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Biomass allocation in herbaceous plants under grazing impact in the high semi-arid Andes

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ABSTRACT

Among the plant traits that affect performance, vitality and herbivore resistance in rangeland vegetation, biomass partitioning ranks top, commonly outweighing processes at single leaves (e.g., photosynthesis, respiration). We explored the allometry of a broad sample of herbaceous species from two high elevation sites in the Andes in order to explain biomass partitioning under harsh climatic conditions and risk of biomass losses under strong camelid grazing pressure. We combined data from NW-Argentina and W-Bolivia from elevations between 4200 and 4250 m in a landscape dominated by tall *Festuca orthophylla* tussocks and a drought driven seasonality (rainfall only between November and March). Across 10–20 taxa per region we found less investment in leaves with a mean leaf mass fraction of only 11% and instead a massive storage in below-ground compartments (rhizomes, tap roots), particularly at the colder Argentinean site. Though grazing pressure was much greater in Bolivia, the foliage mass fraction was there larger than in Argentina. The inter-tussock space in these open, dry plains ('pajonal') was dominated by rosette forming species with a below-ground shoot apex and massive tap roots (70% of all species), rendering these species less sensitive to grazing and trampling. The storage organs of these species represented more than 50% of total biomass. Llamas, which represented the main vertebrate herbivore in these open plains at the Bolivian site, preferred non tap-root herbs and species with low leaf nitrogen concentration. Palatable forbs for llamas (22% of all species at the Bolivian site) only survived when nested (facilitated) in the rigid, tall *Festuca orthophylla* tussocks or thorny shrubs. In conclusion, these extremely high elevation rangeland herbs invest preferentially in structures for persistence (K-strategy) rather than maximizing carbon gain.

Introduction

Plant growth is driven by assimilatory and respiratory processes as well as allocation of photo-assimilates to certain plant compartments. Depending on whether a compartment contributes additional carbon gain (e.g., leaves) or causes carbon costs (heterotrophic plant parts), allocation has a strong influence on overall growth (Weiner, 2004). The effect of this 'investment strategy' of a plant is so large that dry matter allocation commonly outweighs the unit leaf area photosynthetic capacity as a growth determinant (Körner, 2003). These relationships are explored in what has been termed 'functional growth analysis' (e.g., Poorter, 1989; Van der Werf et al., 1993). Functional growth analysis considers the relative amounts of dry matter invested in certain plant compartments and the density of resultant tissues as the two major drivers of plant growth (Lambers and Poorter, 1992; Roy and Garnier, 1994). Plant organs such as leaves, stems, reproductive organs, special storage organs, coarse, and fine roots make up total plant biomass and the investments in these compartments are best described as fractions of the total (Körner, 1991, 1994). The common use of ratios instead of fractions (one part divided by another part, e.g., root:shoot ratio is not advised, because it exaggerates allocation patterns and/or neglects actual function (e.g., pooling stems and leaves into 'shoot' or storage organs and fine roots into 'root' (cf. Mokany et al., 2006, for critical review of root:shoot ratios across many terrestrial biomes).

Tissue quality has successfully been expressed in density-related terms such as specific leaf area (SLA) or its reverse, the leaf mass per area (LMA), and in terms of specific root length. Fast growing plants are generally found to produce a high amount of leaf area per unit dry matter (commonly thin leaves with low LMA), and also produce a great length of fine roots per unit of fine root dry matter (Poorter and Evans, 1998; Ryser, 1996). While high LMA species tend to achieve longer leaf lifespan across a wide spectrum of plant functional types (Wright et al., 2002, 2004), this may not always be seen within individuals of given communities or types of species

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Table 1
Characteristics of the two Andean study sites.

Country	Study site	Elevation [m a.s.l.]	Soil type	Mean air temperature[h] [°C]	Annual precipitation [mm]	Main grazers	Year of plant sampling
Argentina	Huaca-Huasi Cumbres Calchaquíes	4200–4600	Silty sand[a]	4.5[a]	385[a] 200–300[b]	Guanacos	March 1988
Bolivia	Sajama	4250	Volcanic sandy soil[c,d] Regosol[e]	8.8[f]	327–384[g]	Llamas Alpacas Vicuñas Sheep	March 2008

[a] Halloy (1985).
[b] Bianchi et al. (1992).
[c] Lopez et al. (2007).
[d] Buttolph and Coppock (2004).
[e] FAO (2006).
[f] Own measurements 2003–2008.
[g] Own measurements 2006–2008.
[h] During growing season (November–March).

such as alpine and related lowland forb species in the European Alps (Diemer et al., 1992). It rather emerges across samples of a wider spectrum of environmental conditions. The leaf mass fraction, i.e., the total leaf mass per total plant mass and also the leaf area ratio (the total leaf area per total plant mass) are closely and positively related to plant growth rate (Poorter and Nagel, 2000).

