The effects of climate on resource allocation and traits of alpine and boreal herbaceous plants

Master of Science in Biology
Biodiversity, Evolution and Ecology
University of Bergen – Department of Biological Sciences

Lasse Flathaug Søgaard

June 2020

Acknowledgements

First, I would like to thank my supervisors Ragnhild Gya, Joachim Töpper and Vigdis Vandvik, with whose guidance and support made this project possible. I would also like to thank Gunvor Skjelstad, for helpful input on the project and help in the field. A big thanks to Madeleine Dybedahl for providing data for one of the species. Additionally, I want to thank Josh Lynn for help with the statistics and the EECRG for making me feel included and for helpful inputs on the project.

Further, I would also like to thank the SeedClim project and Norwegian research council for funding this project.

Finally, I would like to thank Åshild Sønnesyn Willmann and my family and friends for love and support through the entire process.

Abstract

Climate is rapidly changing, and species are expected to change their ranges to where conditions are now more suitable. Which lowland species that range shift into alpine environments could have potentially different effects of biodiversity and ecosystem functioning. The potential effect of range shifts is dependent on resource allocation and trait response as these can affect the biotic interactions when species meet in a new environment. Furthermore, precipitation has the potential to enhance or mitigate the dynamic between competition and facilitation. This study was conducted along a natural temperature and precipitation gradient in western Norway, six species was sampled. Three sets of species groups were collected along the precipitation gradient, one set of alpine species, one set of lowland species with trait values similarly conservative as in the alpine community ('extant') and the other set of lowland species with more acquisitive trait values than common in alpine communities ('novel'). I found that novel species are generally taller and have a higher biomass compared to the alpine species. In addition, the effects of precipitation on aboveground biomass, vegetative height and number of leaves was generally negative and response varied between the species groups. Moreover, allocation to aboveground decreased in both extant species. Gaining further knowledge on how potential competitor-identity and eventual interactions is important for further predicting how climate change and the indirect effects influence alpine communities.

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Introduction

The biodiversity and functioning of ecosystems are governed by the interplay between the organisms and their environment, including climate, and a change in climate will cause a change in species composition and ecosystem functioning (Dormann & Woodin, 2002; Hooper et al., 2005). To date, the global mean temperature has increased by about 1°C since pre-industrial levels with 8 out of the 10 warmest years ever recorded being in the last decade (NOAA, 2020). Climate projections show that the global mean temperature is likely to increase by 1.5°C within 2052 and that both the amount and seasonality of precipitation is subject to change in several regions (IPCC, 2018). The most severe climatic changes will happen in high latitudes and altitudes, although with regional variation in both magnitude and, for precipitation, the direction of the response (IPCC, 2018).

In alpine and arctic ecosystems, climatic conditions are dominant factors in shaping communities since these factors, and especially temperature, are usually limiting biological activity and rates such as growth and productivity (Billings & Mooney, 1968; Hooper et al., 2005). Climate change is also more drastic in alpine and arctic communities, and so the effects here are further amplified (Bjorkman et al., 2018; Dormann & Woodin, 2002; Elmendorf et al., 2012). For instance, the species richness on mountain summits has increased dramatically over the past 100 years, where climatic warming is thought to be the main driver (Steinbauer et al., 2018). In addition, climatic warming has shown to have indirect negative effects on temporal stability of biomass (Ma et al., 2017), a shift from facilitation to competition at higher elevations (Olsen et al., 2016), decreased species richness (Klein et al., 2004), and negative effect on early seedling survival (Shevtsova et al., 2009; Töpper et al., 2018). The impact on survival can also be attributed to the increased dominance of grass and graminoids over forbs with increasing temperature (Ma et al., 2017; Olsen et al., 2016). Climate is not the only global change driver operating in the alpine however, and the observed advancement of the tree line and shrubification in many low and mid-alpine regions, such as Scandinavia, has been shown to be mainly due land-use changes and abandonment of extensive land-use practices such as mountain summer farms, with increased temperature contributing to shifting climatic niches for trees and shrubs to higher elevations (Bryn et al., 2018; Bryn & Potthoff, 2018).

The relationship between precipitation change and ecosystem functioning is still less known (Moles et al., 2014; Wright et al., 2004), especially in alpine and arctic communities (Elmendorf et al., 2012). Regarding biodiversity, increased precipitation may lead to less biological constraints and higher productivity, where shrubs, grass and graminoids increase in abundance and mosses, lichens and forbs suffer (Klanderud et al., 2015; Ma et al., 2017; Walker et al., 2006). Understanding the impacts on these functional groups is important for our ability to predict future changes on crucial ecosystem services such as carbon storage (Skarpaas et al., 2016).

Resource allocation

Plants are sessile and modular organisms, and thus a major way in which plants respond to their environment is by changing the allocation of accessible resources to different functions and structures. These responses have an important role in ecosystem carbon dynamics, as plant growth and allocation affect carbon flow through the system. Plants take up energy, carbon dioxide, water and nutrients from their surroundings and convert these resources to structures and components of their bodies. As plants are modular organisms capable of allocating resources, these resources can be moved within the plant to where they most efficiently contribute to increase fitness, e.g. into organs or processes that increase survival, growth or reproduction (Brown et al., 2004). A classical way of quantifying how resources are allocated is through "shoot:root" ratios. This ratio provides important information on how plants partition resources to belowground functions like structural support, storage organs and absorption, and aboveground functions, mainly photosynthesis and reproduction (Mokany et al., 2006). A more detailed approach to how plants partition resources categorizes the plant biomass into several categories based on differences in function (Poorter & Nagel, 2000; Skarpaas et al., 2016). This is broadly classified as; **roots** for carbon storage or water and nutrient extraction, **leaves** for increased photosynthetic rate, **stems** for light and reproductive competition or to **reproductive organs** to increase recruitment, dispersal and genetic recombination. A common approach to explain and predict a plant's growth is based on optimal partitioning theory, which states that plants will invest resources into organs that capture the most limiting resource (Bloom et al., 1985). Thus, under water limitation the optimal response is to increase allocation to roots while under light limitation the optimal response is an increase in allocation to leaf and stem structures (Poorter &

Nagel, 2000; Skarpaas et al., 2016). Resource allocation can be considered a trade-off as investment in aboveground biomass comes at the cost of reduced belowground biomass, mainly stem vs. roots in light limitation (Poorter & Nagel, 2000), and leaves vs. roots with water limitation (Poorter & Nagel, 2000; Skarpaas et al., 2016). More precipitation and higher temperatures may lead to less constraints on biological reactions and more resources can thus be invested into reproduction (Moles et al., 2014; Skarpaas et al., 2016), although evidence for this is mixed (Meineri et al., 2014; Ying et al., 2018). In addition, allocations to different plant parts or functions are not necessarily mutually exclusive. For example, allocation to stems that carry both leaves and flowers would support both vegetative growth in terms of light competition and survival (Gruntman et al., 2017; Meineri et al., 2014), and reproduction by making the flower more visible to pollinators (Fornoff et al., 2017; Klanderud & Totland, 2005). As for roots, a plant can invest in carbon storage in the roots one year to use these resources for reproduction the next year (Chiariello & Roughgarden, 1984).

In addition to the broad patterns of allocation of biomass to different plant organs, plants have different physiological and morphological adaptations that optimize their fitness in their respective environments. One way these adaptations are expressed is through traits, which are any measurable features that impact plants in terms of growth, reproduction and survival (Violle et al., 2007). Different traits are coupled to different strategies in terms of resource acquisition rates, where conservative and acquisitive traits are viable under different environmental conditions (Diaz et al., 2004; Grime, 1974). For example, traits associated with high growth rates such as longer stems and larger leaves assure high resource acquisition aboveground (Poorter & Nagel, 2000; Wright et al., 2004). In a high resource environment, this can be a viable strategy. On the other hand, in a low resource environment with more stressors, conservative strategies, that are designed to preserve the structures that valuable resources have been invested in, are more successful (Diaz et al., 2004; Fort et al., 2016; Westoby & Wright, 2006; Wright et al., 2004).

Acquisitive and conservative strategies can both be reflected and measured through traits, where different traits are responding differently to abiotic factors such as temperature and precipitation. For instance, a functional trait which reflects how much a plant invests in each leaf is specific leaf area (SLA; $mm^2\ g^{-1}$), which measures the trade-off between carbon gain

and leaf longevity. With increasing temperatures, plants invest less into each leaf with shorter leaf life spans (Wright et al., 2004), larger leaf area (Guittar et al., 2016; Moles et al., 2014) and higher SLA (Bjorkman et al., 2018; Guittar et al., 2016; Moles et al., 2014; Rosbakh et al., 2015). In addition, max height also increases with temperatures where light competition is thought to be an important factor (Guittar et al., 2016; Moles et al., 2014; Walker et al., 2006). Plants also allocate more resources into reproductive traits like flower production (Meineri et al., 2014), seed number and seed weight (Totland, 1999), with increasing temperatures. However, trait patterns are less clear when precipitation is considered (Moles et al., 2014; Wright et al., 2004). Vegetative trait patterns show inconsistent results in common trait measurements such as max height (Guittar et al., 2016; Moles et al., 2014; Rota et al., 2017) and SLA (Butterfield et al., 2017; Fonseca et al., 2000; Moles et al., 2014; Rota et al., 2017). In addition, leaf area can increase with precipitation (Moles et al., 2014), though no significant effect has also been found (Guittar et al., 2016). Even though allocation to reproduction can increase with precipitation (Skarpaas et al., 2016), the effect of precipitation on reproductive traits is uncertain. While some studies show hints towards an effect of precipitation on seed mass (Moles et al., 2014; Ying et al., 2018), others show non-significant results on seed mass and number of buds (Butterfield et al., 2017; Guittar et al., 2016). There is still a knowledge gap between how allocation patterns and trait response vary with precipitation and between species with different resource acquisition strategies.

