.0101	2.0984
Soil_N	1	0.0833	0.0833	0.4305	151	0.5128	149	0.5128	0.1332
Soil_C	1	0.0202	0.0202	0.1044	151	0.7471	149	0.7471	0.0323
Soil_P	1	0.6844	0.6844	3.5386	151	0.0619	149	0.0619	1.0949
Soil_Ca	1	0.0085	0.0085	0.0441	151	0.8339	149	0.8339	0.0137
soil:Climate_replicate	5	0.3172	0.0634	0.328	151	0.8955	149	0.8955	0.5074

Root Length (Root square)

	npar	Sum Sq	Mean Sq	F value	upper.den.df	upper.p.val	lower.den.df	lower.p.val	expl.dev.(%)
soil	5	14.2547	2.8509	37.467	151	0	149	0	33.0768
Climate_replicate	1	2.2659	2.2659	29.7782	151	0	149	0	5.2578
Soil_N	1	1.0108	1.0108	13.2846	151	4e-04	149	4e-04	2.3456
Soil_C	1	1e-04	1e-04	8e-04	151	0.977	149	0.977	1e-04
Soil_P	1	0.4628	0.4628	6.0826	151	0.0148	149	0.0148	1.074
Soil_Ca	1	0.0592	0.0592	0.7785	151	0.379	149	0.379	0.1375
soil:Climate_replicate	5	0.3592	0.0718	0.9442	151	0.4542	149	0.4543	0.8336

Canopy Height (log)

	npar	Sum Sq	Mean Sq	F value	upper.den.df	upper.p.val	lower.den.df	lower.p.val	expl.dev.(%)
soil	5	1.4517	0.2903	19.6145	151	0	149	0	16.0169
Climate_replicate	1	0.0297	0.0297	2.0089	151	0.1584	149	0.1585	0.3281
Soil_N	1	0.0042	0.0042	0.2821	151	0.5961	149	0.5961	0.0461
Soil_C	1	0.0086	0.0086	0.5824	151	0.4466	149	0.4466	0.0951
Soil_P	1	0.1307	0.1307	8.8285	151	0.0035	149	0.0035	1.4418
Soil_Ca	1	0.0078	0.0078	0.5244	151	0.4701	149	0.4701	0.0856
soil:Climate_replicate	5	0.0732	0.0146	0.9892	151	0.4264	149	0.4264	0.8078

RMF (Root square)

	npar	Sum Sq	Mean Sq	F value	upper.den.df	upper.p.val	lower.den.df	lower.p.val	expl.dev.(%)
soil	5	0.3038	0.0608	11.8517	151	0	149	0	24.5671
Climate_replicate	1	0.0062	0.0062	1.2016	151	0.2748	149	0.2748	0.4981
Soil_N	1	0.0159	0.0159	3.1044	151	0.0801	149	0.0801	1.287
Soil_C	1	0.0179	0.0179	3.4922	151	0.0636	149	0.0636	1.4478
Soil_P	1	1e-04	1e-04	0.0142	151	0.9053	149	0.9053	0.0059
Soil_Ca	1	0.014	0.014	2.7258	151	0.1008	149	0.1008	1.1301
soil:Climate_replicate	5	0.0212	0.0042	0.8267	151	0.5325	149	0.5326	1.7136

Table S2. Analysis of variance (ANOVA) table for the linear mixed effects model with soil sites/subsite as random variable and additive term of plant origin, climate replicate and soil nutrients

Sierra Nevada plants (SNV)

	npar	Sum Sq	Mean Sq	F value	upper.den.df	upper.p.val	lower.den.df	lower.p.val	expl.dev.(%)
homevsaway.soil	1	0.2354	0.2354	3.4135	76	0.0686	42	0.0717	1.3063
homevsaway.climate	1	1.4898	1.4898	21.6052	76	0	42	0	8.2682
Soil_N	1	0.9149	0.9149	13.2687	76	5e-04	42	7e-04	5.0779
Soil_C	1	0.0105	0.0105	0.152	76	0.6978	42	0.6986	0.0582
Soil_P	1	0.5057	0.5057	7.3345	76	0.0084	42	0.0097	2.8069

ALPs plants (SWT)

	npar	Sum Sq	Mean Sq	F value	upper.den.df	upper.p.val	lower.den.df	lower.p.val	expl.dev.(%)
homevsaway.soil	1	0.0521	0.0521	1.036	79	0.3119	45	0.3142	0.4015
homevsaway.climate	1	0.8868	0.8868	17.6443	79	1e-04	45	1e-04	6.8382
Soil_N	1	0.44	0.44	8.7548	79	0.0041	45	0.0049	3.393
Soil_C	1	4e-04	4e-04	0.0089	79	0.9251	45	0.9253	0.0034
Soil_P	1	0.042	0.042	0.8363	79	0.3632	45	0.3653	0.3241

All Plants (SWT + SNV)

	npar	Sum Sq	Mean Sq	F value	upper.den.df	upper.p.val	lower.den.df	lower.p.val	expl.dev.(%)
homevsaway.soil	1	0.2142	0.2142	1.3397	161	0.2488	126	0.2493	0.4971
homevsaway.climate	1	2.3591	2.3591	14.7515	161	2e-04	126	2e-04	5.4742
Soil_N	1	0.9921	0.9921	6.2037	161	0.0138	126	0.014	2.3022
Soil_C	1	0.08	0.08	0.5002	161	0.4804	126	0.4807	0.1856
Soil_P	1	0.4941	0.4941	3.0899	161	0.0807	126	0.0812	1.1466