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EFFECTS OF SIMULATED CLIMATE CHANGE ON BIOMASS ALLOCATION PATTERNS OF SEEDLINGS OF TWO ANDEAN *LEPIDIUM* SPECIES (BRASSICACEAE) WITH DIFFERENT ELEVATIONAL DISTRIBUTIONS

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In tropical mountains, global climate change is expected to lead to increasing temperatures and lifting of cloud condensation layers, possibly also establishing new biotic interactions. These events are likely to force species to either migrate upwards or to adapt to changed environmental conditions (Pounds *et al*. 1999). It is likely that the migratory response of some species will not be fast enough to encompass climate change (Bush 2002), and will be hampered by habitat loss and fragmentation, or simply by the maximum height of mountain ranges, increasing the number of species in danger of extinction (Thomas *et al*. 2004). Even species able to migrate are unlikely to encounter identical climatic conditions at higher elevations, because climate change does not simply imply an increase of temperatures but also shifts in precipitation regimes, cloudiness, and especially the frequency of extreme environmental conditions such as droughts and frost (Vuille *et al*. 2003). It is therefore likely that all species will be forced to some degree to adjust their autoecological behavior. Optimal partioning models and theories suggest that plants respond to variation in the environment by allocating biomass among plant organs to optimize the capture of nutrients, light, water and CO_2 in a manner that maximizes plant growth rates (Bazzaz 1996, McConnaughay & Coleman 1999). Thus the study of the biomass allocation patterns of plant species of tropical mountains at different elevations can indicate how adaptable the species will be to climate change. Little is known about the responses of tropical montane plants to climatic change under field conditions. To date, only one field study has been done to test the predicted effects of climate change on tropical montane epiphyte plant communities (Nadkari & Solano 2002), and comparable studies for other life forms or in other high mountain ecosystems such as *puna* and *páramo* are completely lacking.

The purpose of the present study was to document how the biomass allocation patterns of seedlings of two high-Andean plant species react to a simulated global warming under field condition. For one species we simulated the move to higher elevations, for the other the shift was to lower elevations. We concentrated on the establishment and juvenile stages due to their relevance in the establishment and maintenance of populations (Harper 1977) and susceptibility to environmental stress (Larcher 1994).

METHODS

We selected two species of *Lepidium* (Brassicaceae) because some of the Andean taxa occur at very high elevations and are thus most likely to be affected by climate changes, and because some species of *Lepidium* are of local economic and nutritional value. We chose two species with different elevational distributions: *L. meyenii* Walp. (4050–4600 m) and *L. bipinnatifidum* Dom. Sm. (3100–3900 m). The elevational distributions of the species were obtained from vouchers deposited in the Herbario Nacional de Bolivia (LPB).

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The study was conducted in Bolivia, near the city of La Paz. Plants were cultivated at two localities of different elevation: El Alto (4100 m; 16°28'S, 68°15'W) and Mallasa (3100 m; 16°32'S, 68°08'W). Thus each species was cultivated at one site within its natural elevational distribution and one outside of it. Seeds of each species were collected from a population located within their distribution ranges.

Seeds of each species were planted in 40 plastic pots of 25 cm diameter filled with soil from the upper locality. Half of the pots were located at 4100 m and the other half at 3100 m, under natural conditions of solar irradiation and temperature. The plants were watered regularly to avoid water deficit. Soil elevational translocation was not expected to change soil properties in the short term during the experiment, due to the low organic matter content characteristic of dry *puna* soils, and homogeneous watering, since organic matter and water content are reported to induce changes in soil properties (Scheffer & Schachschabel 2002). Thus by using the same soil and by watering we limited the differences between both sites to climatic conditions (temperature, irradiation, air humidity, etc.).

After two months the plants were collected and the root:shoot ratios were calculated, dividing the root dry weight by the shoot dry weight. A Kruskal-Wallis sum of ranks tests (Fowler *et al.* 1998) were used to test for differences in the weight of below-ground and above-ground structures, and root:shoot ratios between localities for each species. For the test the significance level was $\alpha = 0.05$.

