Genetic differentiation and plasticity interact along temperature and precipitation gradients to determine plant performance under climate change

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Summary

1. Understanding species’ abilities to cope with changing climate is a key prerequisite for predicting the future fates of species and ecosystems. Despite considerable research on species responses to changing climate, we still lack understanding of the role of specific climatic factors, and their interactions, for species responses. We also lack understanding of the relative importance of plasticity vs. adaptation in determining the observed responses.

2. As a model, we use a dominant clonal grass, Festuca rubra, originating from a natural climatic grid of 12 localities in western Norway that allows factorial combinations of temperature (mean growing season temperatures ranging from 6.5°C to 10.5°C) and precipitation (annual precipitation ranging from 600 mm to 2700 mm). We grew clones from all populations in four growth chambers representing the four climatic extremes in the climate grid (warm/cold × wet/dry).

3. Genetic differentiation and direction and magnitude of plastic responses vary systematically among populations throughout the climatic grid. Growth-related plant traits are highly plastic and their degree of plasticity depends on their origin. In contrast, the traits reflecting species’ foraging strategy are not plastic but vary with the climate of origin. Levels of plasticity of growth-related traits and genetically differentiated foraging traits thus might constrain local populations’ ability to cope with novel climates.

4. Synthesis: Shifts in temperature and precipitation, at the scale and direction expected for the region in the next century, are likely to dramatically affect plant performance. This study illustrates how the interplay between genetic differentiation and plasticity in response to both
temperature and precipitation will affect the specific responses of species to climate change. Such complex responses will affect how climate-change impacts scale up to the community and ecosystem levels. Future studies thus need to specifically consider regionally relevant climate-change projections, and also explore the role of genetic differentiation and plasticity and how this varies within local floras. Our study also demonstrates that even widespread species with seemingly broad climatic niches may strongly differ in their population performance and plasticity. Climate-change studies should therefore not be limited to rare and restricted species.

**Keywords:**
Climate change, clonal growth, extravaginal ramets, foraging, genotype × environment interaction, local adaptation, plant performance, reaction norm, reciprocal transplant experiment, tillering.

**Running head: Drivers of plant growth under climate change**
Introduction

Understanding species’ abilities to respond to climate change is important not only for the prediction of future species and ecosystem distribution and loss, but also for effective investment in biodiversity and ecosystem protection (Walther et al. 2002; Moss et al. 2010; Rands et al. 2010; Blume-Werry et al. 2016). While migration to track suitable habitats is an obvious response to changing climate (e.g., Kokko & Lopez-Sepulcre 2006; Nicotra et al. 2010), the slow migration rates of most plant species imply that many species and populations will need to face climate change in situ (e.g., Davis & Shaw 2001; Malcolm et al. 2002; Thomas et al. 2004; Loarie et al. 2009; Bullock et al. 2012; Ravenscroft, Fridley & Grime 2014).

An important mechanism that allows plants to cope with climate change is phenotypic plasticity, i.e. the ability of a genotype to change phenotypic expression in response to different environmental conditions (e.g., Pigliucci 2001; Valladares, Sanchez-Gomez & Zavala 2006; Matesanz, Gianoli & Valladares 2010; Nicotra et al. 2010; Lazaro-Nogal et al. 2015). Phenotypic plasticity allows populations to buffer detrimental effects of rapid climate change – at least in the short term – thereby allowing time for evolutionary changes to occur (e.g., Ayrinhac et al. 2004, Jump & Peñuelas 2005, Kim & Donohue 2011; Anderson et al. 2012; Kim & Donohue 2013; Monty et al. 2013; Padilla et al. 2013). However, phenotypic plasticity is most likely to be effective in coping with weak, short-term, undirected, random, and unpredictable fluctuations in the environment (Gienapp et al. 2008, but see Matesanz, Gianoli & Valladares 2010). Surviving more extensive and directional changes are more likely to require natural selection, favouring genotypes able to grow and reproduce well under the new environmental conditions and resulting in genetic change in the population (Ohsawa & Ide 2008; Matesanz, Gianoli & Valladares 2010; Nicotra et al. 2010). In cases when the specific selection pressures lead to maximized fitness of different local genotypes under different local conditions, this will result in population differentiation and local adaptation (sensu Kawecki & Ebert 2004).

The selection pressures leading to genetic differentiation of populations may not only select for differentiation in mean traits (i.e., genotype × environment interactions), but may also result in differentiation in the degree of phenotypic plasticity (Kawecki & Ebert 2004; Hamann et al. 2016). While plastic variation between populations, reflected by the genotype × environment interaction, has been repeatedly demonstrated (reviewed e.g. in Marais, Hernandez & Juenger 2013 and Franks, Weber & Aitken 2014), only a few studies have explicitly evaluated differences
in the degree of plasticity in plants of different origin (Eranen & Kozlov 2009; Frei, Ghazoul & Pluess 2014). These studies suggest that plants from mesic lower-elevation climates tend to have higher plasticity than plants from more extreme climates at higher elevations. They did not, however, explore the effect of specific climatic drivers on the plasticity, and are thus not able to predict species responses to specific climate changes. Assessment of the degree of genetic differentiation vs. trait plasticity from populations across a range of well-defined environments is thus crucial for understanding species potential to respond to novel climatic conditions. As the degree of trait plasticity (and presumably population differentiation in plasticity) varies across traits (e.g., Sultan & Bazzaz 1993; Sultan 2000; Griffith & Sultan 2006), multiple traits with different functions need to be explored and compared to understand the relative importance of these processes in populations of different origin and across a species’ range.

One key methodology that has proved useful in studies of genetic differentiation vs. phenotypic plasticity in relationship to changing climate and in assessing if genetic differentiation led to local adaptation in the species, is using reciprocal transplant experiments in the field (Hoffmann & Sgro 2011; Hargreaves, Samis & Eckert 2014; Franks, Weber & Aitken 2014). Most reciprocal transplant experiments have been done by transplanting individuals upwards or downwards along elevational or latitudinal gradients and then documenting their performance (e.g., Etterson 2004; Byars, Papst & Hoffmann 2007; De Frenne et al. 2011; Agren & Schemske 2012; Kim & Donohue 2013; Scheepens & Stocklin 2013; Schreiber et al. 2013; Zhou et al. 2013; Hamann et al. 2016). While all these studies allow us to understand the possible consequences of the specific suites of climatic factors correlated to the particular spatial gradient, they do not allow a more general understanding of how performance will be affected by interacting effects of simultaneous change in multiple specific climatic factors. Nor can they be used to assess responses to not yet realized novel climates. Experiments that make use of the reciprocal setup, augmented by the strengths of controlled-condition experiments, e.g., by growing populations of known climatic origin in multiple growth chambers simulating both home climates and specific climatic-change scenarios, can provide mechanistic understanding of species performance in response to specific climatic changes and to novel climates. While a range of previous studies used various alternatives to reciprocal transplant experiments to assess the importance of genetic differentiation and plasticity in response to climate (Hoffmann & Sgro 2011; Franks, Weber & Aitken 2014), we are not aware
of any study which would use such an approach to specifically study plant growth responses to different types of well defined climates.

