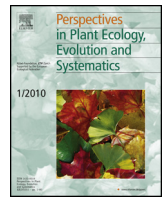


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Research article

## Biomass partitioning in grassland plants along independent gradients in temperature and precipitation



Olav Skarpaas<sup>a,\*</sup>, Eric Meineri<sup>b,c</sup>, Tessa Bargmann<sup>b</sup>, Christine Pötsch<sup>b</sup>,  
Joachim Töpper<sup>b,d</sup>, Vigdis Vandvik<sup>b</sup>

<sup>a</sup> Norwegian Institute for Nature Research, Gaustadalléen 21, NO-0349 Oslo, Norway

<sup>b</sup> Department of Biology, University of Bergen, Thormøhlensgate 53 A, Postboks 7803, N-5020 Bergen, Norway

<sup>c</sup> Department of Ecology, Environment and Plant Sciences, University of Stockholm, Lilla Frescati, SE-106 91 Stockholm, Sweden

<sup>d</sup> Sogn og Fjordane University College, PO 133, NO-6851 Sogndal, Norway

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### ABSTRACT

How plants allocate biomass to different parts strongly affects vegetation dynamics and ecosystem processes and services such as productivity and carbon storage. We tested the hypothesis that plant size explains the majority of variation in the size of plant parts (as predicted by allometric partitioning theory, APT) and that additional variation is explained by optimal responses for a given individual reproductive state and environment (as predicted by optimal partitioning theory, OPT) for alpine-lowland species pairs from three genera of grassland plants (*Veronica*, *Viola* and *Carex*) sampled along orthogonal gradients in temperature and precipitation. We found general patterns of allometric scaling (allometric exponents) of roots, stems, leaves and flowers, more or less as predicted by APT, and these patterns remained fairly constant across temperature and precipitation gradients. In contrast, basic allocation (allometric coefficients) was clearly related to climate, such as less allocation to leaves but more to roots, stems and flowers with increasing temperatures, in accordance with OPT. Furthermore, our results show that basic allocation is related to habitat affinity (alpine, lowland) and individual life-history states (reproductive or not) and that there is greater variability in small plants, which suggests that biomass partitioning theory should consider both the life-history and ecology of small plants to accurately predict climate-related grassland plant allocation and its implications.

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### 1. Introduction

The allocation of resources to different plant parts is a central aspect of plant life histories and responses to environmental change. The net impacts of current climate change on vegetation patterns, processes and functions will therefore also depend on how the allocation of plant biomass to the different parts (i.e. roots, stems, leaves, flowers) relates to climate, and whether such responses vary across species with different growth forms and habitat preferences. For instance, if individuals of different species and functional groups respond differently to climate-driven environmental factors, we may expect diverging population dynamics and changes in community composition and function in the future (i.e. non-analogue communities). Understanding climatic impacts

on allocation strategies may therefore be essential for our ability to predict future changes in functional composition and biodiversity (Liira and Zobel, 2000; Niu et al., 2008) and critical ecosystem processes and services such as productivity and carbon storage (Dukes et al., 2005).

How will global change affect plant biomass allocation? Optimal biomass partitioning theory (OPT) predicts higher allocation to the plant parts that maximize growth or fitness in a given environment: resource uptake theory predicts a higher allocation to the organ increasing the uptake of the most limiting resource for growth (Bloom et al., 1985), and life-history theory predicts a higher allocation to the organs limiting survival or reproduction, optimizing fitness (Stearns, 1992). The optimal response thus varies with the state of the individual plant and its environment, and this variation may be governed by both plastic and genetic responses. For instance, when water and/or nutrients are limiting growth or fitness, root biomass should increase relative to total biomass in order to improve water and/or nutrient uptake. When

\* Corresponding author.

E-mail address: [olav.skarpaas@nina.no](mailto:olav.skarpaas@nina.no) (O. Skarpaas).

light is limiting, more resources should be allocated to leaves and other photosynthetic tissues and/or supporting stems, in order to increase the capture of light by the existing photosynthetic tissue. When temperatures change in a favourable direction for reproductive output, e.g. higher temperatures in cold environments – which may be expected under current global warming – more resources should be allocated to reproduction. The individual plant's choice is likely to depend on environmental cues and adaptations to environmental conditions, although such responses are not always well understood. For instance, it has often been said that alpine species invest more in persistence and growth and less in sexual reproduction than lowland species to ensure survival in a harsh environment (e.g. Billings and Mooney, 1968; Bliss, 1971), but more recent studies have found high seedbank densities (e.g. Chambers, 1993; Vandvik et al., 2015; Zabinski et al., 2000), and diversity of genotypes (e.g. Gabrielsen, 1998; Steltzer et al., 2008) consistent with a history of repeated sexual reproduction in alpine environments. Some studies even report higher allocation to reproduction in alpine species (Fabbro and Körner, 2004; Guo et al., 2012).