The main goal of this study is to investigate how resource allocation is affected by precipitation and trait strategy. For this, alpine species with the range of trait values representative for the alpine community were compared to two sets of lowland species: one set with trait values similarly conservative as in the alpine community (the 'extant' trait set) and the other set with more acquisitive trait values than common in alpine communities (the 'novel' trait set). This comparison is relevant because colonization of these two sets of lowland species can be expected to have quite different impacts on alpine plant communities, with higher impacts of 'novel trait' species than of 'extant trait' species.

Specifically, I compare the alpine species *Veronica alpina* and *Sibbaldia procumbens* to the 'extant' lowland plants *Veronica officinalis* and *Viola canina*, and to the 'novel' *Succisa*

pratensis and *Hypericum maculatum*.

Based on the line of argument presented above, I predict that:

1) Plants allocate less to roots with increasing precipitation, and more to leaves, specifically into traits and structures that maximize leaf competition for light, in form of larger leaf area, increased number of leaves and higher max height with increasing precipitation.
2) An increase in reproductive traits like length of longest inflorescence, number of inflorescences and number of buds, flowers and capsules with increasing precipitation.
3) Alpine species allocate more of their resources to the roots than novel lowland species
4) Extant lowland species have similar resource allocation strategies as the alpine species
5) The novel lowland species are allocating more resources to reproduction than the alpine and extant species

Methods

This project was performed within the SeedClim grid, which is a series of sites that spans throughout south-western Norway (see figure 1, and table 1 for details). The sites use elevation as a natural temperature gradient, with a mean summer temperature from ca. 6.5 ˚C to ca. 10.5 ˚C, and the variation in mean annual precipitation from the wet oceanic climate in the west to the drier continental climate in the east is used as the precipitation gradient (ca. 700-2700mm; climate data provided by Norwegian Meteorological Institute, met.no). The sites are all similar semi-natural grasslands with south-faced slopes, calcareous bedrock and have a history of grazing. In this study, I measured and collected plants within this grid, aiming to sample different types of alpine and lowland species (see below) from as many sites as possible along the precipitation gradient with 2-4 levels, ranging from 600mm to 3000mm. A total of six species were collected, two alpine species selected to have 'alpine' distributions and traits, two lowland species selected to have similar traits to the alpine species, but a more lowland geographical distribution, and two lowland species with more resource-acquisitive traits than the other two. The species chosen for this project were based on average trait values where the species that best describe their functional group in their respective environment (table 2) (Ragnhild Gya, unpublished data). I collected the lowland plants collected at sites representing their upper boreal distributional limit, and alpine plants were collected in the low-alpine zone sites. In most cases for the lowland species, this resulted in sampling collected at the sub-alpine zone SeedClim sites, but one of the lowland species, *Succisa pratensis*, was collected outside the climate grid, in lower-elevation and hence warmer

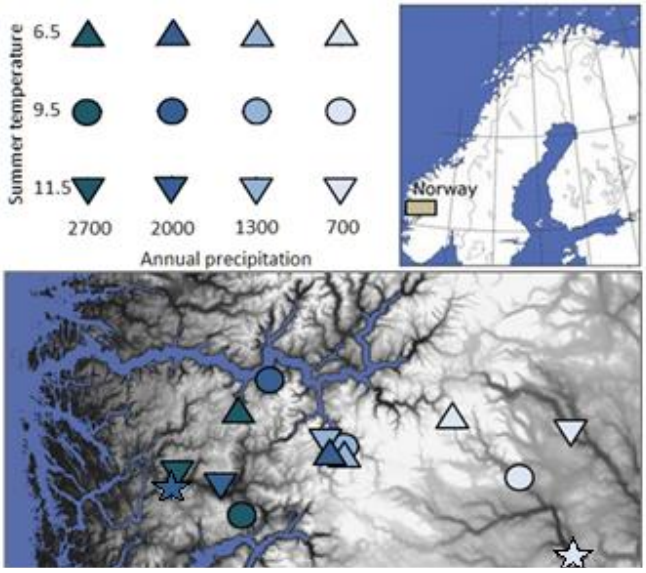

Figure 1. Map of western Norway showing the location of the twelve sites located within the SeedClim grid, with three levels of temperature; boreal, sub-alpine and alpine vegetation types and four levels of precipitation; 650, 1300, 1950 and 2900. Temperature is measured in mean summer temperature (June-September). Precipitation is calculated in mean annual precipitation. Stars indicate sites where *Succisa pratensis* was collected. Figure modified from Klanderud et al., 2015. (Klanderud et al., 2015).

sites that were otherwise similar to the lowland sites. Not all species were present at the sites representing all precipitation levels within their respective environment, but all species were collected at least at two sites (Figure 1; Table 1).

Table 1. **Overview of sites with mean summer temperature, annual precipitation, altitude, coordinates and bedrock.** Bolstadøyri and Kolsrud are sites located outside the SeedClim grid. (Bedrock data collected from: http://geo.ngu.no/kart/berggrunn/; Climate data collected from met.no.) (Table modified from Gya, 2017; Klanderud et al., 2015)

Vegetation zone	Site	Longitude	Latitude	Altitude (m.a.s.l.)	Temperature (°C)	Precipitation (mm year^{-1})	Bedrock
Alpine	Skjellingahaugen	60.9335	6.41504	1088	6.58	2725	Marble
	Gudmedalen	60.8328	7.17561	1213	5.85	1925	Rhyolite. Rhyodacite. Dacite
	Låvisdalen	60.8231	7.27596	1097	6.45	1321	Rhyolite. Rhyodacite. Dacite
	Ulvehaugen	61.0243	8.12343	1208	6.17	596	Rhyolite. Rhyodacite. Dacite
Sub-alpine	Veskre	60.5445	6.51468	797	8.67	3029	(Meta) sandstone Shale
	Rambera	61.0866	6.63028	769	8.77	1848	Phyllite. Mica schist
	Høgsete	60.8760	7.17666	700	9.17	1356	Phyllite. Mica schist
	Ålrust	60.8203	8.70466	815	9.14	789	(Meta)sandstone. Shale
Boreal	Øvstedal	60.6901	5.96487	346	10.78	2923	Rhyolite. Rhyodacite. Dacite
	Arhelleren	60.6652	6.33738	431	10.6	2044	Phyllite. Mica schist
	Vikesland	60.8803	7.16982	474	10.55	1161	Phyllite. Mica schist
	Fauske	61.0355	9.07876	689	10.3	600	Phyllite. Mica schist
Boreal *Succisa Pratensis* sites	Bolstadøyri	60.64793	9.00120	42	13.65*	2223	Phyllite
	Kolsrud	60.44822	9.21242	142	15.10*	820	Quartzite. Gneiss

*Temperature was measured by using an average of mean summer temperature for the last 5 years, which contradicts the protocol for using the temperature 1961-1990. Though, temperature was not used for the analysis.

Table.2 Comparison of trait values between the lowland species and the range of the alpine species. (Gya, 2017)

	Species	Vegetative height (mm)	SLA (cm^2/g)	Leaf area (cm^2)
Alpine	Alpine species range (mean + SD)	73.3 +/- 37.5	242.0 +/- 94.3	2.22 +/- 1.35
Lowland with resource conservative traits	*Veronica officinalis*	56.8	165.0	1.97
	Viola canina	65.8	246.0	2.99
Lowland with resource acquisitive	*Succisa pratensis*	166.0	192.0	14.5
	Hypericum maculatum	260.0	288.5	2.81

***Veronica alpina* (Alpine specialist with resource conservative traits)**

Veronica alpina, alpine speedwell, is an alpine perennial forb common in the Norwegian mountains and arctic areas. It is also found in European mountains, as well as Iceland, northern America and some localities in the Himalayas (Albach et al., 2006; GBIF, 2020). Its range stretches from boreal to high alpine and in Norway, it has been recorded at altitudes up 1920m.a.s.l (Lid & Lid, 2005). Its stem grow vertically 5-15 cm, often bent, and with flowers bundled at the top, and clonal shoots grow vertically out of slightly belowground hypogeogenous rhizomes (Klimešová, 2018; Lid & Lid, 2005; Mossberg & Stenberg, 2012). Leaves are elliptical and slightly hairy (Mossberg & Stenberg, 2012).

Figure 2. Illustration of *Veronica alpina* with belowground architecture and a Fenno-Scandinavian distribution map. (Modified from: Klimešová & Klimeš, 2019; Lid & Lid, 2005; Mossberg & Stenberg, 2012)

***Sibbaldia procumbens* (Alpine specialist with resource conservative traits)**

This perennial herb has a circumpolar distribution and is found in arctic areas and mountain ranges across Eurasia and North-America (GBIF, 2020). It's a characteristic alpine species, known for growing on low-substrate soil, and has been recorded at an altitude of 2130 m.a.s.l. in Lom, Norway(Lid & Lid, 2005). As one can tell from its name, the creeping Sibbaldia grows horizontally with a shy vertical growth height of 3-10cm (Lid & Lid, 2005). Its flowers have small yellow petals that are shorter than the sepals. Each leaf is divided into three leaflets, with a characteristic three toothed tip (Mossberg & Stenberg, 2012).