Climate change is not a unidirectional change in one climatic factor alone, but is predicted to bring about novel combinations of precipitation, temperature and their fluctuations (IPCC 2014). Understanding the interactive effects of specific climatic drivers on species performance, and the specific mechanisms and processes underlying these responses, is thus important for predicting species responses to future climatic changes (Elith & Leathwick 2009; Gotelli & Stanton-Geddes 2015; Meineri et al. 2015; Parmesan & Hanley 2015; Moran, Hartig & Bell 2016). Several studies have assessed the interactive effect of CO$_2$ and temperature or precipitation on species performance (e.g., Volk, Niklaus & Korner 2000; Shaw et al. 2002; Dieleman et al. 2012). To date only (Suseela et al. 2012) and Meineri, Spindelbock & Vandvik (2013) have explored the interactive effects of temperature and moisture - and demonstrated that such interactions can be important. Their studies, however, dealt with soil respiration and seedling recruitment respectively, and we are not aware of any such studies on plant-species performance.

The aim of this study is to understand the importance of genetic differentiation along gradients of temperature and moisture and the degree of plastic response to shifts in the same variables, by determining the performance of a widespread clonal grass, *Festuca rubra*. The species grows across broad climatic gradients and is characterized by considerable genetic differentiation even at the fine scale. It is also plastic in its response to environmental factors (Skálová et al. 1997; Herben et al. 2001). We used plants originating from locations of different temperature and precipitation from a unique natural grassland ‘climate grid’ spanning ~4°C in temperature and ~2100 mm in precipitation established in western Norway (the SeedClim grid, see Meineri, Skarpaas & Vandvik 2012; Meineri, Spindelbock & Vandvik 2013; Meineri et al. 2014; Klanderud, Vandvik & Goldberg 2015). We set up a growth chamber experiment simulating different combinations of temperature and moisture derived from the data on the conditions in the original localities. In this way, we performed a controlled-climate equivalent of a reciprocal transplant experiment, i.e., a ‘reciprocal climate common garden experiment’. This approach has the advantage that it allows us to explore the effects of specific climate change drivers, alone as well as in combination at pre-determined levels, and it ensures that climate is really the only driver of species performance. The climatic prediction for Norway suggests increases in both precipitation (by about 18%) and temperature (by about 1.5°C to 2.2°C) over the next century (Hanssen-Bauer et
In this study, we aim to answer the following questions: (1) *What is the relative importance of genetic differentiation and plasticity in determining plant performance in response to different temperature and precipitation?* We hypothesize that both genetic differences and plasticity will contribute to variation in plant performance along the bioclimatic gradients and in response to climate change, with interactions indicating that climate change responses vary across the species’ climatic niche. 2) *How does the degree of plasticity vary among populations across broad-scale temperature and precipitation gradients?* We hypothesize that plants from warmer and wetter conditions will be more plastic due to higher competition under these conditions (Olsen et al. 2016). (3) *What is the effect of the specific climate-change scenario for the region on species performance, and what is the relative importance of temperature and precipitation change in driving these responses?* We hypothesize that all plants will strongly profit from transplantation to warmer and wetter conditions, i.e. from the projected climate change in the region as such conditions are likely more favourable for the species. Drought might, however, turn the positive effects of warmer conditions to negative as plants in warm conditions will have increased moisture requirements. (4) *How do these patterns differ between different plant traits?* We hypothesize that the degree of plasticity and genetic differentiation will strongly vary between traits due to different developmental constraints underlying different traits (Sharma et al. 2016). High between-trait variation in response to local climate has already been shown in the same system at the community level (Guittar et al. 2016).

**Methods**

**Study species and localities**

*Festuca rubra* L. is a common perennial grass species of temperate grasslands in Europe. In the experiment, we used *Festuca rubra* ssp. *rubra*, a widespread hexaploid type from the *F. rubra* complex. It grows at different densities in grasslands, both as a dominant with only a few other species and also as a subordinate of species-rich stands. It reproduces by seeds as well as vegetatively, producing both intravaginal and extravaginal tillers on rhizomes. *Festuca rubra*
possesses considerable genetic variability and plasticity in growth and foraging-related traits even within a single grassland locality (Skálová et al. 1997; Herben et al. 2001).

The experimental plants were collected along a natural climatic grid established in western Norway (the SeedClim Grid, see Klanderud et al. 2015). It comprises 12 grassland localities representing three levels of summer temperature [the experiment was set up to achieve means of the four warmest months for individual locality types of ca. 6.5°C (alpine, ALP), 8.5°C (sub-alpine, SUB) and 10.5°C (boreal, BOR) combined with each of four levels of mean annual precipitation [ca. 600 (1), 1300 (2), 2000 (3) and 2700 (4) mm, Fig. 1, Meineri et al. 2014; Klanderud et al. 2015]. The target communities are grazed intermediate-rich meadows (Potentillo-Festucetum ovinae; G8 sensu Fremstad 1997) occurring on south-west facing (with the exception of one site, (BOR 3), which was exposed to the east), shallow slopes (5–20°) with relatively base-rich bedrock. Sites were selected specifically to ensure that grazing regime and grazing history, bedrock, slope, aspect and vegetation types are as similar as possible.

Geographical distance between sites is on average 15 km and ranges from 0.65 km (BOR2 and SUB2) to 175 km (BOR1 and BOR4) (Meineri et al. 2014).