A second, and more recent body of allocation theory, allometric partitioning theory (APT), takes the biophysical processes and constraints in the structure and development of plant parts as its point of departure (Enquist, 2002; West et al., 1997). OPT and APT are not mutually exclusive, and should be studied in concert (McCarthy and Enquist, 2007), yet this is rarely done. One of the main predictions of APT is that the allocation of resources to the various plant parts is a function of plant size (Enquist, 2002; Enquist and Niklas, 2002; Enquist et al., 1999). While some plant parts, notably roots and stems, are predicted to scale isometrically with size, relative allocation to leaves and reproductive organs are predicted to decrease with increasing size (Enquist, 2002; Enquist and Niklas, 2002; Price and Enquist, 2006). When looking across a wide range of species spanning sizes of many orders of magnitude, there seems to be a close relationship between allocation and size as predicted by APT (Enquist and Niklas, 2002). However, several aspects of allometric theory also need further consideration (Price et al., 2012; Savage et al., 2008). One important challenge in our context is the validity of APT for small plants. APT has mostly been applied to trees, but as noted by Enquist et al. (2007), small plants do not always meet the assumptions of standard APT (West et al., 1997), which may lead to other scaling patterns for leaves. So far this has only been thoroughly tested for tree saplings (Enquist et al., 2007). Another important challenge is the allometry of reproduction, which may not always follow the log–log linear patterns predicted by APT (Bonser and Aarssen, 2009). It is also still an open question to what extent allometric scaling varies across large-scale gradients in temperature and precipitation, for instance. A recent review with meta-analyses of the literature on allocation to roots, stems and leaves across hundreds of plant species demonstrated that allocation varied in ecologically predictable ways, but that few studies considered allometry or size corrections (Poorter et al., 2012). There was also relatively little data from natural systems, particularly grasslands, where optimal responses may be hard to detect unless size, between-species variation and co-variation, and interactions of important environmental factors are accounted for (McCarthy and Enquist, 2007).

In this study we investigate plant biomass partitioning in a grid of grassland locations where temperature and precipitation vary independently of each other, and where other sources of environmental variability are minimized. Our basic hypothesis is that allometric relationships explain the majority of variation in the biomass of plant parts, and that additional variation is explained by climatically optimized allocation. More specifically, on the basis of the literature summarized above, we predict that (1) allometric scaling follows the same rules across species and climate

gradients; (2) increased temperature increases allocation to roots, stems and flowers, and decreases allocation to leaves; (3) increased precipitation increases allocation to leaves, and decreases allocation to roots and (4) alpine species allocate less to above-ground parts and reproduction than their lowland congeners. Predictions 1–3 are expected to apply to both inter- and intraspecific patterns, and are therefore tested in statistical models at both levels, while prediction 4 can only be tested with the interspecific approach (while controlling for species-specific allocation patterns). As allocation is likely to vary with fertility and site-specific environmental conditions, we also take these factors into account when testing the predictions.

## 2. Materials and methods

### 2.1. Data

The data for this study were collected within the setup of a larger project (SeedClim) that investigates climate change impacts on plants at the individual, population and community level (e.g. Klanderud et al., 2015; Meineri et al., 2014; Vandvik et al., 2015). We selected herb-rich calcareous grasslands in the plant sociological association Potentillo-Festucetum ovinae (Fremstad, 1997) (hereafter referred to as 'grasslands') as the study system for SeedClim, based on high biodiversity, conservation value, relatively wide geographical and altitudinal distribution, and importance as summer pasture. During summer 2008, we selected 12 study sites in western Norway (see Klanderud et al., 2015) to provide a 'climatic grid' where three levels of summer temperature (the mean of the four warmest months; levels of approximately 6.5, 8.5, and 10.5 °C, referred to as 'alpine', 'sub-alpine' and 'boreal') are combined with four levels of total annual precipitation (approximately 600, 1200, 2000 and 2700 mm, referred to as precipitation levels 1–4). We used interpolated temperature and precipitation data from the Norwegian Meteorological Institute (met.no) for the normal period 1961–1990 with a resolution of 100 m (interpolated with the methods described in Tveito et al., 2005 and references therein) for site selection and analyses. The interpolated mean summer temperatures for the normal period were highly correlated (Pearson correlation 0.93,  $N = 12$ ) with local mean summer temperatures in 2009 calculated from on-site temperature measurements (hourly temperature at 2 m height monitored with UTL-3 Scientific Dataloggers, GEOTEST/SLF, [www.utl.ch](http://www.utl.ch)). Precipitation measurements were also set up locally in 2009, but these data contained too many measurement errors to be used in this study. To facilitate comparison between sites, these were selected specifically to contain the target community and to be as similar as possible with respect to potentially important environmental factors other than climate (e.g. grazing regime and history, bedrock, slope and exposure).

The grassland vegetation is herb-dominated (109 species; mean total cover of 62% ± standard deviation of 26.7%) whereas graminoids, notably Poaceae and Cyperaceae, are less prominent (17 and 23 species, respectively, mean total cover of 30.7 ± 14.4%) and woody species are relatively scarce (13 species, mean total cover of 3.0 ± 4.7%). More than 95% of the species are perennial, and the majority have some form of clonality. Three alpine-lowland species pairs, *Veronica alpina* (Alpine speedwell)–*Veronica officinalis* (Heath speedwell), *Viola biflora* (Arctic yellow violet)–*Viola palustris* (Marsh violet), and *Carex capillaris* (Hair sedge)–*Carex pallescens* (Pale sedge) were selected for detailed population studies (Meineri et al., 2014, 2013; Pötsch, 2010; Töpfer, 2015), including the present allocation study, as they were considered representative for the vegetation in terms of functional type and growth form, and as they are among the most commonly occurring species at

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