Figure 3. Illustration of *Sibbaldia procumbens* and Fenno-Scandinavian distribution map. (Modified from: Lid & Lid, 2005; Mossberg & Stenberg, 2012)

***Veronica officinalis* (Lowland generalist with resource conservative traits)**

Common speedwell (*Veronica officinalis*) has a natural range within Europe and the Caucasus mountains, but it has been introduced in countries such as United States and Chile. It thrives in open terrain from deciduous forest to northern boreal and has been recorded at 1150 m.a.s.l. in Norway (Lid & Lid, 2005). It is a perennial who grows mainly horizontally, with adventitious roots and 10-30 cm flowering shoots sprouting out of stolons (Klimešová, 2018; Mossberg & Stenberg, 2012). The oval leaves grow pairwise along the stem and shoots (Lid & Lid, 2005). Because of clonality with overwintering growth, individuals are often long and winding.

Figure 4. Illustration of *Veronica officinalis* with growth form and a Fenno-Scandinavian distribution map. (Modified from: Klimešová & Klimeš, 2019; Lid & Lid, 2005; Mossberg & Stenberg, 2012)

***Viola canina* (Lowland generalist with resource conservative traits)**

The heath dog-violet is a common lowland plant found in places like meadows, roadsides and forest clearings. It is mainly found in Europe and parts of Asia, and in Norway it has been recorded at 860 m.a.s.l. (GBIF, 2020; Lid & Lid, 2005). It is an herbaceous perennial that grows to 5-20 cm in size (Lid & Lid, 2005). They have adventitious roots growing out of an epigeogenous rhizome with vertical reproductive and leaf stalks growing out with one heart—shaped leaf per leaf stalk (Klimešová & Klimeš, 2019; Mossberg & Stenberg, 2012). One flower grows per reproductive stem and they are blue with five petals and an overall quadratic shape (Mossberg & Stenberg, 2012).

Figure 5. Illustration of *Viola canina* with growth form and a Fenno-Scandinavian distribution map. (Modified from: Klimešová & Klimeš, 2019; Lid & Lid, 2005; Mossberg & Stenberg, 2012)

***Succisa pratensis* (Lowland generalist with resource acquisitive traits)**

The devils-bit or Succisa pratensis is a lowland perennial and stretches across Europe and into parts of Russia (GBIF, 2020; Mossberg & Stenberg, 2012). In Norway it grows mainly in fjords and valleys, though it has been recorded up to 1000 meters at Røros (Lid & Lid, 2005). It's polycarpic, with rosettes surviving for many years and sprouts 20-60 cm vertical flower stems annualy, usally with multiple flowers per stem (Jongejans & De Kroon, 2005; Mossberg & Stenberg, 2012). Main root is sooner or later replaced by adventitious roots (Klimešová, 2018). Flowering occurs in late summer, usually from august to september (Mossberg & Stenberg, 2012).

Figure 6. Illustration of *Succisa pratensis* with leaf rosette and a Fenno-Scandinavian distribution map. (Modified from: Klimešová & Klimeš, 2019; Lid & Lid, 2005; Mossberg & Stenberg, 2012)

***Hypericum maculatum* (Lowland generalist with resource acquisitive traits)**

St. Johnswort is a clonal flowering plant and is distributed throughout Europe and into parts of Asia. It is common in Norwegian lowland terrain such as meadows and grazeland, though it has been recorded up to 1260 meters in Jotunheimen (Lid & Lid, 2005). It can grow up to one meter tall and can produce 2-10 new shoots every year, which makes it grow into clusters of ramets (Klimešová & Klimeš, 2019; Lid & Lid, 2005). Yellow flowers sprout at the top, with elongated leaves grow along the stem (Mossberg & Stenberg, 2012).

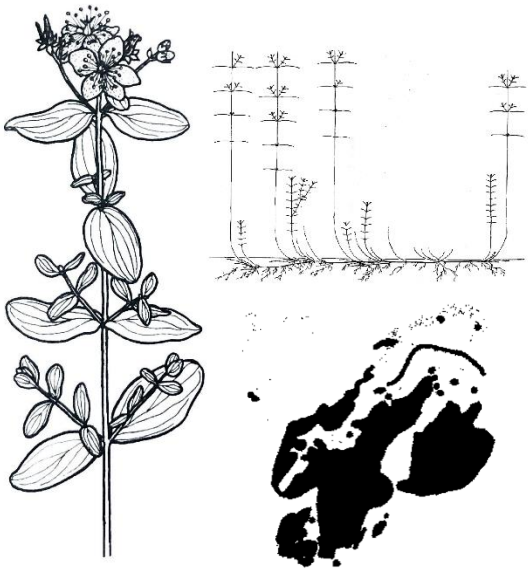

Figure 7. Illustration of *Hypericum maculatum* with growth form and a Fenno-Scandinavian distribution map. (Modified from: Klimešová & Klimeš, 2019; Lid & Lid, 2005; Mossberg & Stenberg, 2012)

Field collection

To capture the plants strategies in a natural environment, traits (see below) were measured in the field and the same individuals were dug up and brought to the lab for weighing of biomass. The goal was to get a minimum of 21 individuals in total from each site to capture a wide enough spectrum of the local population and at least from three different places within the site to ensure genetic diversity. As mentioned earlier, the lowland plants were collected at the sites with their upper boreal limit and the alpine plants were collected at the alpine sites. The plants were collected along the precipitation gradient at each site where the species was present (2-4 sites).

Selecting individuals

To avoid selection bias, the randomization process included throwing a pencil backwards towards an area where I knew the species were present and placed a 25x25cm square facing uphill with its top left corner in the place where the pencils eraser landed. The square was divided into 25, 5x5cm subsquares. After placing the square, the entire square was checked for the species of interest. If no individuals were found, then the square was rejected, and the process was repeated. If at least one individual was found in a search through the square, then the square was treated as follows: First, I thoroughly checked for smaller individuals in the plot. The subsquares were checked in a specific pattern, from top left to bottom right, as a book is read. In the 5x5cm subsquare where the 7^{th} individual was found, all the remaining individuals within that subsquare were also measured and collected to further avoid subconscious selection of individuals. Then the process was repeated until a at least 21 individuals was collected (i.e., if density as high, the whole square would not be sampled). Since some of the plants are clonal, I also needed to assess whether the plants were multiple or one individual. When in doubt, I took note of possible clonality and conservatively counted them as one individual to ensure that the minimum of 21 genetically different individuals requirement was fulfilled. However, because of unpredictable root architecture, unexpected clonality for certain species resulted in lower than planned number of individuals (specifically, for *Hypericum maculatum* at Ålrust, the sampling resulted in only 11 genetically different individuals).

Trait measurement and collection

Traits were measured in the field and length measurements were done in mm by using a

ruler, where I used the vegetative traits shoot height, number of leaves, length of longest leaf, width of the longest leaf, and length of the longest leaf stalk. For reproductive traits, length of longest flowering shoot, number of flowering shoots, number of buds, flowers, potential capsules (or withered flower) and capsules, and inflorescence diameter was measured (specific details in field protocol). Leaf area for the largest leaf was calculated as a square for simplicity. Number of buds, flowers, potential capsules and capsules were added up to total reproductive material. However, not every trait was measured for every species (see appendix I).

Before excavating the plants, I assessed how much soil was necessary to dig up not to damage the roots and marked this area. When digging, getting deep enough was also prioritized. In most cases, most aboveground biomass was removed other than the species of interest. This was done with a scissor to ensure no damage to the roots of the species I was collecting.

Lab

The plants were stored in plastic boxes and in a 2-4°C cooling room within 4-5 days of collection. The plan was to carefully excavate the plants to measure above-and belowground biomass as soon as possible. Unfortunately, the plastic boxes were too airtight, so it got humid and mold started to appear. In addition, it became apparent after a period of storage (5-6 weeks) that 4°C was not cold enough to stop biological activity in these plants. While in storage, the plants started to prepare for the winter by shedding leaves, and most likely drawing resources to the roots.

From October 2019 onwards, therefore I prioritized to get the intact soil samples with the roots in the freezer since removing soil and extracting roots is the most time-consuming task. Therefore, most of the aboveground biomass of the focal individuals was then cut and dried at 65˚C for 72 hours (Pérez-Harguindeguy et al., 2013). The roots were marked to easily find and recognize them in the intact soil turfs. All the roots were frozen within the beginning of November 2019.

For root excavations, soil was thawed in a plastic box with hot water and dish soap for about 30 minutes, as dish soap helps to separate the roots from the soil (Barbez, 2018). Then most

of the soil was washed away in the hot water and roots were carefully extracted. A tweezer was used on species where roots were fragile.

The clean entire roots of each plant were then dried at 65˚C for 72 hours (Pérez-Harguindeguy et al., 2013). Before the biomass could be weighed, both roots and aboveground biomass was dried again overnight and immediately put in a container with silica to ensure that it soaked up as little moisture from the air as possible. Then above-ground and below-ground biomass were weighed on a VMR SM425i scale with 0.01 mg precision.