**Figure 1.** Position of the studied localities along the temperature and precipitation gradient. The dots represent all the localities in the SeedClim grid. The empty circle indicates the locality from which *Festuca rubra* was not available for this study.
Plant material

At each locality, we laid out transects along which we collected at least 40 clones of *F. rubra*, with at least 1 m between neighbour plants, in July 2014. The living plants were transported to the experimental garden of the Institute of Botany, Czech Academy of Sciences, Průhonice, Czech Republic (49°59'38.972"N, 14°33'57.637"E; means of the four warmest months 16.5°C; and regular watering during the vegetation season) and immediately after the transport they were planted into pots (16 × 16 × 16 cm, filled with a mixture of common garden soil and sand at a 2:1 ratio). The common garden soil comprised compost from the experimental garden containing approximately 0.135 % of nitrogen, 1.35% of carbon and 46.5 mg of phosphorus in 1000 g of soil. The plants were allowed to recover from the transport. At the end of August 2014 they were extracted from the pots and reduced to a single ramet. This was done to ensure that there was only one clone per pot, preventing the possibility that we originally collected multiple intermingled clones. At this stage, we also confirmed the identity of plants using flow cytometry (see Castro *et al.* 2011 for methods) and selected only those with a genome size ranging between 9.29 and 10.41 pg. This corresponds to the most widespread hexaploid cytotype of *F. rubra* (Sampoux & Huyghe 2009). From each locality we selected 25 viable genotypes fulfilling this condition. We use the term genotype throughout the subsequent text as Šurinová *et al.* (unpubl.) confirmed that we worked with individuals that were genetically differentiated from each other and therefore true independent genotypes. All the samples from the ALP2 locality belonged to other *Festuca* species, so the study is based on 11 populations.

We continued cultivating the genotypes in the garden until November 2014 to remove possible transgenerational effects. We then transferred the genotypes to the greenhouse. The temperature in the greenhouse was set to be between 5°C and 10°C. At the beginning of February 2015, about 10 single ramets of similar size, each with three leaves and without visible signs of initiating flower buds, were cut from the tussocks and placed into small plastic cups filled with water, to set roots. At the end of February 2015, ramets with developed roots were individually planted into 5 × 5 × 8.5 cm pots filled with a mixture of 1 part common garden soil and 2 parts sand. While the pots may seem quite small, our model species is a tussock grass of small stature and slow growth and the pots were not filled by the plant at the time of harvest. We are thus confident that the results of the experiment are not affected by pot size. For each of the 25 genotypes from all of the 11 populations, we planted 4 ramets resulting in a total of 1100 ramets.
The pots were kept in the greenhouse and ramets that died within the next two weeks were replaced. The plants in single pots will be referred to as individuals in the subsequent text (there were 4 individuals per genotype, one in each growth chamber as described below).

In mid-March 2015, we measured the height of the tallest ramet and noted the number of ramets of each individual providing us with a plant size value at the beginning of the experiment. This was later used as a covariate in the analyses. Individuals were assigned to 4 groups, such that one ramet of each genotype from each population was represented in each group, for cultivation in growth chambers. In each group we had 11 populations × 25 genotypes, i.e. 275 individuals in each growth chamber, comprising 1100 individuals in total. Pots assigned to each growth chamber were fully randomized, placed into three metal trays and moved to the growth chambers. The position of the pots in each growth chamber was randomized monthly. The position of each genotype was always identical across the four growth chambers. For discussion of using only four growth chambers in our study, please see Methodological considerations at the end of the Methods section.

The plants were cultivated in climatic chambers (Vötch 1014) under conditions simulating four different scenarios for the spring to summer climate in the field (second half of April–second half of June). The four scenarios were derived from climate data for the four extreme localities in the SeedClim grid (wettest/driest combined with warmest/coldest), within the technical limits of the climatic chambers and avoiding night frosts (minimum temperature during cultivation being 3°C). Note that this is in effect a controlled-climate equivalent to a reciprocal transplant experiment, and we hence refer to it as a “reciprocal climate common garden experiment”. The temperature in the growth chamber differed between the cold and warm treatments and changed over the growing season following the course of temperature at the natural localities (for details see Table 1). To set the correct moisture level in the growth chambers, we used TMS4 data-loggers to continuously measure soil moisture in the pots (TOMST Co., Hemrová, Knappová & Münzbergová 2016) and identified the correct level of watering to achieve soil moisture comparable to that at the localities. As a result of this calibration, the dry regime plants were watered with about 20 ml of tap water per plant applied to the trays if the soil moisture was lower than 15%. In the wet regime, plants were cultivated under full soil saturation with about 1.5 cm of water in the bottom of the tray. Soil moisture was monitored continuously during the whole experiment and watering was modified to ensure constant moisture throughout the experiment.
Three data-loggers were placed in each growth chamber. Each data LOGGER was placed in a pot
with a growing *Festuca* plant, which was intermixed among the experimental plants and was of
the same size as the experimental plants, but was not a part of the experiment. For all the regimes,
the same day length and radiation were used, i.e. 16 hours of full light (6 am – 10 pm) and 4
hours of full dark with a gradual change of light availability in the transition between the light
and dark period over 2 hours. Over the full light period, the radiation was 360 µmol.m⁻².s⁻¹, red
radiation (R, λ=660 nm) of 26 µmol.m⁻².s⁻¹, and far-red radiation (FR, λ=730 nm) of 15 µmol.m⁻².
².s⁻¹, R/FR = 1.73 (the radiation measured using a SPh 2020 photometer from Optické dílny
Turnov, Czech Republic).

**Plant performance**

Plant performance was recorded three times during the experiment. Specifically, we
counted the number of all ramets and of extravaginal ramets, and measured the length of the
longest ramet (hereafter referred to as plant height) of each individual at the beginning of May,
mid-June and end of August 2015. In mid-June and at the end of August 2015, we also cut all the
aboveground biomass at 3 cm, dried it to constant weight at 60°C and weighed it. The harvest
simulated biomass removal during regular management in the field sites. After the harvest at the
end of August, the remaining parts of the plants were removed from the pots, the belowground
parts were carefully washed and sorted into roots and rhizomes, dried to a constant mass at 60°C
and weighed. In addition, total length of rhizomes was measured before drying. As the total
rhizome length is strongly correlated with rhizome dry mass (r = 0.95), rhizome length is not
considered in the subsequent analyses. The number of extravaginal ramets divided by the total
number of ramets was calculated to give proportional data per plant. Production of extravaginal
ramets by the species indicates the species’ ability to forage in space and thus to occupy areas
further away from the maternal ramet (Ye, Yu & Dong 2006). This may be an important
mechanism that allows species to cope with novel environments.