RESULTS

In the case of the higher elevation species *L. meyenii*, transplantation to a lower elevation led to a greater biomass production by the seedlings in contrast to seedlings growing within their natural elevational ranges (Kruskal-Wallis-Test: $H(1, N = 20) = 6.60$, $p = 0.0102$) (Fig. 1). The seedlings located at the upper site invested nearly 70 % of their dry weight in roots and about 30 % in above-ground biomass, while those at the lower site showed the opposite pattern, allocating

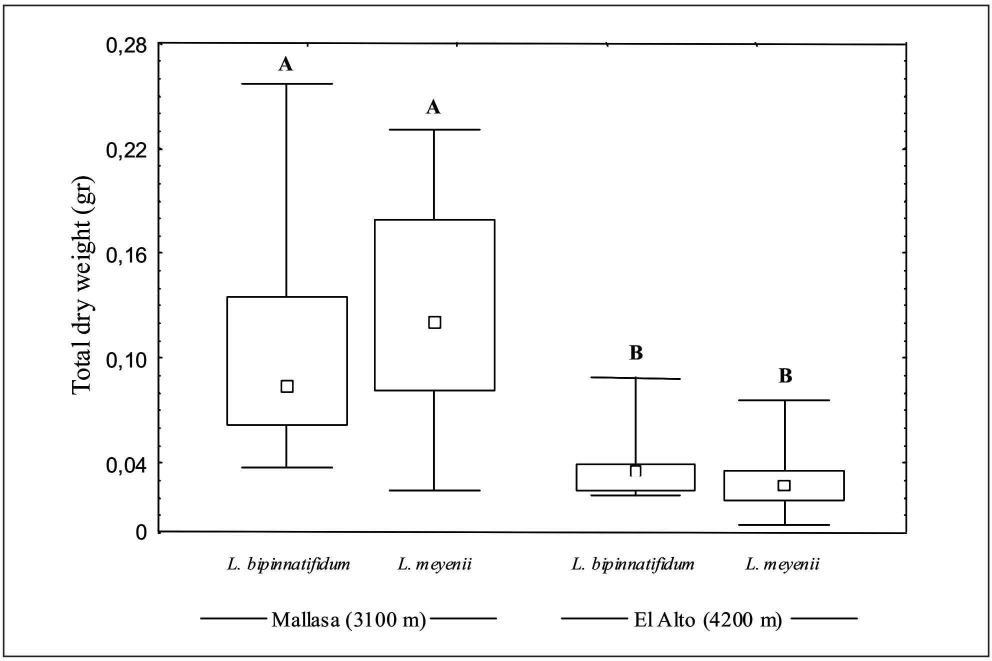

FIG. 1. Median, quartiles (25–75%), maximum, and minimum dry weight of seedlings of *Lepidium meyenii* and *Lepidium bipinnatifidum* after two months at the localities of El Alto and Mallasa. Different letters indicate significant differences between the medians (Kruskal-Wallis test).

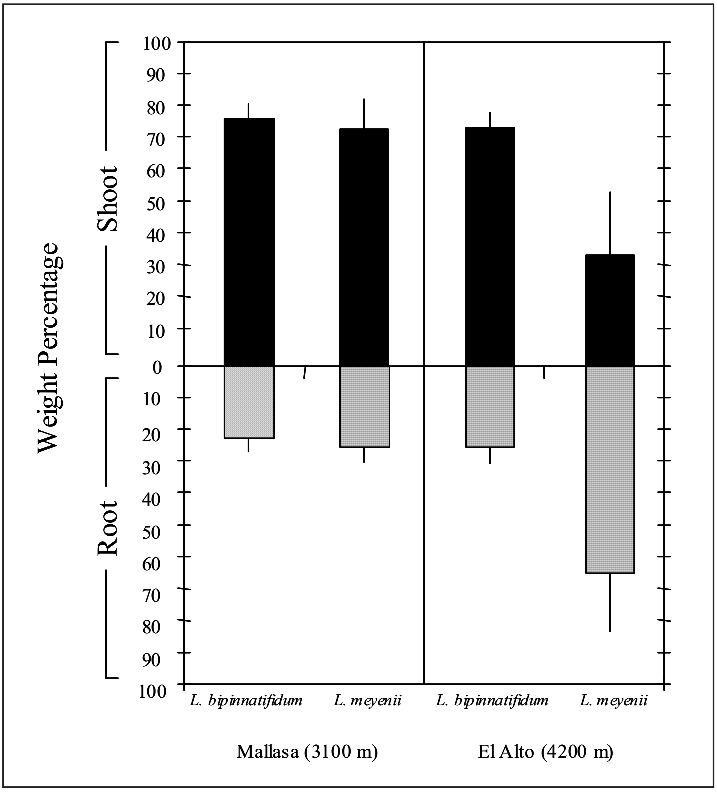

FIG. 2. Biomass allocation in aerial parts and roots in *Lepidium meyenii* and *Lepidium bipinnatifidum* seedlings after two months at the localities of El Alto and Mallasa. The values are medians ± quartile (25–75%) of the percentage of the total dry weight in aerial parts and roots.

30 % and 70 % of the total dry biomass to below- and above-ground structures respectively (Kruskal-Wallis-Test: $H\,(1, N = 20) = 11.57$, $p = 0.0007$) (Figure 2).