For traits analysis, individuals who were found to be clonal were corrected for in the dataset by joining them. For discrete variables like number of leaves and number of flowers, the numbers were then were added together. For continuous variables like length of longest leaf and length of inflorescence shoot, the longest one was selected. When biomass analysis was conducted, a full dataset and a reduced dataset was constructed, the latter where I removed the individuals lost in the process, either because the shoots were too withered to be identified, too hard to detect in the turfs, or if they were lost during sampling. A total of 64 individuals were either lost in sampling or were discovered to be clonal during root washing, leaving the biomass analysis dataset at 407 individuals

Statistical analysis

Before any analysis was conducted, biomass and leaf area were log2-transformed, whereas raw values were used for shoot:root ratio and relative allocation. Data was assumed to be normally distributed and independence of variation based on the sampling method. Precipitation was scaled using the mean and standard deviation of every value, and the mean was subtracted from each of the values and divided by the standard deviation using the scale function in base R. Linear mixed-effect models were used for the analysis, with precipitation as fixed effect and site as a random effect for all models. When testing for differences between species groups, species groups were added as a fixed effect and species as a random effect. Species was used a fixed effect when comparing species in the same model. Whether a quadratic term for precipitation was used in the final model was decided based on the lowest AIC-scores. When comparing species and species groups in the same model, t-values were used to evaluate significance with the lmerTest package and t-values larger than 2. When testing the effect of precipitation on species and species groups, a type

2 Wald chi-square test was used to test for significance of the fixed effects. If there was an interaction in the fixed effects, a type 3 Wald chi-square test was used instead. For species groups analysis, only the traits that the groups all have in common were used (see appendix I).

All analysis was done using R (version 3.6.1) and R-studio (version 1.2.5001.0). Packages used for the analysis were nlme (3.1-140), lme4 (1.1-23), emmeans (1.4-6), lmerTest (3.1-2) and car (3.0-7).

Data is documented and shared through BTF databases and publicly available data documentation. More information in the SeedClim readme file: https://docs.google.com/document/d/1RUOqkf8V_TqwZabu8LUjwQvephE5EClyYegV9wPAgfs/edit?usp=sharing

Results

Precipitation had clear impacts on either absolute biomass or allocation both across species groups and species. Both vegetative and reproductive traits had a general negative response to increasing precipitation in 4 out of 6 species. The novel species were significantly larger that the alpine species compared to the extant species (table 4 & 5).

Size

Aboveground biomass varied significantly between species, and species groups, with the novel species being significantly heavier than extant and alpine species (figure 8; table 4). The above-ground biomass varied by three order of magnitude, where *Veronica alpina* had the lowest above-ground biomass, with population mean biomass ranging from 24-27 mg, whereas *Succisa pratensis* had the highest biomass, with means from 811-1129 mg (table 3). There was an overall tendency across the dataset for aboveground biomass to decrease towards wetter sites (p-value = 0.003). While all species and species groups had consistently negative slopes with precipitation, however, the trend was significant only in the extant species group for *Sibbaldia procumbens* (table 5). For *Sibbaldia procumbens,* has the model suggests lowest aboveground biomass at intermediate precipitation (table 5). The belowground

Table 3. Number of individuals per species per site with population means and standard deviation for above- and belowground biomass**.**

SPECIES	SITE	NUMBER OF INDIVIDUALS	ABOVE-GROUND BIOMASS (mg ±SD)	BELOW-GROUND BIOMASS (mg ±SD)
VERONICA ALPINA	Skjellingahaugen	16	27.0 ± 37.6	28.5 ± 31.8
	Låvisdalen	12	24.9 ± 17.8	52.9 ± 36
	Ulvehaugen	16	23.6 ± 10	22.1 ± 11.9
SIBBALDIA PROCUMBENS	Skjellingahaugen	34	46.2 ± 59.5	117 ± 125
	Gudmedalen	30	55.1 ± 92.2	117 ± 218
	Låvisdalen	34	38.3 ± 27.4	157 ± 109
	Ulvehaugen	30	77.1 ± 58.6	157 ± 104
VERONICA OFFICINALIS	Veskre	24	71.5 ± 49.1	77.9 ± 55.4
	Rambera	20	94.1 ± 86.3	104 ± 67.5
	Høgsete	19	235 ± 348	309 ± 523
	Ålrust	23	161 ± 153	111 ± 88.5
VIOLA CANINA	Veskre	38	21.1 ± 16.3	38.7 ± 28.4
	Høgsete	23	36.7 ± 28.4	80.4 ± 63.1
	Ålrust	25	78.7 ± 63.5	71.1 ± 62.3
SUCCISA PRATENSIS	Bolstadøyri	19	811 ± 743	1028 ± 853
	Kolsrud	19	1129 ± 1402	1365 ± 1438
HYPERICUM MACULATUM	Høgsete	14	229 ± 223	375 ± 328
	Ålrust	11	392 ± 630	713 ± 959

biomass also varied significantly between the groups and species, where the novel species have more belowground biomass than both the extant and alpine species groups (table 4, table 5). The values were broadly comparable to the above-ground biomass, and the mean of *Veronica alpina* populations were ranging from 22-52 mg and *Succisa pratensis* with means ranging from 1028-1365 mg. *Veronica alpina* has the highest below-ground biomass at intermediate precipitation levels.

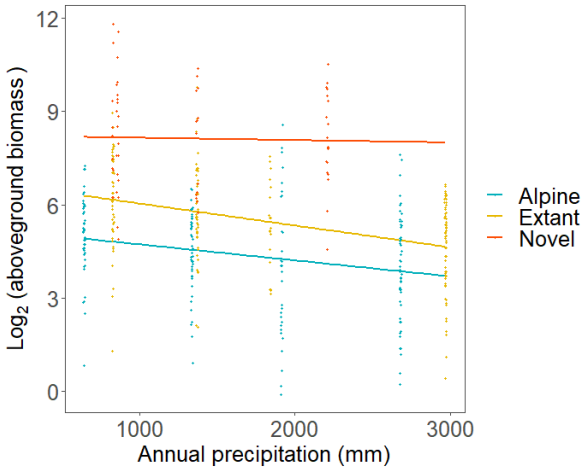

Figure 8. Aboveground biomass between species groups in relation to precipitation. Aboveground biomass decreases with precipitation for all observations (p-value: 0.03), and patterns are significantly different between species groups (p-value:0.02).

Table 4. Summary of full growth and allocation models of the entire dataset. Slope for species groups (alpine, extant, novel) and species (alpine = *Veronica alpina, Sibbaldia procumbens,* extant = *Veronica officinalis, Viola canina,* novel = *Succisa pratensis, Hypericum maculatum*) and per unit of scaled annual precipitation (mm). lmerTest is used to evaluate significance and t-values larger than 2 are evaluated as support that a slope is significant, and those are marked in bold. Effect sizes are based on direct comparison in size or allocation. The alpine species group and Veronica alpine are defined as the base levels in the species groups and species, models, respectively, and slopes all other species groups and species are given as contrasts to their slopes.

Fixed effect	Aboveground biomass (log2)	Belowground biomass (log2)	S:R ratio	Above-ground allocation	Below-ground allocation
Model 1: Precipitation and Species group					
Alpine	**4.36***	**4.87****	**0.95***	**0.42****	**0.58*****
Δ Extant	1.18	1.14	-0.06	0.01	-0.01
Δ Novel	**3.72***	**3.74***	0.01	0.02	-0.02
Precipitation	-0.42	-0.53	0.07	0.01	-0.01
Δ Precipitation * Extant	-0.15	0.31	-0.37	-0.09	0.09
Δ Precipitation * Novel	0.36	0.09	0.40	0.10	-0.10
Model 2: Precipitation and Species					
Veronica alpina	**3.96*****	**3.79*****	**1.3****	**0.52*****	**0.48*****
Δ Sibbaldia procumbens	**0.80****	**2.13*****	**-0.69****	**-0.18*****	**0.18*****
Δ Veronica officinalis	**2.34*****	**2.58***	-0.22	-0.03	0.03
Δ Viola canina	0.79(*)	1.66(*)	-0.6	-0.13	0.13
Δ Succisa pratensis	**5.11*****	**5.76****	-0.51	-0.09	0.09
Δ Hypericum maculatum	**2.98*****	**3.32****	-0.04	-0.02	0.02

Table continues below…

Precipitation	-0.23	-0.42	0.10	0.02	-0.02
Δ Precipitation * Sibbaldia procumbens	-0.27	-0.17	-0.04	-0.01	0.01
Δ Precipitation * Veronica officinalis	-0.24	0.11	-0.20	-0.04	0.04
Δ Precipitation * Viola canina	-0.40	0.03	-0.24	-0.06	0.06
Δ Precipitation * Succisa pratensis	0.13	0.49	-0.15	-0.04	0.04
Δ Precipitation * Hypericum maculatum	0.0002	-1.22	**0.92***	0.22	-0.22

Table 5. Summary of growth and allocation models per species and species group. Slopes for the species and species groups per scaled annual precipitation (mm) on size and allocation. P-values are extracted using a type 3 Wald chi-square test, with values evaluated as: P: 0.1 '(*) 0.05 '*' 0.01 '**'0.001 '***'. AIC scores were used to determine whether a quadratic term was included.