**Data analyses**

To study the effect of the conditions of the original sites as well as the target conditions
under cultivation on performance of the plants in the experiment, we coded the climatic
conditions each individual was subjected to relative to its climate of origin in the field. To do this,
temperature regimes of origin were coded with respect to the mean temperature of the four
warmest months for each locality type, i.e. as 6.5, 8.5 and 10.5°C. Similarly, moisture regimes of
origin were coded by mean annual precipitation at the localities, i.e. 600, 1300, 2000 and 2700
mm. We used the same codes to describe the conditions in the growth chambers, which simulated
the 4 climatic extremes at the sites, i.e. 6.5 and 10.5°C for low and high temperature and 600 and
2700 mm for low and high moisture. We tested the effects of the temperature and precipitation of
the origin and of the target and all their interactions on performance of the plants. We used results
of these tests to express the variation explained by environment of origin, target environment and
their interaction. A significant effect of target conditions will indicate plasticity of the plants, a
significant effect of origin will indicate genetic differentiation, and the interaction between target
and origin will indicate genetic differentiation in plasticity.

While significant interaction between target and origin will indicate genetic differentiation
in plasticity, it does not provide any information on whether these differences are due to a
different direction of the response to the environment, or whether there are any clear differences
in the magnitude of the response. To assess the degree of plasticity of the plants from the
different environments, we thus calculated the phenotypic plasticity index as the difference
between the maximum and minimum value of the trait for each clone (out of the four values
across the growth chambers) divided by the maximum value (Valladares et al. 2000). We use this
index as it is easy to use, robust, widely applied, and can be easily compared among traits
(Valladares, Sanchez-Gomez & Zavala 2006).

To assess whether characterization of populations by their original temperature and
precipitation and their interaction is sufficient, or where there is additional between-population
variation that cannot be explained by these characteristics, we performed tests in which the
temperature and precipitation of the original localities were replaced by locality code. The
original models and the models with the locality code were compared using Akaike information
criteria (AIC, Crawley 2012): models with the locality code were slightly better. The difference
in the AIC values, however, only range between 0.4 and 2.9% for the different dependent
variables suggesting that the two types of models are largely similar. The less parsimonious
locality code models are thus not presented further.

To assess whether the possible genetic differentiation of the populations lead to local
adaptation, we used the local vs. foreign criterion, as suggested by Kawecki & Ebert (2004). To
do this, we included an additional code distinguishing plants grown in their home temperature or
home moisture (i.e. plants grown in conditions simulating conditions of their site of origin) from
plants grown in a foreign environment (i.e. plants grown in all other conditions than the
conditions of their site of origin). We included the effect of home temperature and home moisture
and their interaction with temperature and moisture of origin in the models. The effect of these
factors was tested against original climate × target climate interaction as in previous studies (e.g.,
Raabová, Münzbergová & Fischer 2007). While there are many significant effects in these tests,
most of the patterns detected are also clear from the tests presented below. These results are
therefore only briefly mentioned in the results section and are mainly presented in the
supplementary material Text S1 and Fig. S2.

Finally, we also explored impacts of the directionality of the climate change by subtracting
the above described values of temperature and moisture of the growth chambers from the values
of temperature and moisture at the original localities. In this way we obtained codes ranging from
-4°C to 4°C for temperature and -2100 mm to 2100 mm for moisture with negative values
indicating transplantations to colder or drier conditions and positive values indicating
transplantations to warmer or wetter conditions. Zero indicates plants growing under their home
conditions. We then tested the effect of these differences and their interaction on plant
performance using the models described below. Significant effects detected in this test will
indicate that species performance will be affected by the specific type of climate change to occur.

All of the above described tests were done for each measurement period and the following
dependent variables were used – plant height, number of ramets, and proportion of extravaginal
ramets. In addition, the following variables were tested based on the results at the time of final
harvest of the experiment: total aboveground biomass, total belowground biomass, ratio between
belowground and aboveground biomass, and rhizome biomass. Because the data from the first
and second censuses did not bring any additional insights to data from the third final census, we
only present the latter.

For plant height and number of ramets, we used the same characteristics measured at the
beginning of the experiment as a covariate. We used plant height × number of ramets as a proxy
of plant biomass, and as a covariate when using aboveground, belowground and rhizome biomass
as dependent variables. There was no need for a covariate for number of extravaginal ramets as
there were no extravaginal ramets at the beginning of the experiment. Plant height, number of
ramets and aboveground and belowground biomass were tested assuming a normal distribution of the data. Data on rhizome biomass and belowground to aboveground ratio were log transformed to fit assumptions of normality and homogeneity of variance. The proportion of extravaginal ramets was tested assuming a binomial distribution (number of extra- and intravaginal ramets were linked using cbind function and tested as binary data, (Crawley 2012). All tests were done using mixed effect models as implemented in the lme4 package in R (Bates et al. 2015) with genotype as a random factor.

In this study, we performed each test independently for 7 different traits measured on the same experimental plants. Theoretically, we should apply the Bonferroni correction and reduce the conventional p-level from 0.05 to 0.0071 (Dunn 1961). We decided to use a modification of this approach, the sequential Bonferroni correction (Holm-Bonferroni correction, Rice 1989) as it is considered as less conservative. Still any such correction is considered as too conservative by some authors (e.g., Moran 2003; Garcia 2004; Gotelli & Ellison 2004) and many studies have not applied any correction, for this reason (e.g., Münzbergová 2007; Bowman et al. 2008; Scheepens & Stocklin 2013). Here, we report and illustrate results both with and without this correction (see also Husáková & Münzbergová 2016).

Methodological considerations

It may be argued that our experiment is pseudoreplicated as the growth chambers may theoretically differ in a range of other variables (e.g. light intensity) leading to possible spurious treatment effects (Hurlbert 1984). The conclusions of Hurlbert (1984) on pseudoreplication in growth chamber experiments have, however, been extensively criticized (e.g., Oksanen 2001; Johnson et al. 2016). Later, Hurlbert (2004) concluded that such experiments can be analysed with standard statistical approaches as long as the interaction term is used as an estimate of the error term to test the main effect. In our experiment, the effect manipulated at the growth chamber level, i.e. the target environment, is not the effect of primary interest. Rather, we were primarily interested in the effect of original environment, which is well replicated and the interaction between the original and target environment. In such a case, using the standard error terms is well justified. Thus in line with a range of other studies using similar settings for unreplicated gardens at different elevations (Scheepens & Stocklin 2013; Gugger et al. 2015) or growth chambers (Bezemer, Thompson & Jones 1998; Cavieres & Arroyo 2000; Souther,
Lechowicz & McGraw 2012; Matias & Jump 2014; Zhang et al. 2014), we suggest that such
studies are useful by allowing the separation of genetic differentiation of plants from their
phenotypic plasticity and provide insights into the effect of specific climatic variables without the
confounding effects of other naturally varying factors. For an extended discussion of this issue,
see Text S3.