For the lower elevation species *L. bipinnatifidum*, cultivation at higher elevations reduced the biomass (Kruskal-Wallis-Test: $H\,(1, N = 20) = 10.08$, $p = 0.0015$) (Fig. 1), but did not change the allocation pattern, which was about 50 % to roots and shoots in both localities (Kruskal-Wallis-Test: $H\,(1, N = 20) = 0.82$, $p = 0.36$) (Fig. 2).

Comparing the two species, there was no statistical difference in the dry weight at each of the two cultivation sites nor in biomass allocation patterns at 3100 m, but *L. meyenii* had significantly more below-ground biomass at 4100 m than *L. bipinnatifidum* (Kruskal-Wallis-Test: $H\,(1, N = 20) = 14.28$, $p = 0.0002$).

DISCUSSION

The greater productivity of the seedlings of both species at the lower site likely reflects stronger growth in warmer environments as a result of increased metabolic rates (Precht *et al.* 1978), which leads also to the overall plant size pattern along the elevational gradient (Körner *et al.* 1989).

It is striking that *L. meyenii* had the same growth as *L. bipinnatifidum* about 1000 m below its natural lower elevation limit, indicating that its elevational distribution is unlikely to be limited by temperatures. Possible limiting factors could include higher water stress at the lower site under natural conditions, since precipitation in the study area does not increase significantly at lower elevations, or biotic interactions such as competition or herbivory (Loehle & LeBlanc 1996, Schenk 1996, Vetaas 2002). This suggests that *L. meyenii* may at least be initially favored by increasing temperatures as a consequence of climate change, with phenomena such as interspecific competition becoming important limiting factors. However, it is important to consider the marked change in the allocation pattern in *L. meyenii* growing in warmer environments, with most of the biomass located in above-ground structures. This could make the seedlings of *L. meyenii* more sensitive to the drought and frost events that occur in the austral winter in the region, since plant morphology is one of the main determinants of drought and frost resistance (Larcher 1994). The possible risk of increasing frost damage under elevated temperatures has also been outlined for boreal ecosystems, and has been suggested as one of the main detrimental effects of global warming on plants of cold environments (Kellomaki *et al.* 1995). Strong drought events in the central Andes in the last decades due to climate change are believed to have led to significant losses of biodiversity and decreases in plant growth rates (Halloy 2002). The example of *L. meyenii* in our study shows how a greater susceptibility to climatic extremes may be induced by changes in the biomass allocation as a reaction to growing under warmer environmental conditions. However, warmer conditions imply not only increasing temperatures but also changes in the cloud cover, affecting the irradiation and nutrient availability, factors which have also been documented to lead to changes in the root:shoot ratios (Körner & Renhardt 1987, McConnaughay & Coleman 1999). In this way clarifying the role of each of these factors could help us to understand and predict how high-Andean plants will react to climate change.

The inability to adapt biomass allocation may limit the elevational distribution of potential invasive species in the study area, as has been shown in *L. bipinnatifidum*. While our study does not allow a determination of the cause of a growth response under higher temperatures, it enables us to develop an idea of the factors limiting the upper elevational distribution of the species. At the upper site, *L. bipinnatifidum* grew about as well as *L. meyenii*, but failed to shift its biomass allocation to an increased production of below-ground biomass. During our experimental period no extreme frost events occurred, but based on similar studies elsewhere (Precht *et al.* 1978, Floistad & Kohmann 2003) we suspect that a single strong frost event could have severely damaged the above-ground parts of *L. bipinnatifidum* seedlings, which would then have had fewer resources in their roots to compensate for the damage compared with *L. meyenii*. Thus our study shows that the elevational distribution of the two species of *Lepidium* cannot be explained by mean temperatures alone, but is likely to be more strongly limited by extreme climatic events and biotic factors in their interaction with the adaptability of the individual plant species, particularly with the biomass allocation patterns.

If the relationship of mean temperatures to climatic extremes remains constant in the future, then temperature increases will simply lead to an elevational shift in the distribution of species niches. However, global climate change not only implies changes in temperature but also in CO_2 concentration, precipitation regimes, and irradiation (Root *et al.* 2003). Recent observations from the Bolivian Andes suggest that precipitation and cloudiness are likely to change more strongly than temperatures (Vuille *et al.* 2003). Whereas temperatures show only a moderate increase in this region, precipitation and cloudiness are markedly decreasing, especially in the dry season (austral winter). This implies a higher frequency of extreme climatic events such as frost and drought. This could lead to drastic reductions in the niche area available to plant species as a result of new constraints at both upper and lower elevational limits, and stresses the importance of the adaptability of species to these new conditions. Nevertheless, it is important to note that adaptability via biomass allocation may result from true adjustments or as a consequence of ontogenetic development (Coleman *et al.* 1994). In this way the adaptability of high-Andean species to future climatic scenarios could vary according to species and growing stage.

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