Fixed effect	**Above-ground biomass (log2)**	**Below-ground biomass (log2)**	**S:R ratio**	**Above-ground allocation**	**Below-ground allocation**
Model 1: *Veronica alpina*					
Precipitation	-0.19	-0.17	0.02	-0.002	0.002
Precipitation^2	-0.10	**-0.08***	0.24	**0.10***	**-0.10***
Model 2: *Sibbaldia procumbens*					
Precipitation	**-0.34****	-0.38	0.04	0.01	-0.01
Precipitation^2	**0.40****	0.58	-0.22	-0.04	0.04
Model 3: *Veronica officinalis*					
Precipitation	-0.32	-0.08	**-0.27*****	**-0.05*****	**0.05*****
Precipitation^2	-0.01	-0.2	**0.27*****	**0.04****	**-0.04****
Model 4: *Viola canina*					
Precipitation	-0.95	-0.01	**-0.39*****	**-0.11 *****	0.11 (*)
Precipitation^2	0.47	-0.03	**0.40*****	**0.12 *****	-0.12
Model 5: *Succisa pratensis*					
Precipitation	-0.01	0.004	-0.04	-0.02	0.02
Model 6: *Hypericum maculatum*					
Precipitation	-0.23	-0.50	0.32	0.07	-0.07
Model 7: Alpine species group					
Precipitation	-0.43	-0.54	0.07	0.016	-0.016
Model 8: Extant species group					
Precipitation	**-0.56*****	-0.35(*)	-0.12	-0.03	0.03
Model 9: Novel species group					
Precipitation	-0.09	0.02	0.02	-0.01	0.01

Allocation

There are generally few trends in allocation patters between the species and species groups, and there is no systematic trend in allocation along precipitation (table 4; table 5). The shoot:root patterns along precipitation significantly differed between species groups (figure 9a: p-value: 0.012) although variations within the species groups was evident within the alpine and extant species groups. More specifically, *Veronica alpina* had a higher shoot:root ratio than *Sibbaldia procumbens* (P<0.001), and *Veronica officinalis* had a higher shoot:root ratio than *Viola canina* (P<0.001) (Table 4). Some of the species did respond to precipitation in the species-specific models. *Veronica officinalis* and *Viola canina* both have a decrease in allocation to shoots along precipitation, and a unimodal response with lowest aboveground allocation at intermediate precipitation (table 5; figure 9c). Additionally, *Veronica alpina* did not decrease in allocation to aboveground biomass with precipitation, but it did however show a significant unimodal response, suggesting lowest aboveground allocation at intermediate precipitation. Furthermore, *Hypericum maculatum* allocated more to aboveground biomass along precipitation, compared to *Veronica alpina* (table 4).

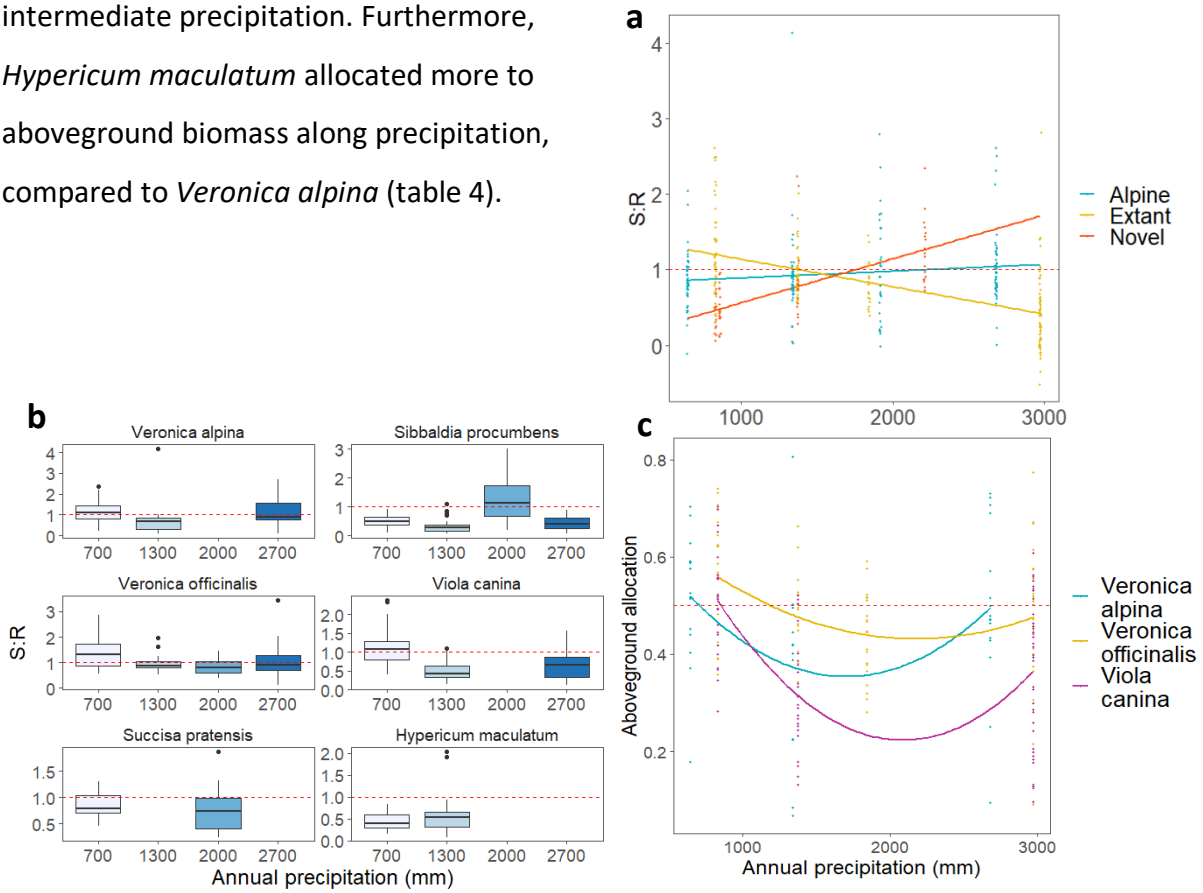

Figure 9. S:R ratio between species and species groups in relation to precipitation. a) aboveground allocation between 3 species who showed a unimodal response to precipitation. b) Shoot:root ratio (S:R) as boxplots for the different species along precipitation. c) S:R species group have different patterns along precipitation (P: 0.012). The red dashed line indicates the point where allocation to aboveground- and belowground biomass is equal.

Vegetative traits

There are differences in traits and trait response to precipitation between species and these differences are less clear between species groups, suggesting variation in response within species groups (appendix I). The alpine species were generally shorter compared to at least one of the lowland species (appendix I). *Hypericum maculatum* was significantly longer than *Veronica alpina* (appendix I) and *Viola canina* had a longer leaf stalk length compared to *Sibbaldia procumbens.* The four lowland species generally had a higher number of leaves, longer length of longest leaf, wider width of the longest leaf and an overall larger leaf area of the longest leaf compared to *Veronica alpina*, while neither number of leaves nor length of longest leaf differed between the alpine species (appendix I). However, the same patterns were not significant between the species groups.

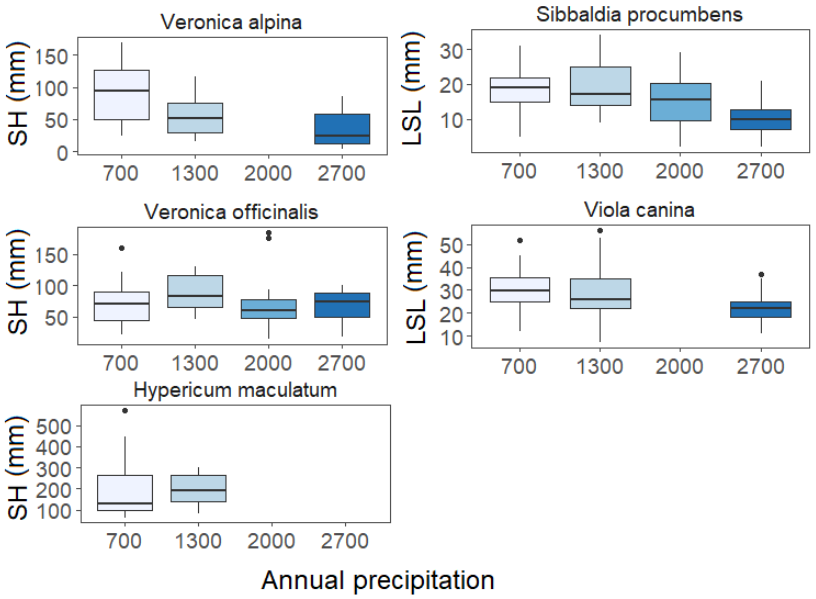

Figure 10. Shoot height and leaf stalk length between species in relation with precipitation. Shoot height (SH) decreases for *Veronica alpina* with precipitation (P: 0.005) and leaf stalk length (LSL) decreases for *Sibbaldia procumbens* (P: 0.001) and *Viola canina* (P<0.001)

The measurements for vegetative height, shoot height and leaf stalk length, shows a general trend to decrease with precipitation (figure 10; appendix I). *Veronica alpina* decreases in shoot height along precipitation, and the leaf stalk length decreased in *Sibbaldia procumbens and Viola canina* (appendix I; figure 10). Interestingly, *Veronica alpina* had more shoots with increasing precipitation, while *Veronica officinalis* decreased in number of shoots and had significantly less in comparison (appendix I). *Viola canina* also decreased in number of shoots along precipitation, but not significantly compared to the other species (appendix I). While *Sibbaldia procumbens* and both extant species decreased in number of leaves with increasing precipitation, only *Veronica officinalis* decreased when compared to *Veronica alpina*.