Results

Target climate

All of the observed plant characteristics were significantly affected by target moisture and
temperature, except for proportion of extravagal ramets and rhizome biomass, suggesting that
the plants respond plastically to the environment (Fig. 2, Table 2). Plants in warm growth
chambers were significantly taller (Fig. S4A), produced more ramets (Fig. S4B), had more
aboveground biomass (Fig. 3A), but had lower belowground biomass (Fig. S4C) and lower below
to aboveground biomass ratio (Fig. S4D) than plants grown in cold conditions. The plants in the
dry growth chambers were also taller, produced more ramets, had greater belowground biomass
and rhizome biomass, and had higher below to aboveground biomass ratio (Fig. S4A-E) and
proportion of extravagal ramets (Fig 3B). The effect of temperature interacted with the effect of
moisture in several cases (Table 2). Specifically, the negative effect of moisture on plant height
was stronger in the cold growth chamber with plants in the cold-wet growth chamber being the
shortest (Table 2, Fig. S4A). Low temperature in the dry growth chambers led to an increased
proportion of extravagal ramets, while low temperature in the wet growth chamber led to a
decrease in the proportion of extravagal ramets (Fig. 3B). Aboveground biomass increased with
temperature in dry but not in wet growth chambers (Fig. 3A). Belowground biomass decreased
with temperature in the wet growth chambers but not in the dry ones (Fig. S4C). All the effects of
target temperature, target moisture as well as their interaction are significant after applying the
Bonferroni correction (Table 2).
Figure 2. Proportion of variation explained by the target environment, the environment of origin and their interaction. The remaining variation is unexplained.

Original climate

Plant height, aboveground biomass and belowground biomass are significantly affected by temperature of origin and aboveground and belowground biomass also by moisture of origin (Fig. 2, Table 2), suggesting genetic differences between the plants originating from different environments. Plants originating from warmer sites were significantly taller and had more aboveground (Fig. 3A) and belowground biomass (Fig. S4C) than those from colder sites. Plants from wetter sites had more aboveground biomass (Fig. 3A) and belowground biomass (Fig. S4C). Temperature and moisture of origin also interacted in their effects (Table 2). Specifically, plants produced less aboveground biomass (Fig. 3A), were shorter and had more rhizomes when originating from wetter colder sites, while the values were opposite when they were from wetter warmer sites (Fig. S4). For proportion of extravaginal ramets, the effect of moisture is more pronounced in plants originating from warmer conditions and thus plants from warm and wet sites produced the lowest proportion of extravaginal ramets (Fig. 3B). The effects of original temperature, original moisture, as well as their interaction are still significant after applying the Bonferroni correction, with one exception: the interactive effect of original moisture and temperature on aboveground biomass (Table 2).
Figure 3. The effect of original environment and target environment on plant performance measured as A) aboveground biomass and B) proportion of extravaginal ramets. ALP denotes the cold alpine sites, SUB denotes sub-alpine sites and BOR denotes warm boreal sites. 1 to 4 indicates moisture at the original localities with 1 indicating the driest and 4 the wettest sites; for the test of significance see Table 2. The graphs show mean ± SE.

Original environment also affects trait plasticity. Specifically, the plasticity index for aboveground (Fig. 4) and belowground biomass (Fig. S5), number of ramets and plant height are
significantly affected by moisture of origin (Table 3) with plants from drier sites being more plastic in all the traits. In addition, plasticity in belowground biomass and plant height is also affected by temperature of origin with plants from the colder sites being more plastic (Table 3, Fig. S5). Three out of six of these significant effects are non-significant after applying the Bonferroni correction (Table 3). Plants from the colder sites are still significantly more plastic in plant height, and plants from drier sites are significantly more plastic in aboveground and belowground biomass after the correction (Table 3).

**Figure 4.** Plasticity index of aboveground biomass of plants of different origin. ALP denotes the cold alpine sites, SUB denotes sub-alpine sites and BOR denotes warm boreal sites. 1 to 4 indicates moisture at the original localities with 1 indicating the driest and 4 the wettest sites.

**Interaction between target and original climate**

There are also a few significant interactions between plant origin and responses in the target growth chambers (Fig. 2, Table 2, Table S6). Two out of the three significant double interactions are non-significant with the Bonferroni correction. As the important interactive patterns are seen from the exploration of the difference between target and original environment presented below, the results are not described in detail here, but only in Text S7.
The tests of the effect of local vs. foreign conditions on species performance exploring local adaptation in the system are shown in detail in Text S1, Fig. S2 and Table S8. There is a number of significant differences indicating that plants grown in their local conditions perform better than plants grown in foreign conditions on average. However, as seen in Fig. 5 and Fig. S9, there is also quite high variation and the effect of local and foreign conditions interacts with plant origin (Table S8). Thus, clear evidence for local adaptation is available only for ramet number (Fig. S9A) and, in some populations, for proportion of extravaginal ramets (Fig. S9B).

**Figure 5.** The effect of difference in temperature and moisture between target and original environment (target-origin) on A) plant height and B) belowground biomass. The colour scale indicates difference in temperature, the sets of columns indicate differences in moisture. Negative values indicate plants grown in colder and drier conditions, positive values indicate plants grown in warmer and wetter conditions and 0 indicates plants grown in conditions corresponding to the conditions from which they originate. The graphs show mean ± SE.
Plants subjected to warming were taller (Fig. 5A), had more ramets, higher aboveground biomass and proportion of extravagal ramets than plants subjected to cooling (Fig. S9, Table 4). Under warming, plants also had lower belowground biomass (Fig. 5B) and ratio of below to aboveground biomass (Fig. S9, Table 4). The effect for number of ramets and proportion of extravagal ramets is non-significant when applying the Bonferroni correction, while the rest are still significant (Table 4).

Plants subjected to a wetter environment were shorter (Fig. 5A), had fewer ramets (Fig. S9A), a lower proportion of extravagal ramets (Fig. S9B), lower rhizome biomass (Fig. S9E), less belowground biomass (Fig. 5B) and a lower below to aboveground ratio (Fig. S9D) than plants grown in drier conditions (Table 4). All these patterns are significant even with the sequential Bonferroni correction (Table 4).