While plant dry matter allocation is to a great part genetically determined for a given species, environmental influences can still cause significant shifts in investments towards needed structures (de Kroon et al., 2009). Evolution selects on such traits, so that species found in certain habitats exhibit certain characteristic allocation patterns (e.g., tundra plants, Bliss, 1981). Important drivers are life history (e.g., plant life span), light, water, nutrients, temperatures (freezing) and disturbance regimes such as grazing or fire. Water shortage (often combined with high radiation and low competition) selects for deep roots, below-ground storage organs and smaller foliage fraction in herbs and grass species (Schulze et al., 1996; Skinner et al., 2006). Disturbance resistance includes the ability to survive repeated losses of foliage by trampling, herbivory, or fire and thus, also selects for large storage tissue and below-ground stems or the complete absence of above-ground stems (below-ground apices instead). The alpine environment, due to its harsh climate conditions can be expected to select for certain allocation regimes (Bowman and Fisk, 2001; Körner, 2003) and the exposure to regular disturbance may further modify dry matter allocation. Thus, biomass partitioning and biomass fractions may follow analogous patterns at high elevation (above the natural tree line) irrespective of their geographic latitudes.

In a broad survey of such characteristics in herbaceous taxa in the European Alps, Körner and Renhardt (1987) showed that roughly 24% of total plant dry matter is allocated to leaves, and, compared to comparable lowland taxa, the stem fraction is halved, whereas the root fraction is doubled. Interestingly, the leaf mass fraction did not significantly change with elevation and turned out to be a rather conservative trait across a range of cold climate regions (Körner, 2003; Körner et al., 1989). Comparable data for tropical and subtropical mountains are scarce, and the much longer growing season may favor investment strategies that differ from those in the temperate zone. Because of the absence of a dormant phase ('winter') one could expect a reduced need in storage organs, permitting greater investments in leaves and thus, an overall enhanced growth and productivity. However, much of the high altitude lands at subtropical latitudes are under the influence of high air pressure cells, leading to very low precipitation, as is the case also for the semi-arid Andean Altiplano. A short growing season driven by summer precipitation in combination with low temperatures and high grazing pressure could select there for even larger below-ground investments than in the temperate zone, and hence, permit only lower productivity. Therefore, we tested the following hypotheses:

Biomass allocation in the cold semi-arid, subtropical regions is not different from that observed in other high elevation regions.

Under similar cold life conditions increased herbivory pressure leads to more pronounced below-ground biomass allocation.

Herbivore pressure may either select for high N, short rotation foliage (low-cost, low LMA) or, more commonly for low N, high LMA, higher longevity foliage (repelling herbivores). For instance, both strategies can be found in semi-arid rangeland (e.g., *Acacia* versus *Combretum* strategy in the African savanna, Scholes and Walker, 1993).

We hypothesized that heavy camelid pressure in combination with a cold climate and water shortage favors short rotation high N foliage. To test this hypothesis, we compared plant biomass allocation in perennial herbaceous plants growing in two semi-arid, high elevation sites in the subtropical Andes (Argentina, Bolivia) which differed mainly in grazing pressure (higher in Bolivia) but were very similar in climate conditions. The comparison across sites of similar elevation and aridity allowed some generalisations for the ecology of herbaceous plants in the high subtropical Andes as well as in a cross-continental comparison to other mountain regions of the world. Both selected sites are representing larger regions. For instance, the Altiplano covers an area of 200,000 km^2, taking into account Peru, Bolivia and Argentina (Wirrmann and Mourguiart, 1995). More than the half of this area is covered by semi-arid grasslands such as the Bolivian grassland studied here.

Materials and methods

Study sites and sampling

The present study was carried out in two semi-arid sites in the subtropical Andes: one in the Cumbres Calchaquíes in NW-Argentina and the other in the central Andean Altiplano (W-Bolivia; Table 1).

Cumbres Calchaquíes (Argentina)

The Argentinean site was in the Cumbres Calchaquíes mountains on the Huaca-Huasi plain around Laguna Nostra (26°40′S, 65°44′W; Halloy, 1985, 1998; Halloy and Mark, 1996, cf. Table 1). This high plateau at 4200–4600 m elevation receives on average 385 mm rainfall per year (measured 1976–1979, Halloy, 1985). However, more recent (but extrapolated) data indicate lower annual precipitation means between 200 and 300 mm (Bianchi et al., 1992). Rain amounts have decreased particularly since the late eighties (Bianchi et al., 2005). The mean air temperature during the main growing season (November–March) is 4.5, −1.6 °C during the winter season, with minima down to −23 °C (Halloy, 1985). The mean soil temperature at −30 cm depth is +8.1 °C in summer and −1 °C in winter (Halloy, 1985). Similar climate conditions and accordingly, very comparable vegetation units (compared to the