The extant species group decreased in number of shoots with increasing precipitation (appendix I). While the novel species group decrease in length of the longest leaf with increasing precipitation, where they decrease significantly more than the alpine species group (figure 11). Even with this decrease, the width of the longest leaves for the novels is slightly increasing with precipitation, though not significant, resulting in no change in overall leaf area in comparison with *Veronica alpina*. Though this is highly likely to be caused by the simplified form of leaf area calculation, which increases the impact of width in compared to length for elliptical leaves.

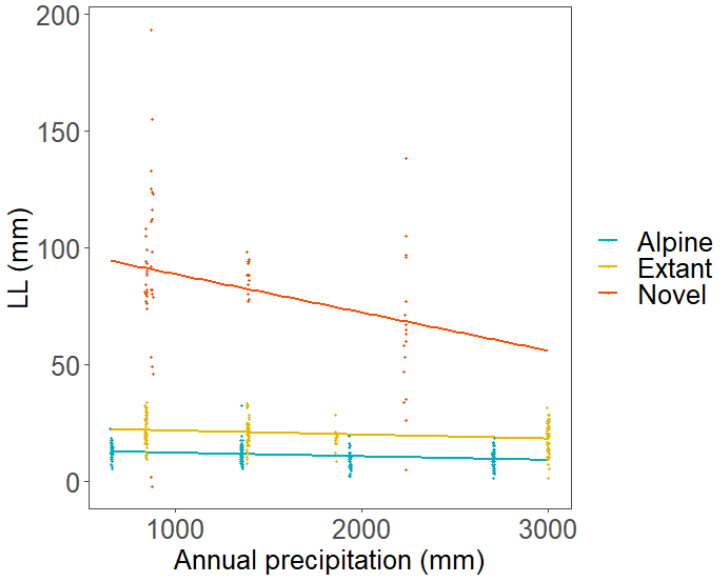

Figure 11. Length of longest leaf between species groups in relation with precipitation. Length of the longest leaf (LL) decreases for the novel species (P: 0.01) and might decrease for the alpine (P: 0.09) and the extant (P: 0.06) with increasing precipitation.

Reproductive traits

The novel species have longer inflorescence shoots and more buds compared to the other species (appendix I). All the species had shorter inflorescence shoots than *Succisa pratensis,* in addition the alpine and extant species had shorter inflorescence shoots than *Hypericum maculatum*. Only *Sibbaldia procumbens* had significantly fewer number of flowering shoots than *Succisa pratensis*. *Hypericum maculatum* had more buds than *Succisa pratensis* (P<0.001), *Viola canina* (P<0.001) and *Veronica alpina* (0.01), This could be attributed to *Hypericum maculatum* producing more buds in general in combination with sampling too early. *Veronica officinalis* had more potential capsules, and total reproductive material compared to the *Succisa pratensis*. Additionally, *Veronica officinalis* have more capsules compared to *Veronica alpina* (P: 0.046), *Sibbaldia procumbens* (P: 0.02), *Viola canina* (P<0.001), *Succisa pratensis* (P: 0.03) and *Hypericum maculatum* (P: 0.02),

The novel species group did have a higher investment in some reproductive traits in comparison with the other species groups. Length of longest inflorescence shoot might be

higher in the novel species, but higher biomass in general and higher temperatures attribute to this difference (appendix I; but see table 1). The novel species had more buds compared to the other species groups, which was significant compared to the extant species group (appendix I).

Four of the six species had significant reproductive trait patterns along precipitation (appendix I). *Hypericum maculatum* showed a diverging pattern in two reproductive traits, while increasing the number of buds, but decreasing the length of inflorescence shoot with increasing precipitation (figure 12). There was a general trend to decrease in some reproductive traits for three of the species, as *Viola canina* decreased in total reproductive material, *Sibbaldia procumbens* decreased in number of flowering shoots and number of capsules and *Veronica officinalis* decreased in number of flowering shoots, potential capsules, capsules and total reproductive material (figure 12; appendix I).

Species seem to have different reproductive strategies along precipitation, but the general trend seem to be an overall decrease or no significant response. *Viola canina* have shorter inflorescence shoots with increased precipitation compared to *Veronica officinalis* (P:0.005). *Hypericum maculatum* decreased significantly in length of inflorescence shoot in comparison to *Succisa pratensis*. Although *Hypericum maculatum* had significantly more buds than *Succisa pratensis* with increasing precipitation. The species show different patterns in number of flowering shoots with precipitation. While number of flowering shoots decreased for *Sibbaldia procumbens* and *Veronica officinalis*, no difference in patterns were revealed in pairwise comparisons by the post-hoc. For the total reproductive material, both *Veronica officinalis* (P<0.001) and *Viola canina* (P:0.049) decreased with precipitation.

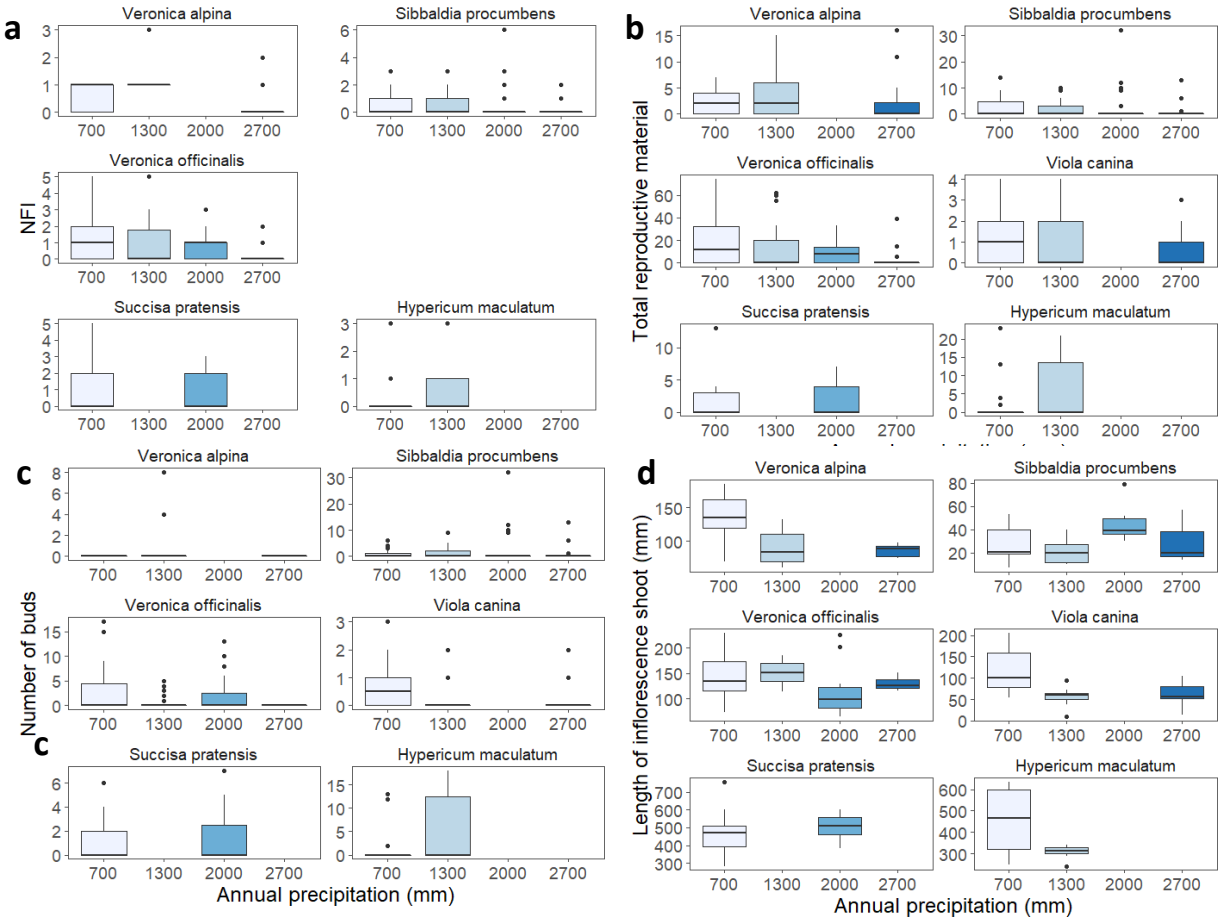

Figure 12. Traits distribution along precipitation between species. a) number of flowering shoots (NFI), b) length of inflorescence shoot, c) number of buds and d) total reproductive material.

Patterns for reproductive traits along precipitation are clearer for the extant species group compared to the other two (appendix I; figure 13). All the reproductive traits for the extant species had negative slopes, though they were only significant for length of inflorescence shoots, number of flowering shoots, potential capsules and total reproductive material (appendix I; figure 13). When comparing patterns along precipitation, the extant ($P<0.001$) and alpine (P: 0.02) species groups are allocating less to buds with increasing precipitation compared to the novel species. The extant species group are allocating less to total reproductive material with increasing precipitation compared to the novel species.