For plant height (Fig. 5A), aboveground (Fig. S9C) and belowground biomass (Fig. 5B) and rhizome biomass there is also a significant interaction between difference in temperature and moisture (Table 4). Plant size increased much more with increasing temperature when the plants were grown in wetter conditions, while warming did not have any effect in drier conditions (Fig. 5A). All these patterns are significant even with the sequential Bonferroni correction (Table 4).

**Discussion**

Performance of our model species, *Festuca rubra*, depends strongly on plant origin, suggesting genetic differences between populations, with some signs of local adaptation. At the same time, the plants also show a high degree of phenotypic plasticity and populations from different climates also differ markedly in their degree of plasticity. Such combined genetic and plastic responses to climate seem to be a common pattern. Indeed, the review by Franks, Weber & Aitken (2014) conclude that all studies that explicitly study both of these processes find both to be important. In line with our study, this review also demonstrates that the importance of plasticity vs. genetic differentiation strongly varies among traits. Our results, however, add unique insights into the specific mechanisms behind the differentiation by demonstrating that both temperature and moisture of cultivation and of origin affect plant performance, and that these effects strongly interact.
Plasticity and genetic differentiation

High plasticity in relation to temperature as well as moisture and high variation in plasticity between different traits is in line with a range of previous studies demonstrating that target conditions impact plant performance (e.g., Raabová, Münzbergová & Fischer 2011; Couso & Fernandez 2012; Černá & Münzbergová 2015; Lazaro-Nogal et al. 2015; Malyshev et al. 2016). Specifically, target conditions explain most of the variation in the growth-related traits (plant height, number of ramets, aboveground and belowground biomass) in our study, although the plasticity of these traits strongly varies with origin. In contrast, the traits reflecting species ability to forage for resources (proportion of extravaginal ramets, rhizome biomass) are primarily explained by the environment of origin. Traits related to foraging are also found to drive community responses to climate change in a community-wide field study in the same study system (Guittar et al. 2016). Plasticity of the foraging-related traits is low and constant across origins. Our results thus suggest that size is highly plastic, and that the species has an ability to take advantage of suitable conditions through increased growth (number of ramets, plant height and biomass). In contrast, the foraging behaviour is a more fixed trait under changing climatic factors, which nevertheless varies between populations. The fact that the foraging traits do not vary may suggest presence of strong stabilizing selection working on these traits (Pelabon et al. 2010). These traits therefore seem to be the primary drivers of a species’ ability to respond to climate (see also Guittar et al. 2016). However, Herben et al. (2001) and Skálová (2010) demonstrated that the proportion of extravaginal ramets is highly plastic in Festuca rubra in relation to neighbour density and light availability. Plasticity in foraging traits could thus still occur in our system, and even vary with climate, as the changing climate is expected to be linked to increased competition and reduced light availability under natural conditions (Olsen et al. 2016).

The interaction between origin and target climate always explains the lowest proportion of the variation in our models, suggesting relatively low genetic differentiation in plasticity between environments (sensu Pigliucci 2001). This is in line with other studies testing interactions between genotype (represented by origin in our study) and environment (represented by target in our study, e.g., Gugger et al. 2015).

In spite of the limited magnitude of the interaction between origin and target climate impacts, the degree of trait plasticity described by the plasticity index (expressing the
proportional change of a trait across different environments) is affected by conditions of origin, suggesting that phenotypic plasticity itself is a trait under selection (Thompson 1991) and that selection can change the degree of plasticity depending on the conditions (e.g., Emery, Chinnappa & Chmielewski 1994; Springate et al. 2011; Gugger et al. 2015). Specifically, plants coming from drier and colder environments are most plastic in growth-related traits (mainly in production of aboveground and belowground biomass). The link between dry conditions and plasticity is in line with previous studies demonstrating that drought is a key factor exerting selection on trait plasticity (Couso & Fernandez 2012, Lazaro-Nogal et al. 2015). While those two studies come from much drier environments and suggest that the plasticity may be caused by high variation in water availability, our results suggest that greater plasticity can also be found in plants from mesic conditions compared to sites which are very wet.

The higher plasticity in growth-related traits in plants from colder climates may reflect that plants from cold environments need to be able to make use of short ‘windows of opportunity’ when favourable conditions occur in the harsh alpine environment to rapidly increase their growth. This pattern contrasts with expectations of previous studies, predicting and, in some cases, confirming that plants from extreme environments at higher elevations tend to be less plastic (e.g., Emery, Chinnappa & Chmielewski 1994; Eranen & Kozlov 2009; Frei, Ghazoul & Pluess 2014). All these studies only worked along elevational gradients, and did not explicitly test the effect of different climatic variables. We are not aware of any previous study that explicitly isolated and compared plasticity of plants across different temperatures while controlling for precipitation differences and vice versa. While Lemke et al. (2015) attempted to separate effects of temperature and precipitation along a wide transect across Europe and suggested a contrary pattern, i.e. higher phenotypic plasticity under warm and wet conditions, their study did not separate phenotypic plasticity from genetic differentiation. Our study is thus the first study demonstrating higher growth plasticity of plants from colder conditions. More studies using other species and systems using controlled designs similar to ours are now needed to confirm the generality of our conclusions.

In addition to high plasticity, this study demonstrates that both temperature and moisture of origin play an important role in plant performance, with plants from warmer and drier sites growing larger, indicating genetic differentiation between populations. Reduced plant size in plants from colder conditions is in line with studies showing similar patterns from localities at
higher elevations or latitudes (e.g., Nunez-Farfan & Schlichting 2001; Kollmann & Banuelos 2004; Byars, Papst & Hoffmann 2007; Gonzalo-Turpin & Hazard 2009; Monty & Mahy 2009; Fischer et al. 2011; Scheepens & Stocklin 2013; Dostálek et al. 2016). In addition, Guittar et al. (2016) indicate that plants from warmer sites tend to be larger in a community-wide study and Meineri et al. (2014) show an increased size at flowering for Veronica officinalis, both working in the same model system as us.

Decreased plant stature is usually expected to be maladaptive (van Kleunen & Fischer 2005). We, however, suggest that reduced stature of plants in extreme conditions at high elevation may in fact be seen as an adaption allowing plants to withstand the extreme weather conditions, such as low temperature, high snow cover and shorter growing season (Kollmann & Banuelos 2004). It may also be an adaptation to higher wind speed and higher light exposure as these might be more important stress factors at higher elevations than temperature (McIntire, Piper & Fajardo 2016). In addition, increased plant size might be viewed as a result of selection pressure for increased ability to compete for light in a warmer climate while there is no need to invest excessively in aboveground biomass in a colder climate with much lower competition (Olsen et al. 2016). While we attempted to select our sites to be as similar as possible, differences in these factors cannot be fully excluded and have to be considered as an alternative explanation for the effect of temperature of origin on plant size. In general, our results are in line with previous studies suggesting the importance of climate for performance of various rare as well as widespread species (e.g., Fournier-Level et al. 2011; Bennington et al. 2012; Kim & Donohue 2013; Mendola et al. 2015; Malyshev et al. 2016) and reviews of older studies in Hereford (2009) and Alberto et al. (2013).

The effect of climate of origin might suggest that the plants are locally adapted. Despite our data showing a significant effect of local vs. foreign environment for a range of traits, the indication of local adaptation in our data is only convincing for number of ramets. This is due to strong interactions between foreign vs. local contrast for moisture and temperature and also the interaction of the foreign vs. local contrast with population origin. This result contrasts with conclusions of previous studies suggesting that local adaptation to climate is one of the key factors limiting species ability to cope with climate variation and thus to adapt to changing climates even for widespread species with apparently wide climatic niches (e.g., De Frenne et al. 2011; Aitken & Whitlock 2013; Mendola et al. 2015).
The contrasting results might be caused by the numerous interactions described above and the fact that we study adaptation to two different factors. This makes our results very complex. The absence of a clear indication of local adaption in the majority of the traits we study may be attributed also to the lack of a clear link between the traits and life-time fitness. While it is clear that having data on life-time seed production would indeed be better (see e.g., Volis et al. 2015), our species is a long-lived clonal species and measuring life-time fitness is definitely not straightforward. It has been estimated that a single genet of Festuca rubra can live for several hundred years (Harberd 1961; de Witte & Stocklin 2010). In addition, our experimental plants flowered very rarely and early flowering in long-lived perennials may not be an indication of high fitness, but a response to stress (Ahmad & Prasad 2012). The trait showing local adaptation most clearly—the number of ramets—is a trait that might be most closely linked to fitness in the clonal species (note that number of ramets is a growth-related trait, while proportion of extravaginal ramets is a foraging-related trait, so these two traits have very different biological meaning).

Previous studies specifically exploring local adaptation of species (sensu Kawecki & Ebert 2004) in relation to climate mainly assessed adaptation to temperature (Williams & Black 1993; Mimura & Aitken 2010; De Frenne et al. 2011; Souther, Lechowicz & McGraw 2012) and demonstrate that temperature is an important factor driving local adaptation of species. For moisture, Gimenez-Benavides, Escudero & Iriondo (2007) demonstrate that soil moisture may also be an important factor affecting species adaptation and Garcia-Fernandez et al. (2013) confirm that the ability to cope with drought is a key factor driving performance of their model species. The only study comparing the effects of precipitation of origin to the effect of temperature of origin on plant performance concludes that elevation and temperature of origin, but not precipitation of origin, affect species performance (Scheepens & Stocklin 2013). Compared to our system, their precipitation gradient is much shorter and precipitation partly correlated with elevation and temperature (Scheepens & Stocklin 2013). In contrast, precipitation of origin, and, importantly, also its predictability, has been shown to be an important determinant of performance of species coming from semi-arid environments, with plants from wetter sites being larger (Couso & Fernandez 2012; Lazaro-Nogal et al. 2015). In our system, there is an opposite trend with plants from wetter climates tending to be smaller, likely due to the negative effect of high snow cover resulting in shorter growing seasons at the wetter sites.
Interestingly, there is a strong interaction between precipitation and temperature in our system, such that plants originating from cold and wet sites were the smallest. This is likely due to persistent snow cover at these locations and linked to the strongly reduced growing-season length. While a range of previous studies have demonstrated the effect of length of the growing season on plant size (e.g., Natali, Schuur & Rubin 2012; Liu et al. 2016), most of the patterns previously reported are just a matter of plastic response and not linked to genetic differences between the genotypes. The different genotypes of *F. rubra* are thus clearly adapted to their local conditions and any shift in the environment may at least partly restrict their growth. Few previous studies have simultaneously explored adaptation to moisture and temperature. One of these studies, Allan & Pannell (2009), conclude that moisture but not temperature plays a role for plant performance. In contrast, Andalo, Beaulieu & Bousquet (2005) demonstrate that adaptation to temperature but not to moisture is important for performance of white spruce. Neither of these, however, explicitly study interactions between the two factors. Thus our study is unique in demonstrating that temperature and moisture may interact to determine plant adaptations and suggest that both of these factors need to be studied simultaneously when attempting to understand the consequences of climate change.

**Effects of changing climate**

The general climatic prediction for Norway suggests increases in both precipitation and temperature over the next century (Hanssen-Bauer et al. 2005). The expected change in mean annual temperature ranges from 1.5°C to 2.2°C, with the change being stronger in winter and spring than in summer. In addition, precipitation is expected to increase by about 18%, with the change being stronger in winter than in summer (Hanssen-Bauer et al. 2005). We find that plant performance is generally higher under warmer and wetter conditions, suggesting that our model species is likely able to take advantage of climate change. Increased performance of plants exposed to warmer and wetter climates suggests that even though the plants show certain levels of genetic differentiation and local adaption, they will still be able to profit from more favourable growth conditions under future climate change in the region. This is in line with our finding that plants from the environments most endangered by climate change, i.e. the coldest and driest sites, are the most plastic.
As the species is dominant in the studied systems, it may be expected that it will increase its dominance in the sites in the future, leading to a potential loss in subordinate species and thus a reduction in the diversity of the plant communities (Olsen *et al.* 2016). Other scenarios, such as its suppression due to even higher profit of other native or invasive plant species or increased negative interactions with other trophic levels, are, however, also possible (e.g., Plowman & Richards 1997; Robinson, Ryan & Newman 2012). Importantly, the results demonstrate that the change in temperature interacts with the change in moisture, suggesting that these two factors should be studied in combination.