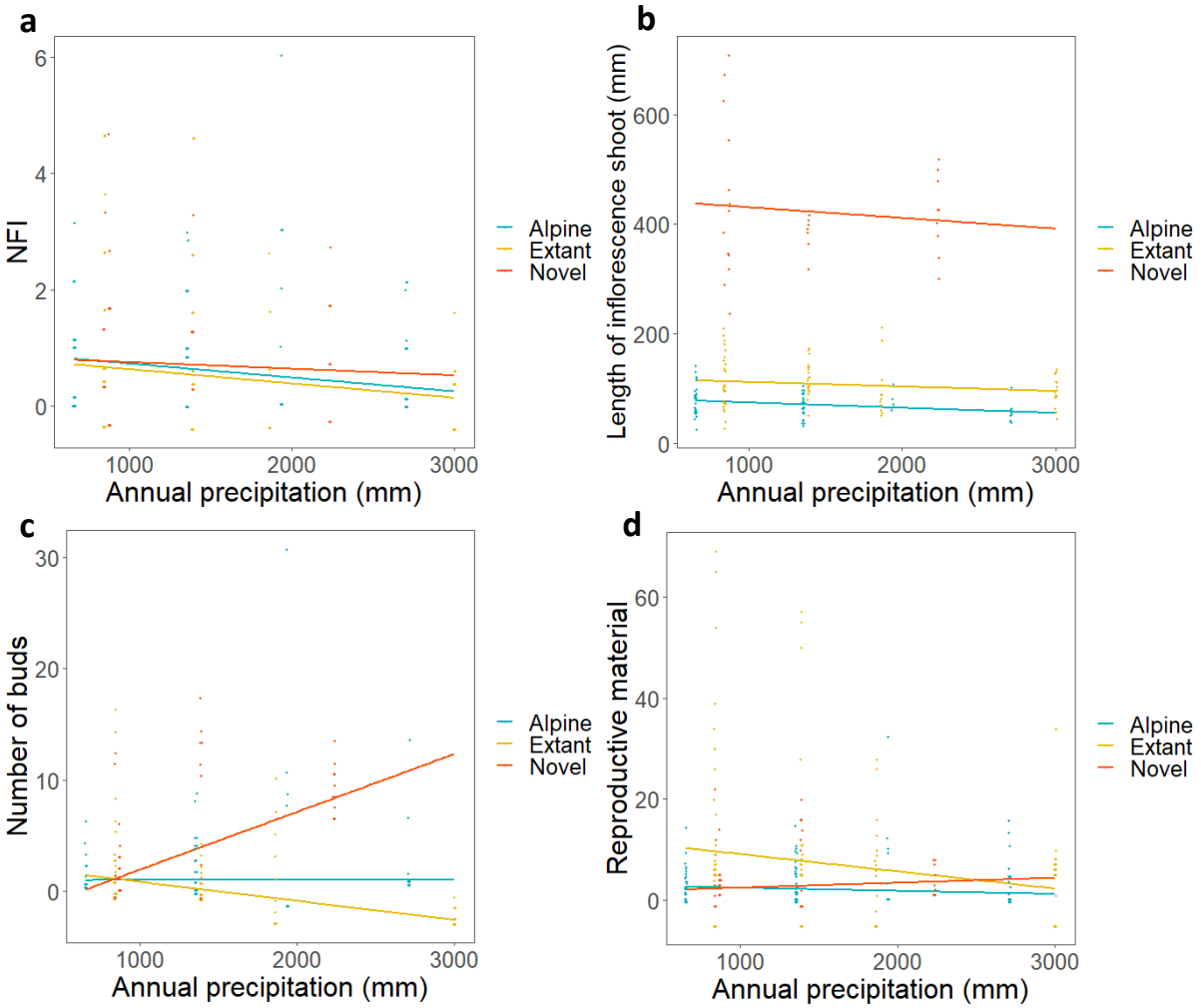

Figure 13. Traits distribution along precipitation between the species groups. a) the extant species group significantly decline in number of flowering shoots (NFI), with precipitation. b) length of inflorescence shoot, where novel species are significantly taller than the other two species groups. c) number of buds, where the novel species are increasing significantly more along precipitation compared to the other two species groups. d) total reproductive material significantly decreases with precipitation for the extant. (More detailed info in appendix I)

Discussion

The goal of this study was to investigate the effect of precipitation on allocation and plant traits and compare these responses between three different species groups, where the groups were chosen based on trait similarities and differences compared to a typical alpine community. The overall effect of increasing precipitation was mostly negative or was not significant, which contradicted my predictions based on literature that generally finds that precipitation shows an increase in increases in root allocation, taller plants with more and larger leaves and higher reproductive output. This may be due to a large range of precipitation where in the drier end precipitation may be limiting, and in the wetter end other factors, such as longer spring snow cover, may counteract the effects of higher water availability. Moreover, there were differences between species groups and the potential range shifts from the extant and novels species may affect alpine communities differently, as strategies and response to changing climates differ.

Novel vs extant range shifts

The ongoing warming of climate change will introduce new species to alpine communities as lowland species expand their ranges and thus new interactions will occur (Steinbauer et al., 2018). These interactions are defined by which species shift their ranges to alpine environments , and the identity of the species that shift ranges has consequences in terms of competitive interactions (Alexander et al., 2015). Compared to alpine species, novel species are considered more competitive than extant species. I found that extant species may have similar above- and belowground biomass to the alpine species, whereas the novel species have larger biomass. If the novel species expand into alpine communities, this increase in biomass could have larger impacts on the alpine communities, as they may be less conservative with their resources and invest more resources into light competition and reproduction (Alexander et al., 2015, 2016; Bruelheide et al., 2018; Díaz et al., 2016; Donovan et al., 2011). Additionally, the extant species allocating differently, as *Veronica officinalis* is allocating more to aboveground biomass than *Viola canina*. This suggests that *Veronica officinalis* may increase aboveground competition more than *Viola canina* in a potential range expanse.

The competition for light is important for plants and allocation to plant parts and traits that confer to an increase in light capture are predicted to be better competitors for light. I found that the resource acquisitive novel species, *Hypericum maculatum* is both taller and has a higher shoot:root ratio compared to *Veronica alpina*, whereas the extant species were not. Thus a potential range shift from the novel *Hypericum maculatum* to alpine environments could have potential negative effects for *Veronica alpina*, as *Veronica alpina* is predicted to be a weak competitor for light (Olsen et al., 2016). Furthermore, the extant species may not be as competitive as the novel species, because. In addition, other studies within the same system found that *Veronica alpina* decreased in survival with increasing temperatures (Töpper et al., 2018). Altogether, both direct effects of climate and which species shift range can affect the alpine species ability to compete for light.

I expect a higher allocation to reproductive parts in the novel species because of their resource acquisitive strategies. I found that the lowland novel species did have higher reproductive output in the form of longer inflorescence shoots compared to the alpine and extant species groups, and more buds compared to the extant species group. The fact that lowland have a higher number of buds compared to the extant species and not the alpine species group, may because alpine species may have higher allocation to reproduction compared to lowland plants (Körner & Fabbro, 2004). Although one would assume that this would also apply for the extant species group, although one needs to account for the difference in resource acquisition strategies between the novel and extant species group, which is further exemplified in the significantly higher inflorescence shoots. Furthermore, the lack of difference in total reproductive material may because seed mass is not accounted for which may vary with elevation, though evidence for this claim is contradicting (Baker, 1972; Bu et al., 2007; Pluess et al., 2005)

The effects of precipitation on size, allocation and trait response

The general consensus is that precipitation has a positive effect on aboveground biomass for a given plant community (Kardol et al., 2010; Ma et al., 2017). This is thought to be because water is an enhancing factor for plant growth within these studies, as water is a crucial resource of plant growth (Bloom et al., 1985). Interestingly, I found an overall decrease in aboveground biomass with increasing precipitation. These contrasting results could be attributed to the large range of precipitation within the gradient, where water limitation

may not be an issue, even at the drier end of gradient (600mm). Additionally, where increased soil moisture may be a constraining factor as wet soil may require more heat to warm up, thus increasing precipitation may have indirect effects on growth (Roxy et al., 2014). In addition, more precipitation may come as snow at wetter sites, delaying or even decreasing growing season. Moreover, the increased precipitation may wash away nutrients from the soil, which may explain the decrease in shoot:root ratio in the extant species, meaning they invest more into roots than to shoot to obtain the nutrients in the soil. So, allocation to roots may still increase even though water is not considered a limiting factor.

In previous studies, allocation to roots decreases with precipitation (Mokany et al., 2006; Skarpaas et al., 2016). This is in accordance with optimal partitioning theory, which suggests that plants will invest resources into the plant organs that is the most limiting, and less into plant organs that are not limiting. In contrast, I found that allocation to roots increases with precipitation for two of the six species. One possible explanation for these contrasting results can be the difference in range of precipitation, where the increase in shoot:root ratio suggests that water may not be a limiting factor in our system, but more evident at lower levels of precipitation, as one of the studies had a majority of data collected beneath 1000mm (Mokany et al., 2006). Another explanation can be the use of graminoids in addition to forbs (Skarpaas et al., 2016). Furthermore, there is also evidence supporting not a decrease, but a shift in distribution from shallow to deeper roots of belowground biomass with lower amounts of precipitation (Zhang et al., 2019).

I expected a higher allocation to vegetative traits with increasing precipitation, such as increase vegetative height, number of leaves and leaf area (Guittar et al., 2016; Moles et al., 2014; Skarpaas et al., 2016). Though I find that the traits that show significant patterns with precipitation generally decrease, such as number of leaves and vegetative height, which contrasts my predictions. Although the species that have negative trait responses associated with precipitation also decrease in shoot:root ratio.