Most previous studies looking at the interacting effect of changed moisture and temperature are field climate-change experiments that also modified the level of CO$_2$. While several of these studies demonstrate the interactive effects of moisture and temperature on various aspects of soils (e.g., Wan *et al.* 2007; Larsen *et al.* 2011; Selsted *et al.* 2012), the only study that investigates plant biomass and plant community composition concludes that the effect of moisture and temperature are largely additive (Kardol *et al.* 2010). Our study is thus the first to demonstrate a strong interaction between changes in temperature and changes in precipitation on species performance in response to changing climate. It suggests that future studies aiming to understand species responses to changing climate need to consider carefully the specific changes expected and attempt to understand the effect of all the potentially changing factors, separately as well as in combination.

**Conclusions**

A key result of our study is that both temperature and moisture of cultivation and of origin affect plant performance, and that these effects strongly interact. This allows us to make predictions about the species’ response to future climate change. Specifically, our results imply that our target species, *Festuca rubra*, will profit from warming provided the climate gets wetter at the same time, while the species will not show any significant response to climate warming under simultaneous climatic drying. As the plants have the ability to compensate for increased drought by investing more in belowground structures independent of temperature, they are able to perform equally well under drought as under warm and wet conditions. Cold and wet conditions thus seem to be the most stressful for this species.
Species response to climate change necessarily also depends on response of the remaining species in the community. *F. rubra* tends to be more abundant in lower elevations as long as the productivity of the stands is not too high. We thus expect that climate change in the nutrient poor alpine environment, as was studied here, will lead to increased dominance of the species. This general prediction is, however, constrained by the fact species’ response to climate change is strongly modified by the plasticity of plants from different origins, with plants from the extreme cold and dry conditions being the most plastic. This may allow the plants from cold and dry conditions, i.e. from the environments most endangered by climate change, to profit from the future climate change more than plants from the other environments. In contrast, the specific genotypes from cold and wet environments are likely to be lost in the course of climate change. The response of the species as a whole, commonly predicted by species distribution models, may thus be overly optimistic in some parts of the range and too pessimistic in others. Global response of the species will thus also crucially depend on the specific structure of the landscape and the specific genotypes available to occupy the novel environments in the landscape. Present day species distribution can thus not be easily used to predict how the specific populations and thus the species as a whole will behave under climate change.

**Author contributions**

Planning the project ZM, VH, VV, HS; Executing the experiment VH, ZM, HS; Analysing the data ZM; Writing the manuscript ZM; Commenting on the manuscript VV, VH, HS.

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sites and climate stations in the field was supported by the Norwegian Research Council NORKLIMA project SeedClim (project 184912).
Table 1. The specific regime settings in the growth chambers providing information on minimum (min), maximum (max) and average (av.) temperature in the growth chamber each day. The regimes mimic the course of temperatures at the localities during the day as well as over the course of the growing season.

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<td></td>
<td>Min</td>
<td>Max</td>
<td>Av</td>
<td>Min</td>
<td>Max</td>
<td>Av</td>
<td></td>
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<td>16°C</td>
<td>10.1°C</td>
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<tr>
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<td>3°C</td>
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<td></td>
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<td>23.8°C</td>
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**Table 2.** The effect of original (O) and target (T) temperature (temp) and moisture (mois) and their two-way interactions on plant performance in the growth chambers. Higher-order interactions are shown in Table S6. Plant size at the beginning of the experiment was used as a covariate and genotype as a random factor. Df Error = 1078. Significant values (p ≤ 0.05) are in bold. Results marked with * are significant after correcting for multiple testing. Dev. indicates deviance explained by the given variable.

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<td></td>
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<td>p</td>
<td>dev.</td>
<td>p</td>
<td>dev.</td>
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</tr>
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<td>&lt;0.001*</td>
<td>21.70</td>
<td>&lt;0.001*</td>
<td>63.03</td>
<td>&lt;0.001*</td>
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<td>244.52</td>
<td>&lt;0.001*</td>
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<td>0.21</td>
<td>0.65</td>
<td>119.59</td>
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</table>

Prop. extravag. = Proportion of extravaginal ramets; Aboveg. b. = aboveground biomass; Belowg. b. = belowground biomass
Table 3. The effect of temperature (Otemp) and moisture (Omois) of origin on plasticity index based on the single traits. Most of the tests were done using linear regressions and the reported values are F-values. The tests for proportion of extravaginal ramets were done using GLM assuming a binomial distribution of the dependent variable and the reported values represent explained deviance. Df Error = 269. Significant values (p ≤ 0.05) are in bold. Results marked with * are significant after correcting for multiple testing.

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<td></td>
<td>p 0.002*</td>
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<td>0.008*</td>
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Prop. extravag. = Proportion of extravaginal ramets; Aboveg. b. = aboveground biomass; Belowg. b. = belowground biomass
Table 4. The effect of difference in temperature and moisture between localities of origin and target conditions and their interaction on plant performance. Significant values (p ≤ 0.05) are in bold. Results marked with * are significant after correcting for multiple testing. Df Error = 1094.

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<td>29.52</td>
<td>6.91</td>
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<td>300.22</td>
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<td>Diff. temp × diff. mois</td>
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<td>dev. p</td>
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Prop. extravag. = Proportion of extravaginal ramets; Aboveg. b. = aboveground biomass; Belowg. b. = belowground biomass
References


Supporting Information captions

Text S1. Detailed description of the results comparing plant performance in local vs. foreign conditions

Figure S2. The effect of cultivation in local vs. foreign moisture and temperature on proportion of extravaginal ramets created by the plants.

Text S3. Detailed consideration of the possible pseudoreplication issue in the experiment.

Figure S4. The effect of original environment and target environment on plant performance measured as A) plant height, B) ramet number, C) belowground biomass, D) proportion of aboveground and belowground biomass and E) rhizome biomass.

Figure S5. Plasticity index of belowground biomass of plants of different origin. ALP denotes the cold alpine sites, SUB denotes sub-alpine sites and BOR denotes warm boreal sites. 1 to 4 indicates moisture at the original localities with 1 indicating the driest and 4 the wettest sites.

Table S6. The effect of original and target temperature and moisture and all their interactions on plant performance in the growth chambers.

Text S7. Detailed description of the results testing target and origin interaction

Table S8. The effect of foreign vs. local temperature and moisture and their interactions with temperature and moisture of origin on plant performance in the growth chambers.

Figure S9. The effect of difference in temperature and moisture between target and original environment (target-origin) on A) number of ramets, B) proportion of extravaginal ramets, C) aboveground biomass, D) proportion of aboveground and belowground biomass and E) rhizome biomass.