Limitations of the study

Using only aboveground and belowground biomass has its conceptual flaws, mainly that adding stems, leaves and reproductive biomass into one unit doesn't take into account the different functions they have (Poorter & Nagel, 2000). In addition, belowground biomass as measurement of resource uptake without considering surface area of the roots might

underestimate function (Weiner, 2004). This can be true for the alpine species have shown to allocate more biomass to fine roots, which has increased surface area and hence a larger water uptake potential (Körner & Renhardt, 1987). Furthermore, allocation as a measurement of function fails to address that a plant parts have different functions, for example roots accounts for resource uptake, storage and anchoring (Weiner, 2004). In addition, the traits that are measured or calculated may under- or overestimates their function. For example, the effects on the simplified measurement for leaf area should be interpreted with caution, as it may not accurately reflect the actual area. Another example is the fact that *Succisa pratensis* flowers are actually compound flower heads with several flowers per flower head. Since these flower heads were counted as one flower it may underestimate how much it invests into reproduction. Furthermore, the statistical analysis itself comes with a chance of error, as the p-value cutoff at 0.05 will cause an incorrect rejection of the null hypothesis five percent of the time (type 1 errors), In addition, there are a lot of variables measured and used in different tests, which increases the chance of false positives.

Concluding remarks

I found that increasing precipitation had an overall negative effect on aboveground biomass. In addition, the trait response and allocation along precipitation is interspecific, thus understanding plant response regarding the direct effects on climate change is crucial for predicting changes in ecosystem functioning. Furthermore, this research may help in gaining further insight about the potential interactions caused by extant and novel range shifts, as competitor-identity may influence the survivability of focal species (Alexander et al., 2015). Further research on the interactions between species, perhaps between several functional groups, is needed to gain more knowledge about how alpine systems may react in the future.

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Appendix I

Abbreviations: SH = shoot height, LSL = length of longest leaf stalk, NS = number of shoots, NL = number of leaves, LL = length of longest leaf, WL = width of longest leaf, LL_{area} = leaf area of the longest leaf, LIS = length of longest inflorescence shoot, NFI = number of inflorescence shoots, #B = number of buds, #F = number of flowers, #PC = number of potential capsules, #C = number of capsules, #R = total number of reproductive material.

Table 6. Vegetative traits compared to *Veronica alpina* and the alpine species groups and individual species and species group models in response to precipitation. Parentheses indicate only one species is measured within the species group. Significant values are marked in bold and are evaluated using t-values larger than 2.

	SH (mm)	LSL (mm)	NS	NL	LL (mm)	WL (mm)	LL_{area} (log2)
Model 1: Precipitation * Species							
Veronica alpina	**57.14****		**1.98*****	**14.98*****	**11.59*****	**5.78*****	**5.85*****
Δ Sibbaldia procumbens		**INT 15.7*****		5.54	-0.84		
Δ Veronica officinalis	17.93		**1.81****	**14.81*****	**9.41*****	**5.24****	**1.87****
Δ Viola canina		**11.81****	-0.57	**-8.73***	**8.51*****	**10.02*****	**2.24****
Δ Succisa pratensis				-1.49	**131.54*****	**21.38*****	**5.94*****
Δ Hypericum maculatum	**137.57****		-0.71	**58.28*****	10.15(*)	**7.76*****	**2.25*****
Precipitation	-21.26 (*)		0.61(*)	2.66	-1.0	-0.82	-0.41(*)
Δ Precipitation * Sibbaldia procumbens		**INT -3.55***		-7.51(*)	-0.47		
Δ Precipitation * Veronica officinalis	16.97		**-1.48****	**-9,71***	0.64	0.92	0.39
Δ Precipitation * Viola canina		0.31	-0.73(*)	-3.21	-1.12	-0.49	0.11
Δ Precipitation * Succisa pratensis				-0.05	**-1.14*****	1.36	0.33
Δ Precipitation * Hypericum maculatum	21.6		-0.65	13.21	1.68	3.73	1.01(*)
Model 2: Precipitation * Species group							
Alpine			1.98	17.82	11.16	5.78	0.1
Δ Extant			0.64	0.26	9.25	7.68	2.07
Δ Novel			-0.64	21.12	66.25	13.87	3.9
Precipitation			**(0.61*)**	-1.5	-1.26	(-0.82)	**(-0.41***)**
Δ Precipitation * Extant			**-1.04***	-1.72	-0.14	0.09	0.23(*)
Δ Precipitation * Novel			(-0.57)	5.2	**-12.2*****	1.59	**0.41***
Model 3: Veronica alpina							
Δ Precipitation	**-21.58****		**0.6****	2.72	**-1.0****	**-0.82*****	**-0.41*****
Model 4: Sibbaldia procumbens							
Δ Precipitation		**-4.11****		**-5.73***	-1.73(*)		
Model 5: Veronica officinalis							
Δ Precipitation	-5.11		**-1.02****	**-8.24***	-0.45	0.09	-0.03
Model 6: Viola canina							
Δ Precipitation		**-3.37*****	**-0.14***	**-0.71***	-2.6	-1.57	-0.35
Model 7: Succisa pratensis							

Δ Precipitation				3.05	-18.3	0.62	-0.09
				Model 8: Hypericum maculatum			
Δ Precipitation	1.31		0.15	0.18	0.79	2.2	0.54
				Model 9: Alpine			
Δ Precipitation				-1.5	-1.36(*)		
				Model 10: Extant			
Δ Precipitation			**-0.43***	**-3.28(*)**	**-1.44(*)**	-0.75	-0.19
				Model 11: Novel			
Δ Precipitation				3.168	**-13.42***	1.2	-0.006

Table 7. Reproductive traits compared to *Succisa pratensis* and the novel species groups and individual species and species group models in response to precipitation. Parentheses indicate only one species is measured within the species group. Significant values are marked in bold and are evaluated using t-values larger than 2.

	LIS (mm)	NFI	#B	#F	#PC	#C	#R
			Model 1: Precipitation * Species				
Succisa pratensis	**489.5*** **	**0.98*** **	1.42(*)	0.27	0.18	0	1.88
Δ Hypericum maculatum	**-254.6*** **	-0.27	**7.26*** **	0.16	-0.07	-1.28	6.4(*)
Δ Veronica alpina	**-387.5*** **	-0.34	-0.85	-0.06	-0.13	1.76	0.5
Δ Sibbaldia procumbens	**-457.5*** **	**-0.49***	-0.17	-0.23		0.46	-0.12
Δ Veronica officinalis	**-356.9*** **	-0.09	0.14	0.49	**2.96*** **	**7.0***	**10.6*** **
Δ Viola canina	**-408.8*** **		-0.84	0.17	-0.17	-0.57	-1.06
Precipitation	16.1	-0.21	0.23	-0.02	-0.11	0	0.08
Δ Precipitation * Hypericum maculatum	**-225.2*** **	0.62	**7.13*** **	-0.01	-0.1	-1.0	6.05
Δ Precipitation * Veronica alpina	-34.67	0.02	-0.22	-0.04	00.06	-0.12	-0.43
Δ Precipitation * Sibbaldia procumbens	-9.22	0.01	-0.25	0.006		-0.57	-0.71
Δ Precipitation * Veronica officinalis	-24.15	-0.24	-1.14	-0.24	**-1.42** **	-3.92(*)	**-6.73*** **
Δ Precipitation * Viola canina	34.75		-0.36	0.001	0.12	-0.008	-0.28
			Model 2: Precipitation * Species group				
Novel	**417.03*** **	0.67	**5.52***	0.34	0.17	-0.27	3.18
Δ Alpine	**-349.6***	-0.11	-4.51	-0.22	-0.15	1.37	-1.1
Δ Extant	**-311.3***	-(0.21)	**-5.86*** **	0.24	1.43	3.64	3.63
Precipitation	-16.1	-0.09	4.3(*)	-0.04	-0.13	-0.1	0.8
Δ Precipitation * Alpine	8.23	-0.1	**-4.27***	0.003	0.1	-0.27	-1.3
Δ Precipitation * Extant	9.32	(-0.1)	**-5.7*** **	-0.06	-0.49	-1.53	**-3.62***
			Model 3: Veronica alpina				
Δ Precipitation	-17.7	-0.18	-0.08	-0.05	-0.05	-0.1	-0.33
			Model 4: Sibbaldia procumbens				
Δ Precipitation	4.39	**-0.2***	-0.02	-0.02		**-0.57** **	-0.62
			Model 5: Veronica officinalis				
Δ Precipitation	-8.96	**-0.46*** **	-0.91	-0.27	**-1.53** **	**-3.91*** **	**-6.64*** **
			Model 6: Viola canina				
Δ Precipitation	-17.2		-0.14	-0.03	0.01	-0.02	**-0.19***

			Model 7: Succisa pratensis				
Δ Precipitation	0.16	-0.21	0.3	0.02	-0.11		0.08
			Model 8: Hypericum maculatum				
Δ Precipitation	**-221.3***	0.41	**8.28***	0.06	-0.22	0.002	6.14
			Model 9: Alpine				
Δ Precipitation	-7.75	-0.19(*)	0.003	-0.04	-0.02	-0.36(*)	-0.5(*)
			Model 10: Extant				
Δ Precipitation	**-15.59***	**(-0.18**)**	-0.45	-0.12	**-0.62****	-1.64	**-2.82****
			Model 11: Novel				
Δ Precipitation	14.31	0.21	1.79	-0.02	-0.12	-0.005	0.17